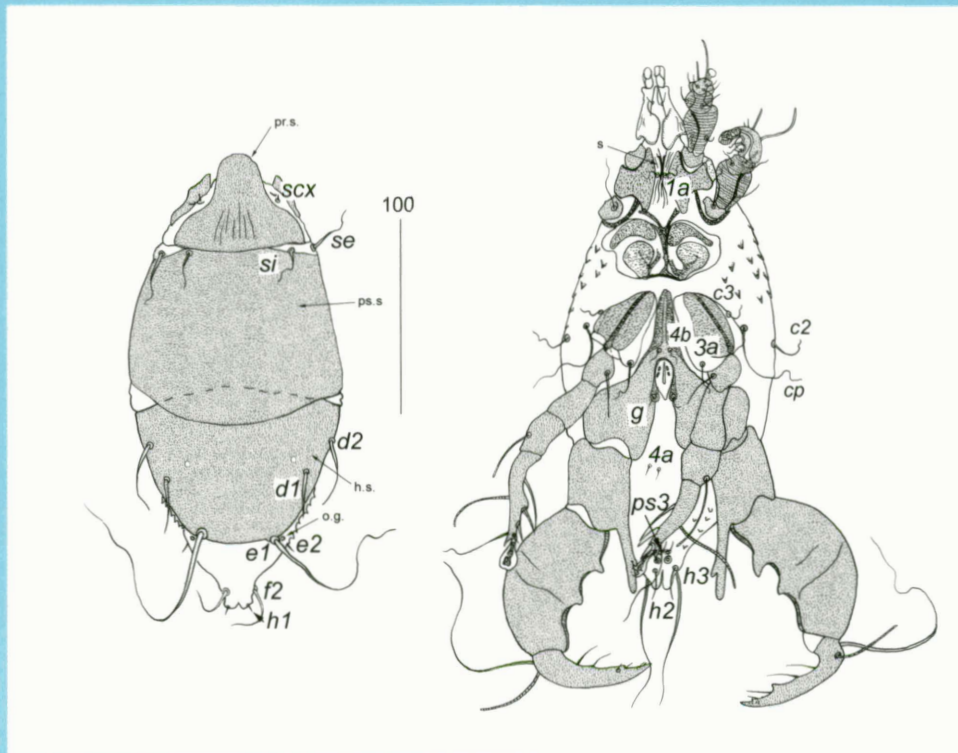


FUR-MITES OF THE FAMILY ATOPOMELIDAE (ACARI: ASTIGMATA) PARASITIC ON PHILIPPINE MAMMALS: SYSTEMATICS, PHYLOGENY, AND HOST-PARASITE RELATIONSHIPS

BY
ANDRE V. BOCHKOV and BARRY M. OCONNOR



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COVER ILLUSTRATION — *Atopomelus crocidurae*, male.

MISCELLANEOUS PUBLICATIONS
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**Fur-Mites of the Family Atopomelidae
(Acari: Astigmata) Parasitic on Philippine
Mammals: Systematics, Phylogeny, and
Host-Parasite Relationships**

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Andre V. Bochkov^{1,2} and Barry M. OConnor¹

CONTENTS

	PAGE
Abstract	iii
Introduction	1
Material and methods	1
Systematics	
Key to the genera and subgenera of Philippine Atopomelidae Günther, 1942	2
Key to Philippine species of the subgenus <i>Listrophoroides</i> (s.s.) Hirst, 1932	8
Key to Philippine species of the subgenus <i>Marquesania</i> Womersley, 1943	27
Phylogenetic analysis	52
Host-parasite relationships	54
Acknowledgements	60
Literature cited	61

ABSTRACT

Fur-mites of the family Atopomelidae (Acari: Astigmata) from the Philippines are revised. Among 74 potential host species of 24 genera belonging to the families Muridae (Rodentia) and Soricidae (Soricomorpha) known from the Philippines, 54 species of 23 genera were examined for ectoparasites, and atopomelid mites were collected from 31 species in 10 genera. A total of 18 atopomelid species belonging to the genera *Atopomelus* Trouessart, 1917 and *Listrophoroides* Hirst, 1923, including 12 previously undescribed species, were recovered: *Atopomelus crocidurae* Fain and Lukoschus, 1977, *Listrophoroides* (s.s.) *mindanensis* Fain and Lukoschus, 1981, *L. (s.s.) batomys* sp.n., *L. (s.s.) palawanensis* Fain, 1976, *L. (s.s.) brachypyx* Fain, 1974, *L. (s.s.) crunomys* sp.n., *L. (s.s.) insularis* sp.n., *L. (s.s.) chrotomys* sp.n., *L. (Marquesania) cucullatus* (Trouessart, 1893), *L. (M.) paracucullatus* sp.n., *L. (M.) postsquamatus* Fain, 1976, *L. (M.) apomys* sp.n., *L. (M.) heaneyi* sp.n., *L. (M.) faini* sp.n., *L. (M.) limnomys* sp.n., *L. (M.) bullimus* sp.n., *L. (M.) luzonicus* sp.n., and *L. (M.) corpuzrarosae* sp.n. All species are described or redescribed, host and geographic ranges are recorded, and keys to all species are provided. To clarify relationships of the Philippine species with other Southeast Asian *Listrophoroides*, a phylogenetic analysis was conducted using parsimony methods on morphological characters. The Philippine species of the subgenus *Listrophoroides* (s.s.) belong to a cluster including Southeast Asian species of the *rajah* and *borneoensis* species groups. *Listrophoroides batomys* and *L. mindanensis* form a separate clade that is sister to all other members of this cluster. Three other newly described species of *Listrophoroides* (s.s.) (*L. crunomys* and *L. insularis*+*L. chrotomys*) are represented by two independent lineages situated in the core of this cluster, between the *borneoensis* and *rajah* groups. The species of the subgenus *Marquesania* form a monophyletic group sister to the Southeast Asian species of the subgenus *Listrophoroides* (s.s.). The phylogenetic relationships of the Philippine atopomelids are partially correlated with the host phylogeny, and there are several groups of closely related species that are associated with particular rodent taxa. However, this underlying co-evolutionary pattern is often complicated by probable cases of host switching.

Keywords: Atopomelidae, parasites, mites, Philippines, fauna, mammals, systematics, phylogenetics, co-evolution

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Fur-Mites of the Family Atopomelidae (Acari: Astigmata) Parasitic on Philippine Mammals: Systematics, Phylogeny, and Host-Parasite Relationships

INTRODUCTION

The mammalian fauna of the Philippine Archipelago has one of the highest per-area levels of endemism in the world. Among 175 currently known native mammal species inhabiting this archipelago, 112 species are endemic (Heaney *et al.*, 1998; Esselstyn *et al.*, 2004). Such high diversity and endemism of the Philippine fauna make this region especially interesting for taxonomic and island biogeographical studies. Unfortunately, many Philippine species are threatened because their natural habitats are increasingly impacted by human activity (Heaney, 1993; Oliver & Heaney, 1996). Many of the Philippine mammals are strongly limited in their distribution to montane forests and cannot live in agricultural lands or even in secondary forests (Heaney *et al.*, 1989; Heaney & Rickart, 1990). For these reasons, the Philippine mammals have been the subject of intensive investigation from both conservation and basic scientific perspectives (for references see Heaney, 2001).

In contrast with the mammals, the mites (Acari) parasitizing these hosts in the Philippines are relatively poorly studied (Corpuz-Raros, 1993). Mite lineages including permanent, highly specific parasites have great potential for co-phylogenetic and biogeographical studies (Balashov, 1982; Brooks, 1990; Clayton & Moore, 1997; Fain, 1994), and a number of groups parasitizing mammals or birds have been recently analyzed using modern methods (O'Connor, 1987; Klompen, 1992; Mironov & Dabert, 1999; Ramery *et al.*, 2000; Bochkov, 2001; Dabert *et al.*, 2001; Ehrnsberger *et al.*, 2001; Dabert, 2003). Detailed study of mites associated with Philippine mammals may provide useful data in understanding problematic elements of host phylogeny and particularly for reconstruction of the process of dispersal of the mammal hosts from Indochina to the Philippines via islands of the Sunda shelf. However, to date, only a relatively small number of papers containing taxonomic descriptions of acariform mites parasitizing mammals in the Philippines have been published (*e.g.*, Brown & Goff, 1988; Uchikawa *et al.*, 1991; Klompen, 1992; Fain, 2001; Bochkov & O'Connor, 2003).

The present work is a monographic study of the Philippine species of the fur-mite family Atopomelidae, common parasites of Philippine rodents and shrews. Because this family contains only permanent parasites that are highly specialized to live in the fur of small mammals, marsupials, "insectivores", primates, carnivores, and rodents (O'Connor, 1982), it has been the subject of recent co-evolutionary studies (Fain, 1994; Bochkov & Fain, 2003; Bochkov *et al.*, 2005; Bochkov & O'Connor, 2005). The family is widely distributed, being known from both hemispheres, but is largely limited to tropical or subtrop-

ical climates. About 47 genera and more than 380 species of atopomelid mites have been described, and five centers of biodiversity recognized, *i.e.*, mainland Africa, Madagascar, Southeast Asia, Australia-Oceania, and the Neotropical region (Fain, 1972a, b, 1976a, 1979, 1981). Some prior studies of Southeast Asian Atopomelidae have been conducted (Fain, 1981; Bochkov & Fain, 2003; Bochkov *et al.*, 2004, 2005; Bochkov & O'Connor, 2005), but no comprehensive study of this group in the Philippines has been attempted, and to date only four species have been recorded from this region, *Atopomelus crocidurae* Fain and Lukoschus, 1977, *Listrophoroides cucullatus* Trouessart, 1893, *L. postsquamatus* Fain, 1976, and *L. palawanensis* Fain, 1976.

The mammal fauna of the Philippines includes 29 genera and 81 species of potential hosts of atopomelids belonging to the families Muridae, Sciuridae (Rodentia), Soricidae (Soricomorpha), and Erinaceidae (Erinaceomorpha). We have examined specimens of 75% of these host species and collected 18 atopomelid species, including 12 previously undescribed, belonging to the genera *Atopomelus* Trouessart, 1917 and *Listrophoroides* Hirst, 1923. In this work, we provide descriptions or re-descriptions and keys to all Philippine species as well as their host ranges and distributions. We also conducted a phylogenetic analysis of the Philippine *Listrophoroides* species to determine the relationships of the new species to other Southeast Asian *Listrophoroides*, and to develop hypotheses of historical host-parasite associations.

MATERIAL AND METHODS

Material

Most of the more than 1500 mite specimens examined in this study originated from hosts collected by Dr. Lawrence Heaney, currently of the Field Museum of Natural History, Chicago, USA (FMNH), and his collaborators, who have been surveying the small mammal fauna of the Philippines since 1981. Field collections of mammals were conducted using techniques that minimized contact between host specimens to reduce the potential for parasite contamination. Host specimens were individually bagged, and those to be preserved in fluid were wrapped in cheesecloth before fixation in formalin and subsequent transfer to 70% ethanol for preservation. Wrapping minimizes both loss of ectoparasite specimens and contamination from other hosts, both serious problems when existing museum collections are surveyed for ectoparasites. Upon return to the USA, mammal specimens were borrowed by one of us (BMOC), unwrapped, and examined under a dissecting microscope. Ectoparasites were removed with fine forceps, sorted by

family group and location on the host, and preserved in 70% ethanol. During the 1987 and 2003 field expeditions, freshly collected hosts were examined in the field and mites collected by Hans Klompen and Ashley Dowling respectively. These collections were supplemented by examination of previously collected dry and fluid-preserved mammal specimens in FMNH and the U.S. National Museum of Natural History, Washington, USA (USNM), A total of 643 host individuals were examined in this study. The following collection data (as available) were recorded for each Philippine host specimen examined and entered into a database in the laboratory of BMOC: BMOC catalog number; host genus, species, order and family; island, province, specific locality, latitude, longitude, elevation, collection date, collector, field number, institutional acronym and catalog number of host depository; identification and location on host of each parasite species.

Mite specimens were cleared in lactophenol and mounted in Hoyer's medium. Specimens were studied using Zeiss and Leica compound microscopes equipped with phase contrast and differential interference contrast optics. Drawings were made with a camera lucida and measurements taken using a calibrated ocular micrometer. Specimens of previously described species were compared by AVB with specimens from the type series deposited in the collection of Dr. Alex Fain at the Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (IRSNB). The lectotype of *Listrophoroides cucullatus* (Trouessart, 1893), housed in the Muséum National d'Histoire Naturelle, Paris, France (NHMV) was examined earlier (Bochkov & Fain, 2003).

In the species descriptions, idiosomal chaetotaxy follows Griffiths *et al.* (1990) with modifications for coxal setae proposed by Norton (1998). The leg chaetotaxy follow Grandjean (1939). All measurements are given in micrometers (μm) and were taken as follows: body length = the total length from the anterior extremity of the gnathosoma to the posterior border of the body; body width = maximum width taken at whatever level it occurs; length of dorsal shields = maximum length, measured in the median line of the shields; length of the posterior legs = length from the most basal point of the trochanter to the apex of the tarsus, excluding pretarsus; length of the tibiotarsus = length from the most basal point of this segment to the apex of the tarsus, excluding pretarsus. Measurements for holotypes are given in parenthesis. Type and voucher specimens are deposited in institutions as determined by regulations and permits in force at the time the material was collected.

Host taxonomy and systematics follow Hutterer (2005) and Heaney *et al.* (1998) for insectivores and Musser and Carleton (2005) for rodents. Specimen depositories and reference numbers are cited using the following abbreviations:

BMNH—The Natural History Museum, London, England
 BMOC #—B.M. OConnor reference number
 FMNH—Field Museum of Natural History, Chicago, USA
 IRSNB—Institut royal des Sciences naturelles de Belgique, Brussels, Belgium

NHMV—Muséum National d'Histoire Naturelle, Paris, France
 NMP—National Museum of the Philippines, Manila, Philippines
 OSAL—The Acarology Laboratory, Ohio State University, Columbus, USA

SMF—Senckenberg Museum, Frankfurt, Germany.

UMMZ—Museum of Zoology, University of Michigan, Ann Arbor, USA

USNM—National Museum of Natural History, Smithsonian Institution, Washington, USA

ZISP—Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia

SYSTEMATICS

Key to the genera and subgenera of Philippine Atopomelidae Günther, 1942

MALES

- Attachment organs of coxae I absent. Anterior apodemes of coxae I–IV each fused mesally. Attachment organs of coxae II represented by pair of distinctly developed valves. Adanal suckers present. Pretarsal ambulacra of legs II–III strongly flattened dorso-ventrally. Legs IV hypertrophied, 1.6–2 times longer and much wider than legs III. Setae *pRII* and *sRIII* present on trochanters II and III, respectively. Trochanters IV with ventral spur; femur and genu IV fused; tibiotarsus saber-like, without ambulacra and modified setae. genus *Atopomelus* Trouessart, 1917
 (one species *A. crocidurae* Fain and Lukoschus, 1977; Fig. 1)

Attachment organs of coxae I distinctly developed, represented by striated membranes. Anterior apodemes of coxae I fused to each other, anterior apodemes of coxae II–IV widely separated. Attachment organs of coxae II represented by pair of distinctly developed striated membranes, fused to coxae II. Adanal suckers absent. Ambulacra of legs II–IV present, unmodified. Legs IV only slightly longer than legs III, femur IV maximally 2 times wider than femur III. Trochanters of all legs without setae. Trochanter IV without spurs; femur and genu IV separated; tibiotarsus not modified, setae *ra* modified genus *Listrophoroides* Hirst, 1923 (Fig. 5) 2.

- Femur and genu I not expanded dorsally. Hysteronotal shield without lateral incisions. Striated membranes of coxae II not reaching lateral margins of body, except in *L. (L.) batomys* sp.n. Anterior projections of aedeagal-supporting sclerite fused to each other. Postgenital sclerite present or absent, without lateral projections. Anal fold present or absent, not sclerotized subgenus *Listrophoroides* Hirst, 1923 (Fig. 5)

Femur and genu I strongly expanded dorsally. Hysteronotal shield with lateral incisions. Striated membranes of coxae II reaching lateral margins of body. Anterior projections of aedeagal-supporting sclerite fused to each other or separated. Postgenital sclerite present, with well developed Y, U or V shaped lateral projections. Anal fold present, distinctly sclerotized subgenus *Marquesania* Womersley, 1943 (Fig. 20)

FEMALES

- Attachment organs of coxae I absent. Anterior apodemes of coxae II fused to each other. Attachment organs of coxae II represented by pair of distinctly developed valves. Hysteronotal shield absent. Setae *f2* macrosetae. Setae *pRII* and *sRIII* present on trochanters II and III, respectively. Pretarsal ambulacra of legs II–IV strongly flattened dorso-ventrally.
 genus *Atopomelus* Trouessart, 1917 (one species in the Philippines *A. crocidurae* Fain and Lukoschus, 1977, Fig. 2)

Attachment organs of coxae I well developed, represented by coxal membranes. Attachment organs of coxae II represented by pair of distinctly developed striated membranes fused to coxae II. Hysteronotal shield present,

covering most part of hysteronotum. Setae *f2* short, not longer than other hysteronotal setae. Trochanters of all legs without setae. Ambulacra of legs II–IV not modified . . . genus *Listrophoroides* Hirst, 1923 (Fig. 6) . . . 2.

2. Femur and genu I not expanded dorsally. Striated membranes of coxae II not reaching lateral margins of body, except in *L. (L.) batomys* sp.n. Basal cap of spermatheca not sacculiform subgenus *Listrophoroides* Hirst, 1923 (Fig. 6)

Femur and genu I strongly expanded dorsally. Striated membranes of coxae II reaching lateral margins of body. Basal cap of spermatheca sacculiform subgenus *Marquessania* Womersley, 1943 (Fig. 21)

Atopomelus Trouessart, 1918

Type species: *Atopomelus locusta* Trouessart, 1918, by monotypy.

This genus includes five species associated exclusively with "insectivore" hosts of the families Erinaceidae (Erinaceomorpha), Talpidae and Soricidae (Soricomorpha). It has recently been revised by Bochkov *et al.* (2005), and the Philippine records below were previously included in that work.

Atopomelus crociduræ Fain and Lukoschus, 1977 (Figs 1–4)

Atopomelus crociduræ Fain and Lukoschus, 1977: 29, figs 1–2.

DIAGNOSIS. *Male*: dorsal shields without ornamentation. Setae *d1* and *d2* subequal in length. Setae *e2* microsetae. Femurogenu IV with two ventral spurs. Ventral spur of trochanter IV bifurcate; dorsal spur absent. *Female*: postscapular shield with large posterior median incision, length ratio of this incision and this shield 2:3, width ratio 1:3. Median scales of hysterosoma in form of narrow triangles. Genital papillae separate.

MALE (Fig. 1). Body 330–360 long (in 10 specimens), 130–140 wide, length/width ratio 2.5 : 1. *Gnathosoma* 55–60 long, 40–45 wide. *Idiosoma*. Dorsal shields without ornamentation. Prescapular shield 73–77 long. Postscapular shield 120–130 long. Hysteronotal shield 100–110 long, trapeziform, bearing 3 pairs of setae, *d1*, *d2*, *e1*, and pair of round unsclerotized patches situated near to bases of setae *d2*. Diameter of these patches subequal to bases of setae *d2*. Setae *d1* and *d2* slightly thickened, subequal in length, or *d1* slightly longer. Setae *e1* 3–4 times longer than *d1*. Length ratio between postscapular and hysteronotal shields subequal, 1.2:1. Unsclerotized integument of opisthosoma without ornamentation, and only few scales present laterally. Setae *e2* microsetae, setae *f2* about 3 times longer than *h2*. Setae *h3* about 3 times longer than *f2*. Aedeagus short. Length of idiosomal setae: *si* 17–27, *se* 20–30, *c2* 30–45, *c3* 30–35, *cp* 50–70, *d1* 50–55, *d2* 35–45, *e1* 70–75, *e2* 7–8, *f2* 45–60, *h1* 6–7, *h2* 13–15, *h3* 140–150, *3a* 28–32, *g* 10–12, *4a* 6–7, *4b* 23–25, *ps3* 5–6. Setae *d* I–II 4–5, III 57–65, IV 180–190. *Legs* IV 2 times longer than legs III. Leg III 135–145 long; leg IV 210–230 long; femurogenu IV 130–150 long; tibiotarsus III 60–65 long; tibiotarsus IV 105–110 long; ventral spur of trochanter IV about 45 long; anterior ventral spur of femurogenu IV 9–10 long; posterior ventral spur of femurogenu IV about 5 long. Setae *d* I–II much shorter than

respective solenidia *ω1*; seta *d* III subequal in length to tibiotarsus, excluding ambulacrum. Trochanter IV without dorsal spur, ventral spur well developed, subequal in length to this segment, with two apices unequal in length. Femurogenu IV with two ventral spurs. Tarsus IV with two unequal apices (Fig. 1F). Length of solenidia: *ω1* I–II 14–15, *ω3* I 20–22; *φ* I–II 40–43, III 48–53, IV 38–40; *σ* I–II 11–12, III 30–32.

FEMALE (Fig. 2). Body 420–435 long (in 10 specimens), 125–135 wide. *Gnathosoma* 55–60 long, 35–40 wide. *Idiosoma*. Prescapular shield 68–75 long. Postscapular shield 45–50 long, 87–90 wide, well developed, covered by scale-like pattern, with large posterior median incision. Length ratio of this incision and postscapular shield 2:3, width ratio 1:3. Setae *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, and *ps3* short, subequal in length. Hysteronotum covered medially by triangular scales that are longer than wide. Genital papillae separated. Genital valves triangular, widely separated each from other, each bearing setae *3a* and *g*. Distal part of spermatheca narrow. Length of idiosomal setae: *si* 10–12, *se* 14–16, *c2* 18–20, *c3* 14–15, *cp* 38–42, *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, *ps3*—all 10–12, *f2* 170–175, *h3* 125–130, *3a* 20–22, *g* and *4a* 18–20, *4b* 12–14. Setae *d* I–II 4–5, III–IV 45–50. *Leg* III 95–100 long; leg IV 100–115 long; tibiotarsus III–IV 38–40 long. Setae *d* I–II much shorter than respective solenidia *ω1*; seta *d* III–IV slightly longer or subequal to respective tibiotarsi, excluding ambulacra. Length of solenidia: *ω1* I–II 15–20, *ω3* I 19–20; *φ* I–III 38–43, IV 10–12; *σ* I–II 12–13, III 10–11.

LARVA (Fig. 3A–E). *Gnathosoma* as in adults. *Idiosoma* as in female but postscapular shield absent. Anterior apodemes I and II fused medially, and apodemes IV fused in anterior part. Idiosomal setation: *scx*, *si*, *se*, *c2*, *c3*, *cp*, *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, *1a*, *3a*. Leg sensilla: I trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*, *σ1*), tibia 2 (*gT*, *φ*), tarsus 9 (*wa*, *ra*, *la*, *ba*, *d*, *e*, *f*, *ε*, *ω1*); II trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*, *σ*), tibia 2 (*gT*, *φ*), tarsus 8 (*wa*, *ra*, *la-ba*, *d*, *e*, *f*, *ω1*); III trochanter 0, femur 0, genu 1 (*σ*), tibiotarsus 8 (tibia—*kT*, *φ*, tarsus—*w*, *r*, *s*, *d*, *e*, *f*).

PROTONYMPH (Fig. 3F–L). Postscapular shield absent. Setae *f2*, *h3*, *ps3*, and *g* added. One pair of indistinct genital papillae present between coxae IV. Apodemes IV fused mesally. Leg IV added with tarsal setae *d*, *r*, and *w*.

TRITONYMPH (Fig. 4). Postscapular shield absent. Setae *4a* and *4b* added on idiosoma, setae *pR* added on trochanter II, setae *kT* and solenidion *φ* added on tibia IV, and setae *e*, *f* added on tarsus IV.

MATERIAL EXAMINED. Eleven males, 10 females, and 1 tritonymph (BMOC 92-1400-100) ex *Crocidura mindorus* (FMNH 146790), Sibuyan Isl., Romblon Prov., 6.75 km S, 4.5 km E Magdiwang, 12°26'N, 122°33'E, 1325 m, 9 March 1992, coll. S.M. Goodman (SMG 5153); 12 males, 7 females, 6 tritonymphs, 1 protonymph, and 1 larva (BMOC 92-1400-097) ex *C. mindorus* (FMNH 146789), same data, 7 March 1992, coll. S.M. Goodman (SMG 5131); 11 males, 9 females, and 5 tritonymphs (BMOC 92-1400-092) ex *C. mindorus* (FMNH 146788), same data, 6 March 1992, coll. S.M. Goodman (SMG 5116); 4 males and 4 females (BMOC 01-0920-008) ex

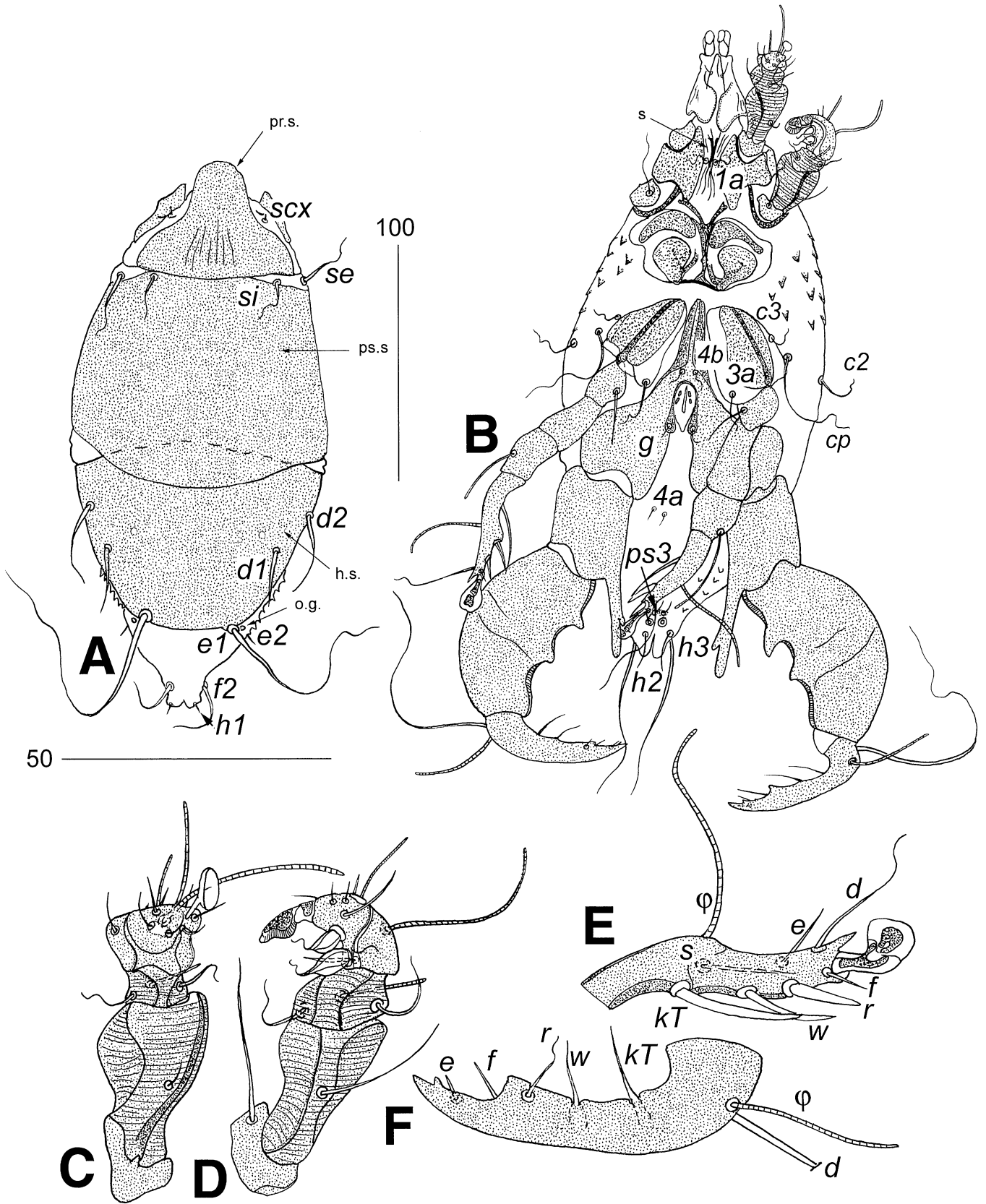


Fig. 1. (A-F). *Atopomelus crocidurae* Fain and Lukoschus, 1977, male. A.—Dorsal view. B.—Ventral view. C.—Leg I, ventral view. D.—Leg II, ventral view. E.—Tibiotarsus III, lateral view. F.—Tibiotarsus IV, lateral view. Abbreviations: h.s.—hysteronotal shield, o.g.—opening of opisthosomal glands, pr.s.—prescapular shield, ps.s.—postscapular shield, s—sternum. Scale bars 100 μ m (A-B) and 50 μ m (C-F).

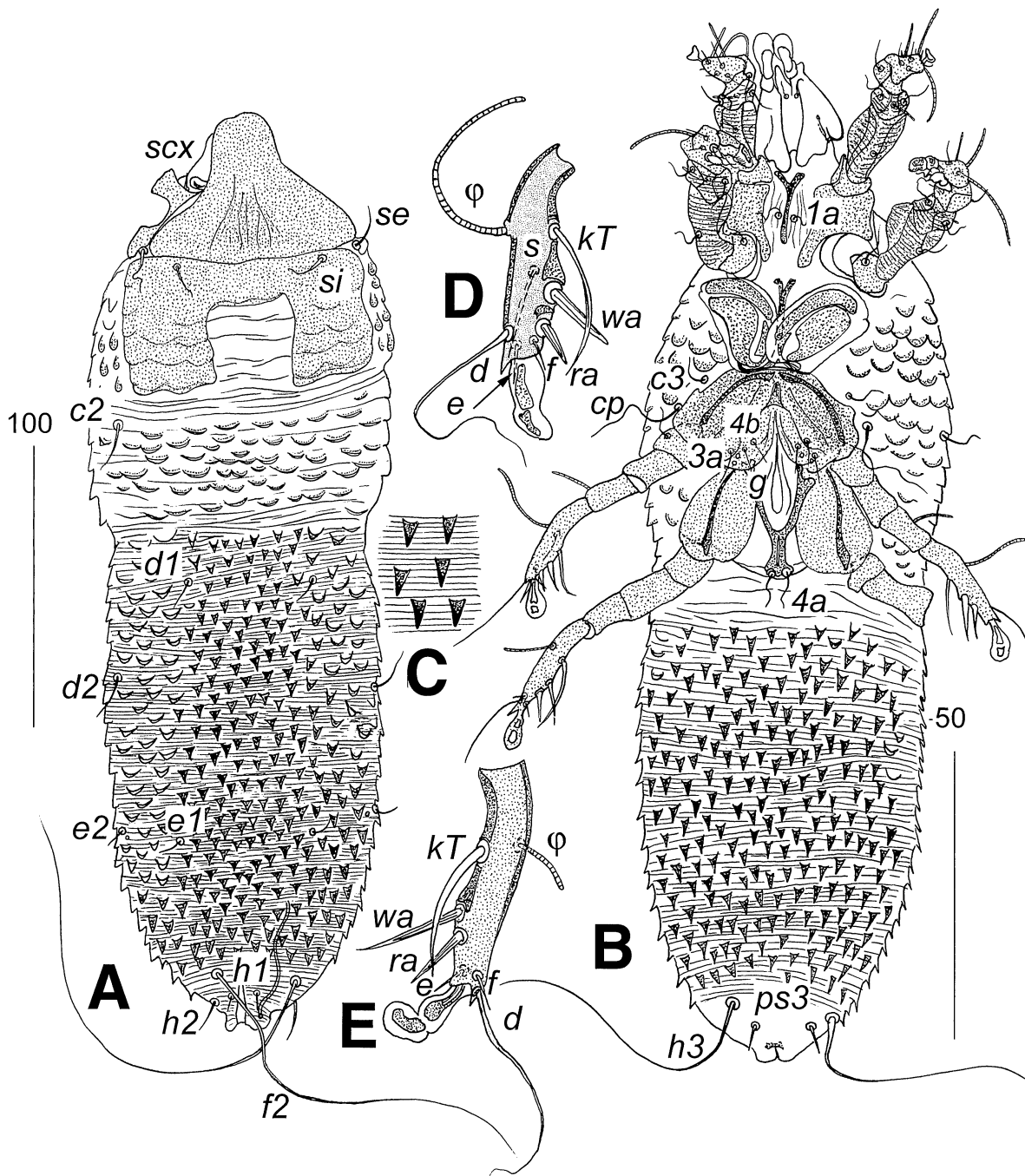
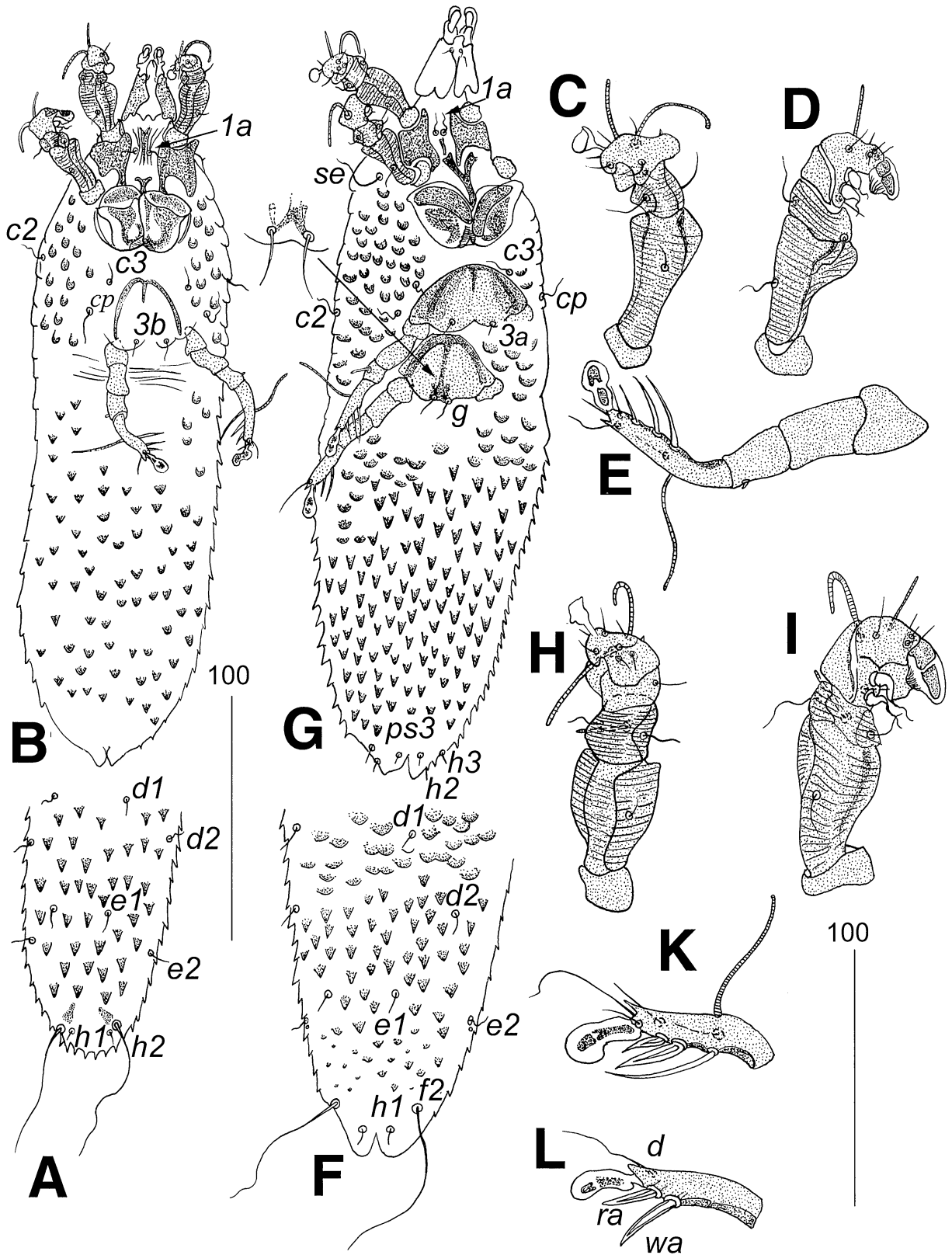


Fig. 2. (A–E). *Atopomelus crocidurae*, female. A.—Dorsal view. B.—Ventral view. C.—Dorsal scales of idiosoma. D.—Tibiotarsus III, lateral view. E.—Tibiotarsus IV, lateral view. Scale bars 100 μm (A–B) and 50 μm (C–E).

Crocidura grayi (FMNH 168976), Luzon Isl., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Am-licao, 17°26'30"N, 121°04'15"E, 1800 m, 25 March 2001, coll. L.R. Heaney (LRH 6436); 2 males and 1 female (BMOC 01-0920-007) ex *C. grayi* (FMNH 168975), same data, 20 March 2001, coll. E.A. Rickart (EAR 4583); 2 males, 4 females, 4 tritonymphs, and 1 protonymph (BMOC 01-0920-009) ex *C. grayi* (FMNH 168977), same data, 25 March 2001, coll. E.A. Rickart (EAR 4615); 1

male (BMOC 01-0920-008) ex *C. grayi* (FMNH 168976), same data, 25 March 2001, coll. L.R. Heaney (LRH 6436); 2 tritonymphs (BMOC 01-0920-006) ex *C. grayi* (FMNH 168974), same data, 19 March 2001, coll. L.R. Heaney (LRH 6363); 2 females, 8 tritonymphs, 5 protonymphs, and 2 larvae (HK 87-0620-001) ex *Crocidura beatus* (USNM 458960), Bohol Isl., Bohol Prov., 1 km S, 2 km E Bilar, 9°43'N, 124°7'E, 20 June 1987, coll. L.R. Heaney (LRH 3747); 3 males, 2 females,



50

Fig. 3. (A-L). *Atopomelus crocidurae* Fain and Lukoschus, 1977, immatures. Larva (A-E). A.—Hysterosoma, dorsal view. B.—Ventral view. C.—Leg I, ventral view. D.—Leg II, ventral view. E.—Tarsus III, lateral view. Protonymph (F-L). F.—Hysterosoma, dorsal view. G.—Ventral view. H.—Leg I, ventral view. I.—Leg II, ventral view. K.—Tibiotarsus III, lateral view. L.—Tibiotarsus IV, lateral view. Scale bars 100 μ m (A-B, F, G) and 50 μ m (C-E, H-I).

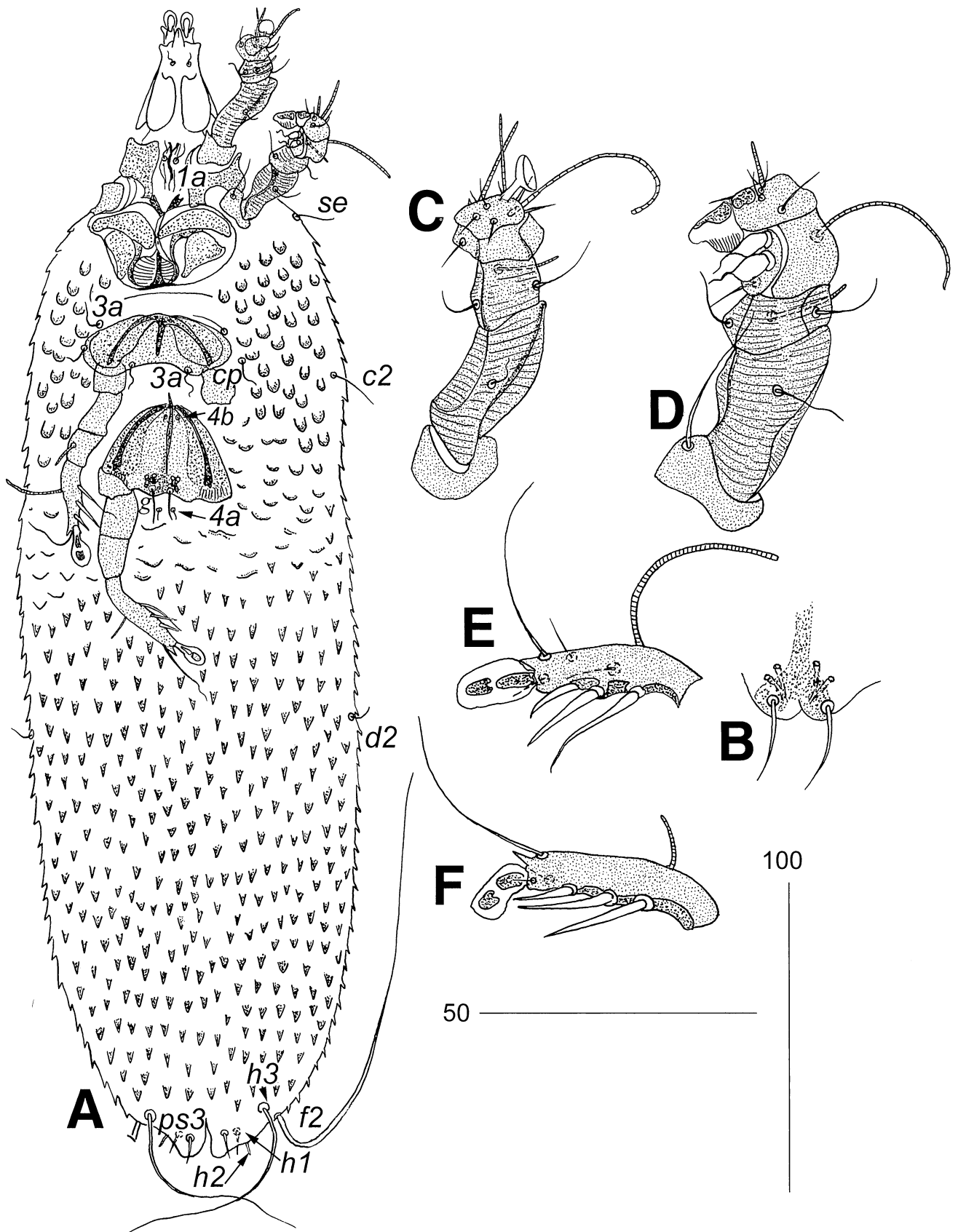


Fig. 4. (A-F). *Atopomelus crocidurae* Fain and Lukoschus, 1977, tritonymph. A.—Ventral view. B.—Genital acetabulae. C.—Leg I, ventral view. D.—Leg II, ventral view. E.—Leg III, lateral view. F.—Leg IV, lateral view. Scale bars 100 μm (A) and 50 μm (B-G).

9 tritonymphs, 3 protonymphs, and 3 larvae (BMOC 95-1214-002) ex *C. beatus* (FMNH 167854), Camiguin Prov., Mt. Timpoong, 2 km N, 6.5 km W Mahinog, 9°11'N, 124°43'E, 1000 m, 22 May 1994, coll. B.R. Tabaranza (BRT 135); 3 males, 5 tritonymphs, 5 protonymphs, and 6 larvae (BMOC 95-1214-003) ex *C. beatus* (FMNH 167855), same data, coll. B.R. Tabaranza (BRT 148).

TYPE DEPOSITION. Holotype is deposited in NHMV, voucher specimens from this study in FMNH, NMP, OSAL, UMMZ.

HOST ASSOCIATIONS AND DISTRIBUTION. This species was originally described from two females collected from *Crocidura attenuata* Milne-Edwards, 1872 (= *aequicaudata*) from Sumatra (Fain & Lukoschus, 1977). *Atopomelus crocidurae* is widely distributed on Indo-Malayan shrews of the genus *Crocidura* (tribe Crocidurini): *Crocidura monticola* Peters, 1870, and *C. foetida* Peters, 1870 from southwestern Borneo (Indonesia), *C. malayana* Robinson and Kloss, 1911 from west Malaysia, *C. beatus* Miller, 1910, *C. grayi* Dobson, 1890, and *C. mindorus* Miller, 1910, all Philippine endemics (Bochkov *et al.*, 2004). We did not collect this species from the single specimen of *C. negrina* Rabor, 1952 that was available to us; however, this specimen was in poor condition having been found dead on a road on Negros Island. We also did not recover any *Atopomelus* mites from 33 individuals of the gymnure, *Podogymnura truei*, collected on Mindanao Island, although species are known from mainland Asian gymnures of the genus *Hylomys* (Bochkov *et al.*, 2005).

TAXONOMIC NOTES. *Atopomelus crocidurae* is more similar to *Atopomelus talpae* Fain, Lukoschus and Cauwenberge, 1973 than to the species known from Erinaceidae. In males of these two species, the postscapular shield is without ornamentation, the opisthonotal surface posterior to the hysteronotal shield is unornamented, the opisthosomal venter is sparsely covered by scales laterally, trochanter IV lacks a dorsal spur, and its ventral spur is bifurcate; in females, the hysteronotum is covered by numerous scales, which are longer than wide, the genital papillar remnants are separated, and the distal part of the spermatheca is not inflated. These species differ from each other by the following characters. In both sexes of *A. crocidurae*, seta *la* is absent on all tarsi, seta *f* of tarsus II is filiform; in males, the hysteronotal shield is trapezoidal in shape, with a pair of rounded unsclerotized patches near the bases of setae *d2*, setae *e2* are microsetae, setae *ps2* are absent, femur-genu IV has two ventral spurs, the ventral spur of trochanter IV has two points unequal in length, tarsus IV has two unequal apical points; in females, the postscapular shield is rectangular, with a deep and wide posterior median incision; it is covered by a scale-like pattern, setae *4a* are situated on the fused sclerotized areas of coxae IV, they are subequal in length to setae *g*. In both sexes of *A. talpae*, seta *la* is present on tarsi I and II, seta *f* of tarsus II is inflated; in males, the hysteronotal shield is mushroom-shaped, without the discernible non sclerotized patches, setae *e2* are macrosetae, subequal in length to *e1*, setae *ps2* are present, femur-genu IV is without any spurs, the ventral spur of trochanter IV has two subequal points, tarsus IV has two subequal

apical points; in females, the postscapular shield is triangular, with a strongly sclerotized median band, setae *4a* are situated on the soft cuticle between the sclerotized areas of coxae IV and are almost 2 times longer than setae *g*.

Genus *Listrophoroides* Hirst, 1923

Type species *Listrophoroides aethiopicus* Hirst, 1923, by monotypy

This large genus has been divided into 17 subgenera (Fain & Bochkov, 2003). Among them, the subgenera *Listrophoroides* (*s.s.*), *Marquesania*, and *Paklistrophoroides* Fain and Hyland, 1980 are associated primarily with Asian murine rodents and form a monophyletic complex (Bochkov & OConnor, 2005). The morphology of immatures is described below for *Listrophoroides* (*M.*) *postsquamatus* Fain, 1976.

Subgenus *Listrophoroides* Hirst, 1923

This subgenus includes 57 species, along with four newly recognized species described below (Bochkov *et al.*, 2004; Bochkov & OConnor, 2005).

Key to Philippine species of the subgenus *Listrophoroides* (*s.s.*) Hirst, 1923

MALES

- Anus situated ventro-terminally. Anal fold absent. Lobar membrane with median incision. 3
Anus situated ventrally. Anal fold present. Lobar membrane without median incision. 2
- Striated membranes of coxae II reaching lateral margins of body. Median sclerotized band on postscapular shield absent. Anal fold sclerotized. Lobar membrane weakly developed. *L. (L.) batomys* sp.n. (Fig. 7)
Striated membranes of coxae II not reaching lateral margins of body. Median sclerotized band on postscapular shield present. Anal fold not sclerotized, but pair of elongated adanal shields present inside of anal fold close to anal opening. Lobar membrane well developed
L. (L.) mindanensis Fain and Lukoschus, 1981 (Fig. 5)
- Dorso-basal projection of femur I distinctly developed. Postscapular shield covered by short straight, curved or scalloped lines arranged into transverse rows. Hysteronotal shield unornamented posterior to level of setae *e2*. Coxal fields IV without medial sclerotized projections 5
Dorso-apical projection of femur I indistinct. Postscapular shield covered by entire transverse lines. Hysteronotal shield covered by distinct ornamentation posterior to level of setae *e2*. Coxal fields IV with medial sclerotized projections 4
- Projections of coxal fields IV wide and relatively long, reaching posteriorly to level of setae *4a*. Lobar membrane with distinct lateral expansions
L. (L.) chrotomys sp.n. (Fig. 19A–B)
Projections of coxal fields IV narrow and short, not reaching level of setae *4a*. Lobar membrane weakly developed, without lateral expansions.
L. (L.) insularis sp.n. (Fig. 17)

5. Hysteronotal shield covered by ornamentation in anterior half. Lobar membrane weakly developed, smooth laterally 6

Hysteronotal shield covered by ornamentation only in anterior third. Lobar membrane distinctly developed, dentate laterally

L. (L.) brachypyx Fain, 1974 (Fig. 11)

6. Striated membranes of coxae II subequal in width to striated membranes of coxae I. Aedeagus thick and short, about 9 long. Supporting sclerite of aedeagus distinctly developed. Postgenital shield long and narrow, extending posteriorly to anal opening. Opisthogaster without sclerotized bands or patches other than postgenital shield

L. (L.) palawanensis Fain, 1976 (Fig. 9)

Striated membranes of coxae II distinctly wider than striated membranes of coxae I. Aedeagus thin and elongated, about 22–24 long. Supporting sclerite of aedeagus strongly reduced. Postgenital shield absent. Pair of narrow sclerotized bands flanking aedeagus present

L. (L.) crunomys sp.n. (Figs 13, 15)

FEMALES

1. Dorso-apical projection of femur I indistinct 4

Dorso-apical projection of femur I distinctly developed 2

2. Anterior half of postscapular shield without short straight lines in lateral margins. Soft cuticle of hysteronotum with lateral scales restricted to region posterior to level of setae *el* 3

Anterior half of postscapular shield without ornamentation in lateral margins. Soft cuticle of hysteronotum with numerous lateral scales between levels of setae *el* and *e2* *L. (L.) brachypyx* Fain, 1974 (Fig. 12)

3. Basal cap of spermatheca globose, inflated. Striated membranes of coxae II narrow, subequal in width to striated membranes of coxae I. Coxal fields III without transverse line. Coxal fields IV with short transverse line

L. (L.) palawanensis Fain, 1976 (Fig. 10)

Basal cap of spermatheca sacculiform. Striated membranes of coxae II distinctly wider than striated membranes of coxae I. Coxal fields III with transverse line. Coxal fields IV without transverse line.

L. (L.) crunomys sp.n. (Figs 14, 16)

4. Striated membranes of coxae II not reaching lateral margins of body. Ends of epigynal apodeme not bifurcate 5

Striated membranes of coxae II reaching lateral margins of body in their anterior half. Ends of epigynal apodeme bifurcate.

L. (L.) batomys sp.n. (Fig. 8)

5. Postscapular shield with indistinct median band. Lateral opisthogaster with numerous scales extending from level of coxae IV to level of setae *ps3* *L. (L.) mindanensis* Fain and Lukoschus, 1981 (Fig. 6)

Postscapular shield without median band. Lateral opisthogaster without scales 6

6. Median ventral scales of opisthosoma posterior to setae *4a* distinctly developed and numerous in most specimens

L. (L.) chrotomys sp.n. (Fig. 19C)

Median ventral scales of opisthosoma posterior to setae *4a* relatively few and indistinct *L. (L.) insularis* sp.n. (Fig. 18)

Listrophoroides (Listrophoroides) mindanensis

Fain and Lukoschus, 1981

(Figs 5–6)

Listrophoroides (Listrophoroides) mindanensis Fain and Lukoschus, 1981 in Fain, 1981: 75, figs 89–92.

DIAGNOSIS. Postscapular shield with indistinct median band. *Male*. Genital organ situated posterior to level of coxae III. Aedeagus short, about 6 long. Anus situated ventrally. Lobar membrane distinctly developed, without median incision. *Female*. Ends of epigynal apodeme slightly bifurcate.

MALE (Fig. 5). Body 335–345 long, 117–135 wide in 10 specimens. Length and width of gnathosoma subequal, about 35. *Dorsum*. Postscapular shield 70–77 and 110–125 wide, with indistinct median band and 7–8 transverse lines. Hysteronotal shield 155–165 long, completely covering dorsal surface of hysteronotum, ornamented with 4–5 transverse lines in its anterior third and fine, slightly reticulate pattern medially, extending to level of setae *el*. Distance *el-el* 29–33. Setae *e2* situated on hysteronotal shield. Setae *h3* 33–37 long. *Venter*. Striate membranes of coxae II well developed, about 30 wide. Genital organ situated between levels of coxae III and IV. Aedeagus short, about 6 long. Postgenital shield small, only slightly wider than bases of setae *g*. Coxae III without transverse lines. Coxal fields IV with indistinctly sclerotized projections, reaching level of setae *4a*. Pair of sclerotized patches present immediately posterior to bases of setae *4a*. Anus situated ventrally. Anal fold well developed, V-shaped. Pair of adanal shields present adjacent to anal opening. Lobar membrane well developed, triangular, covered by longitudinal striations, without median incision. *Legs*. Dorso-apical projection of femur I indistinct. Femur IV about 18 wide, 1.4 times wider than femur III (13). Legs III and IV 80–85 and 100–105 long, respectively. Tibiotarsi III and IV 25–30 and 33–35 long, respectively. Length ratio of femur: genu: tibiotarsus IV 1.6:1:1.5. Solenidia φ of legs III and IV 11–13 and 35–40, respectively.

FEMALE (Fig. 6). Body 370–395 long, 130–140 wide in 10 specimens. Gnathosoma about 45 long, 37 wide. *Dorsum*. Postscapular shield 77–85 long, 120–130 wide, with indistinct median band and 7–8 transverse lines. Hysteronotal shield 160–175 long, covered by 10–12 transverse lines extending from the anterior margin to level of setae *el*. Third anterior line curved laterally; lines situated in posterior half of hysteronotal shield fine and interrupted. Distances *d1-d1* and *el-el* 75–78 and 50–57 long, respectively. Distance *el-el* 2.4–2.8 times longer than distance *el*-posterior margin of hysteronotal shield, 18–25. Basal cap of spermatheca sacculiform. *Venter*. Striated membranes of coxae II well developed, about 35 wide. Coxae III with transverse line. Opisthogaster sclerotized and covered laterally by scales reaching level of setae *f2*. Median part of opisthogaster with indistinct, broadly rounded scales in anterior half. *Legs*. Dorso-apical projection of femur I indistinct. Legs III and IV 80–90 and 90–100 long, respectively. Solenidia φ of legs III and IV, 9–10 and 2–3 long, respectively.

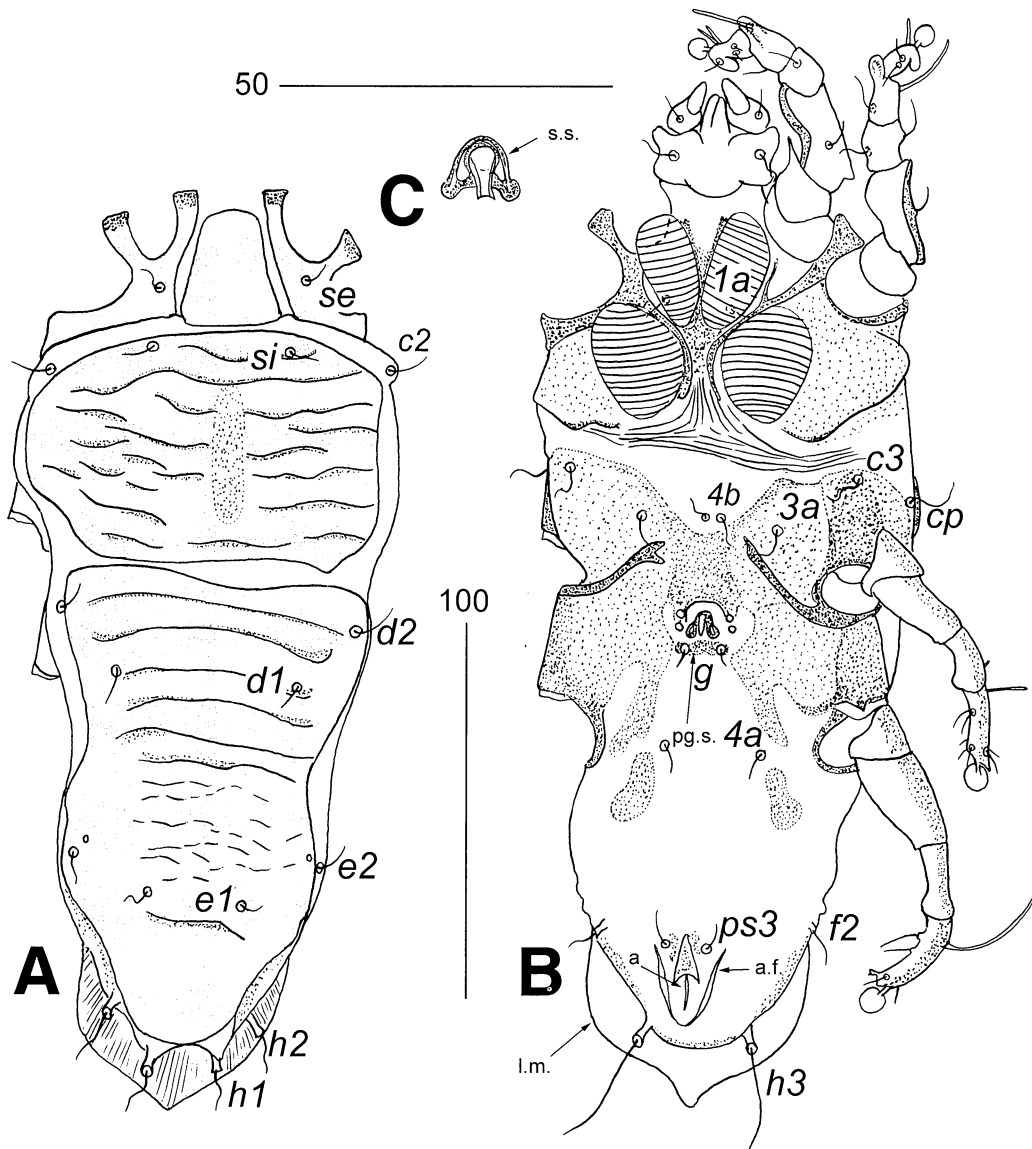


Fig. 5. (A-C). *Listrophoroides mindanensis* Fain and Lukoschus, 1981, male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. Abbreviations: a—anus, a.f.—anal fold, l.m.—lobar membrane, pg.s.—postgenital shield, s.s.—supporting sclerite. Scale bars 100 μ m (A-B) and 50 μ m (C).

MATERIAL EXAMINED. Nine males and 24 females (BMOC 93-1300-043) ex *Batomys salomonseni* (FMNH 147932), Mindanao Isl., Bukidnon Prov., Mt. Katanglad Range, 18.5 km S, 4 km E Camp Phillips, 08°09'30"N, 124°51'E, 2250 m, 28 March 1993, coll. E.A. Rickart (EAR 2553); 8 males and 29 females (BMOC 93-1300-042) ex *B. salomonseni* (FMNH 147931), same data, coll. E.A. Rickart (EAR 2552).

TYPE DEPOSITION. Holotype is deposited in SMF. Voucher specimens from this study deposited in FMNH, NMP, OSAL, UMMZ.

HOST ASSOCIATIONS AND DISTRIBUTION. This species was originally described from *Batomys salomonseni* from Mindanao Island (Fain, 1981) and has not been subsequently reported. It is a monoxenous parasite of the Old Philippine endemic, *Batomys salomonseni* (Sanborn, 1953).

***Listrophoroides (Listrophoroides) batomys* New Species**
(Figs 7-8)

DIAGNOSIS. Striate membranes of coxae II wide, reaching lateral margins of body. *Male.* Genital organ situated posterior to level of coxae III. Aedeagus short, 7-8 long. Anus situated ventrally. Lobar membrane weakly developed, without median incision. *Female.* Ends of epigynal apodeme bifurcate.

MALE (Fig. 7) Body 328-339 long (339), 123-129 wide in 9 paratypes (129). Length and width of gnathosoma subequal, 35-40. *Dorsum.* Postscapular shield 73-77 long (73), 121-128 wide (123), completely covered by 7-9 transverse lines, 2-3 posterior lines interrupted. Hysteronotal shield 154-165 long (165), completely covering dorsal surface of hysteronotum, ornamented with 9-11 transverse lines extending from ante-

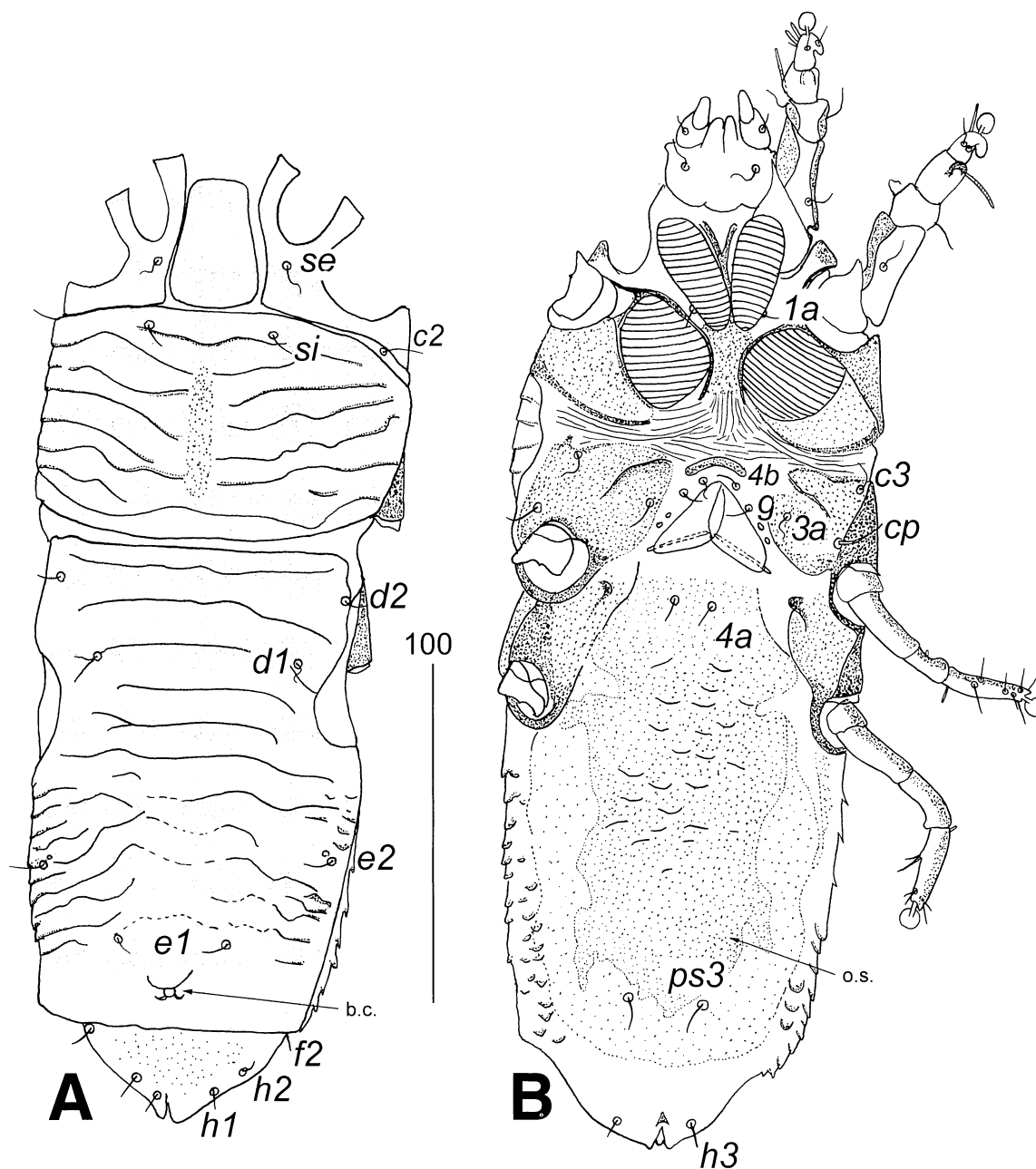


Fig. 6. (A-B). *Listrophoroides mindanensis* Fain and Lukoschus, 1981, female. A.—Dorsal view. B.—Ventral view. Abbreviations: b.c.—basal cap of spermatheca, o.s.—opisthogastric shield.

rior margin to level of setae *e1*, 2–3 posterior lines interrupted in some specimens. Distance *e1-e1* 40–46 (46). Setae *e2* situated on hysteronotal shield. Setae *h3* 18–22 long (20). *Venter*. Striate membranes of coxae II wide, reaching lateral margins of body. Genital organ situated between levels of coxae III and IV. Postgenital shield small, only slightly wider than bases of setae *g*. Aedeagus short, length 7–8 (7). Coxae III with 2–3 transverse lines. Coxal fields IV with indistinctly sclerotized projections, reaching level of setae *4a*. Pair of sclerotized patches present immediately posterior to bases of setae *4a* present. Anus situated ventrally. Anal fold distinctly developed, shaped

like an inverted-V. Adanal shields present. Lobar membrane weakly developed, without median incision, slightly elongated in median part. *Legs*. Dorso-apical projection of femur I indistinct. Femur IV about 18 wide, 1.3 times wider than femur III (13). Legs III and IV 77–90 (79) and 99–108 long (103), respectively. Tibiotarsi III and IV 24–31 (26) and 33–35 long (33), respectively. Length ratio of femur: genu: tibiotarsus IV 2 : 1 : 1.6. Solenidia φ of legs III and IV 11–13 (11) and 33–37 long (33), respectively.

FEMALE (Fig. 8). Body 357–380 long, 135–146 wide in 10 paratypes. Length and width of gnathosoma subequal, about

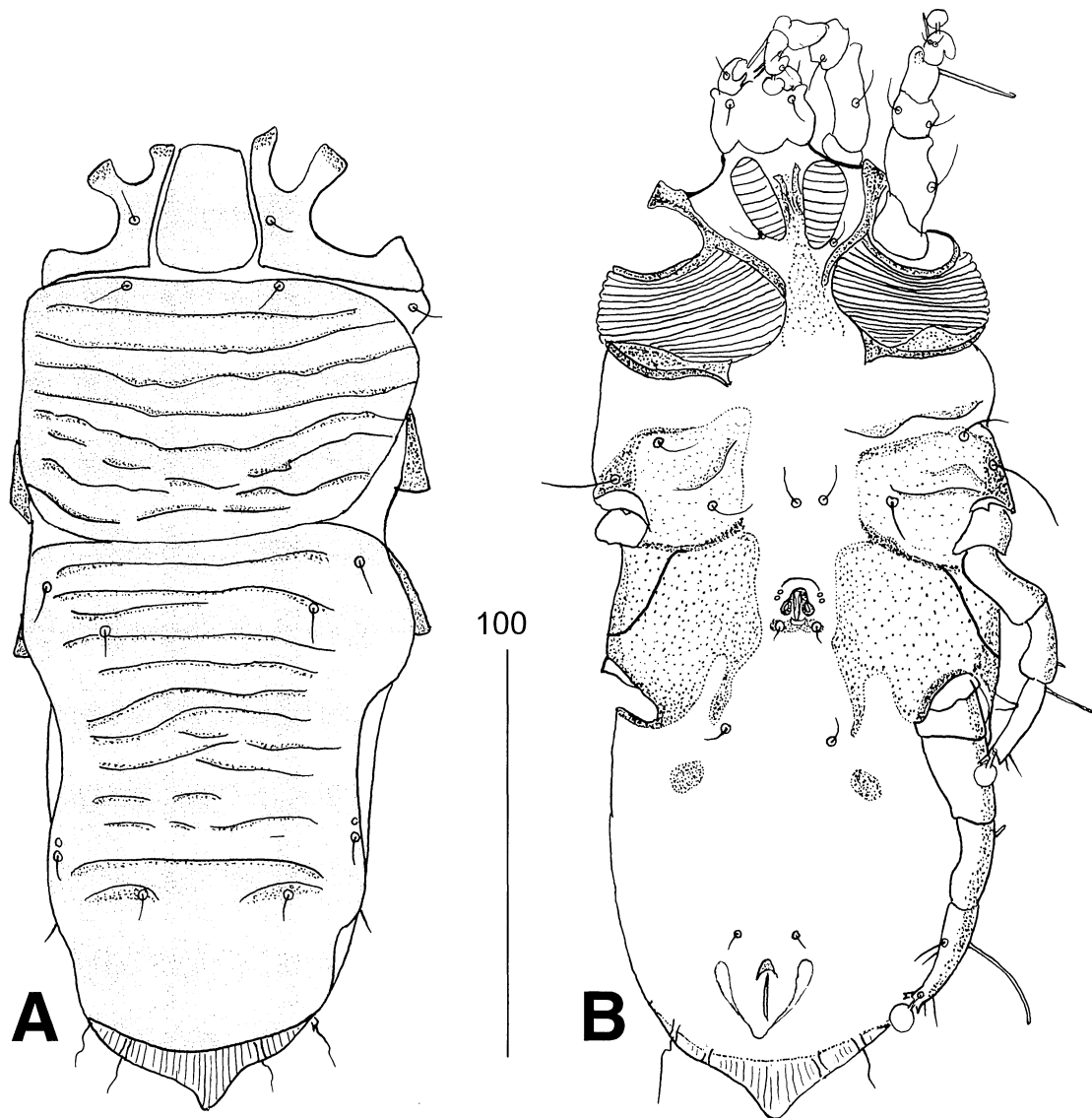


Fig. 7. (A-B). *Listrophoroides batomys* sp.n., male. A.—Dorsal view. B.—Ventral view.

45. *Dorsum*. Postscapular shield 85–88 long, 120–143 wide, completely covered by 7–9 transverse lines. Hysteronotal shield 165–178 long, covered by 10–14 transverse lines extending from anterior margin to level of setae *e1*; median lines curved laterally. Hysteronotal shield 103–117 wide at level of setae *d1* and 112–120 wide at level of setae *e1*. Distance *e1-e1* 50–66, 1.6–1.7 times longer than distance *e1*-posterior margin of hysteronotal shield, 29–35. *Venter*. Basal cap of spermatheca sacculiform. Striated membranes of coxae II wide, reaching lateral margins of body. Coxae III with 2 transverse lines. Opisthogaster sclerotized. Lateral parts of opisthogaster covered by furrows in anterior third and scales reaching level of setae *f2*. Median part of opisthogaster with weakly developed, widely rounded scales extending from level of setae *4a* to level of setae *ps3*. *Legs*. Dorso-apical projection of femur I. weakly developed. Legs III and IV 81–92 and 90–95 long

respectively. Solenidia ϕ of legs III and IV, 11–13 and 2–3 long, respectively.

ETYMOLOGY. The species name is derived from the generic name of the host and is a noun in apposition.

TYPE MATERIAL. Male holotype (BMOC 88-1710-037, 1), 3 male and 1 female paratypes (BMOC 01-0920-037, 2–5) ex *Batomys granti* (FMNH 169125), Luzon Isl., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Magdala, 17°27'30"N, 121°04'06"E, 1600 m., 15 March 2001, coll. E.A. Rickart (EAR 4560); 1 male and 12 female paratypes (BMOC 88-1710-038, 1–13) ex *B. granti* (USNM 458950), Luzon Isl., Camarines Sur Prov., Mt. Isarog, 4 km N, 21 km E Naga, 13°40'N, 123°22'E, 1350 m., 29 April 1988, coll. E.A. Rickart (EAR 2024); 6 male and 4 female paratypes (BMOC 88-1700-008, 1–10) ex *B. granti* (USNM 458339), same data, 22 April 1988, coll. L.R. Heaney (LRH 4150).

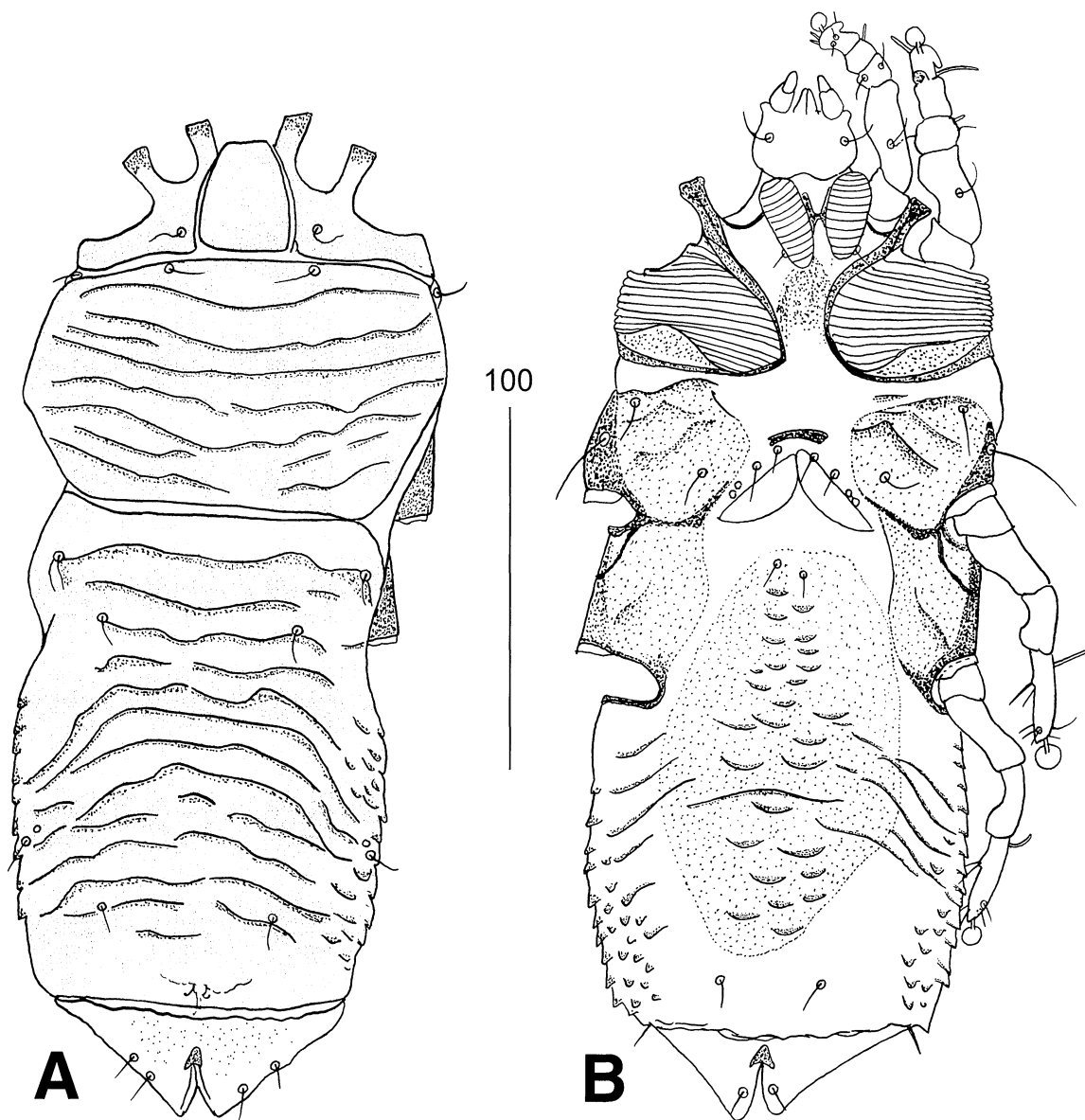


Fig. 8. (A-B). *Listrophoroides batomys* sp.n., female. A.—Dorsal view. B.—Ventral view.

SPECIMEN DEPOSITION. Holotype is deposited in NMP, paratypes in FMNH, NMP, UMMZ, USNM, OSAL, ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION. This species is a monoxenous parasite of the Old Philippine endemic *Batomys granti* Thomas, 1895 and occurs with its host in both northern and southeastern Luzon.

TAXONOMIC NOTES. The new species is clearly distinguished from all other species of the subgenus by the wide striate membranes of coxae II, reaching the lateral margins of the body. *L. (L.) batomys* is most similar to *L. (L.) mindanensis* and differs from this species by the following characters. In both sexes of *L. (L.) batomys*, the striated membranes of coxae II reach the lateral margins of the body; the median sclerotized band of the postscapular shield is absent; in males, the lobar membrane is weakly developed; in females, the lateral parts of opisthosoma

are covered by distinct furrows in the anterior third. In both sexes of *L. (L.) mindanensis*, the striated membranes of coxae II do not reach the lateral margins of the body; the median sclerotized band of the postscapular shield is present; in males, the lobar membrane is well developed; in females, the lateral parts of the opisthosoma are without furrows in the anterior third.

***Listrophoroides (Listrophoroides) palawanensis* Fain, 1976**
(Figs 9–10)

Listrophoroides (Listrophoroides) palawanensis Fain, 1976b: 61; Fain, 1981: 31, figs 13–16.

DIAGNOSIS. *Male.* Genital organ situated posterior to level of coxae III. Aedeagus short, about 9 long. Anus situated ventro-

terminally. Postgenital shield extended as a long, narrow median band, reaching anus. *Female*. Basal cap of spermatheca narrowly cylindrical. Bursa copulatrix opening on terminal papilla.

MALE (Fig. 9) Body 385–395 long, 155–160 wide in 3 specimens. Length and width of gnathosoma subequal, about 45. *Dorsum*. Postscapular shield 75–80 long, 155–160 wide, completely covered by short curved lines arranged in 6–7 rows. Hysteronotal shield 155–165 long, completely covering dorsal surface of hysteronotum, ornamented with 6–8 transverse rows of short curved lines, extending from anterior margin of this shield to level of setae *e2*. Distance *e1-e1* 44–48. Setae *e2*

situated on hysteronotal shield. Setae *h3* 40 long. *Venter*. Striate membranes of coxae II distinctly developed, about 25 wide. Genital organ situated between levels of coxae III and IV. Aedeagus short, length about 9. Postgenital shield extending posteriorly as long (145–160), narrow (30–35), median band, reaching anus. Coxae III without transverse lines. Coxal fields IV without projections. Anus situated ventro-terminally. Anal fold not developed. Adanal shields absent. Lobar membrane weakly developed, with median incision. *Legs*. Dorso-basal projection of femur I distinctly developed. Femur IV about 27 wide, 1.7 times wider than femur III (16). Legs III and IV 130–135 and

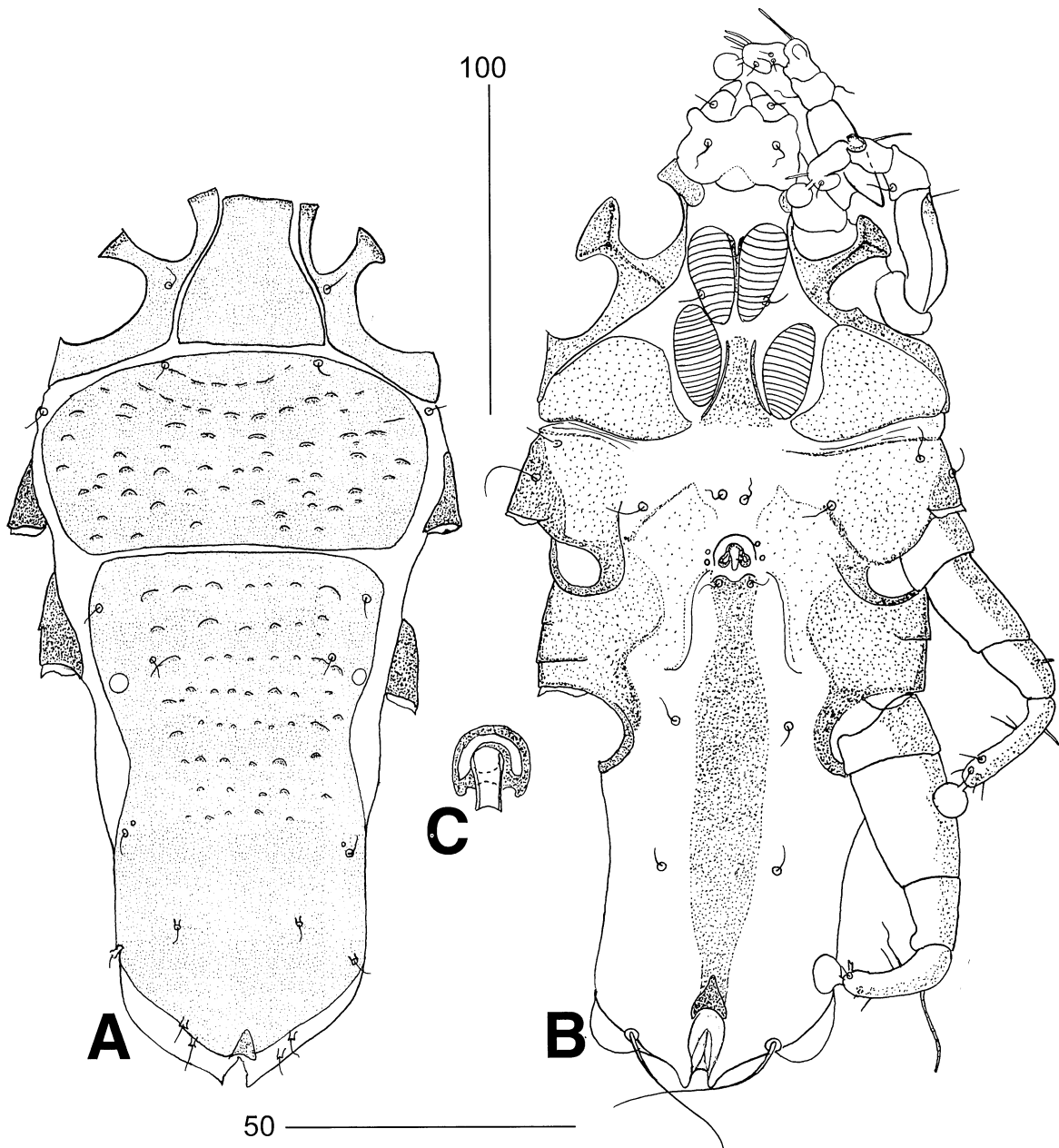


Fig. 9. (A–C). *Listrophoroides palawanensis* Fain, 1976, male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. Scale bars 100 μm (A–B) and 50 μm (C).

140–145 long, respectively. Tibiotarsi III and IV 45 and 45–48 long, respectively. Length ratio of femur: genu: tibiotarsus IV 1.5 : 1 : 1.3. Solenidia φ of legs III and IV 11 and 40, respectively.

FEMALE (Fig. 10). Body 425–475 long, 145–175 wide in 10 specimens. Length and width of gnathosoma subequal, about 50. *Dorsum*. Postscapular shield 80–88 long, 155–165 wide, completely covered by 7 transverse rows of short curved lines. Hysteronotal shield 165–187 long, completely covered by 12–14 transverse lines. Lines in anterior half of this shield curved

laterally, lines posterior to level of setae *e2* interrupted. Distances *d1-d1* and *e1-e1* 73–77 and 50–65 long, respectively. Distance *e1-e1* 2.8–3 times longer than distance *e1*-posterior margin of hysteronotal shield, 15–22. Basal cap of spermatheca narrowly cylindrical. *Venter*. Striated membranes of coxae II narrow, about 25 wide, subequal in width to striated membranes of coxae I. Coxae III without transverse line. Coxae IV with short transverse line. Opisthosoma with large opisthogastric shield. Lateral parts of opisthosoma covered by scales pos-

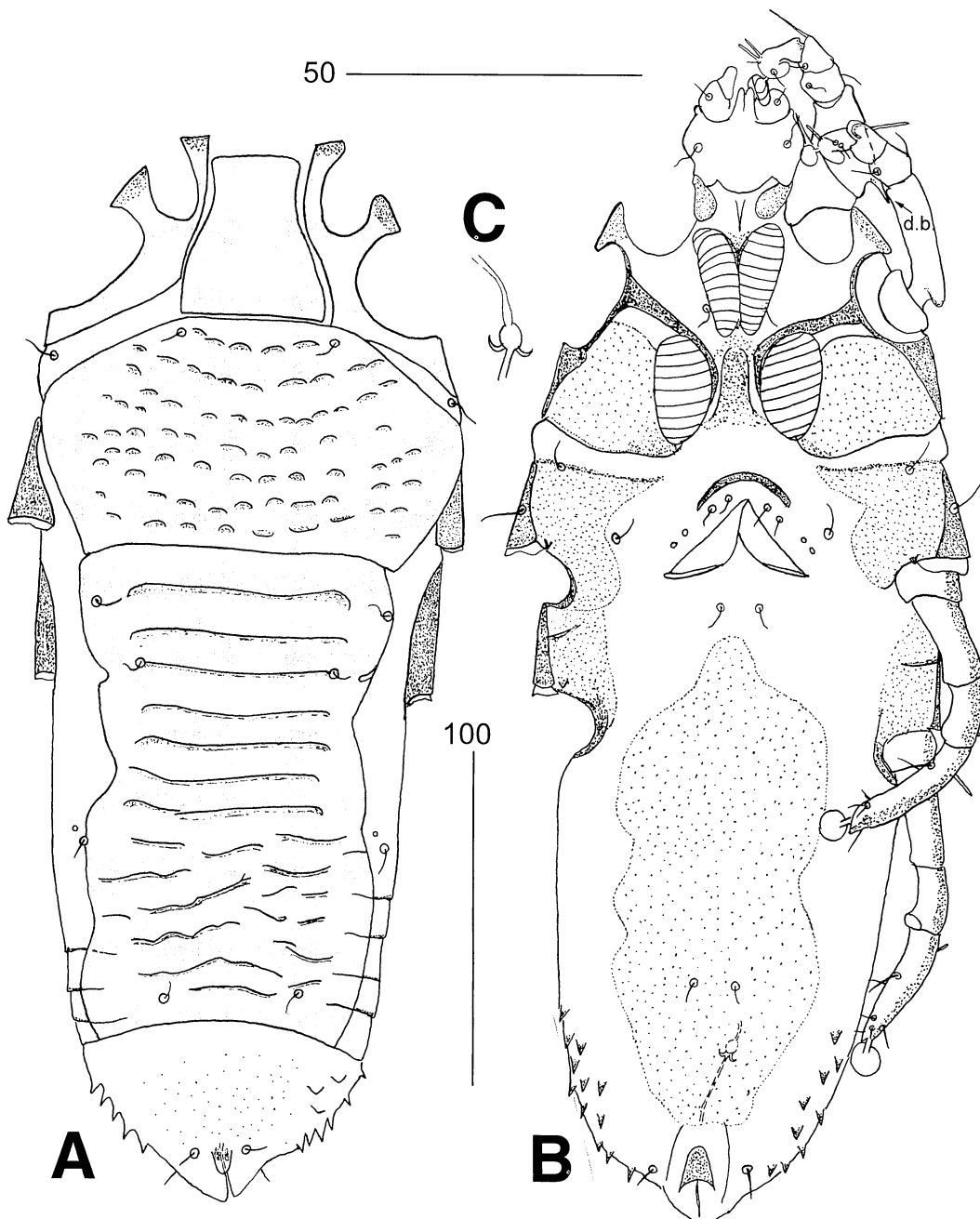


Fig. 10. (A–C). *Listrophoroides palawanensis* Fain, 1976, female. A.—Dorsal view. B.—Ventral view. C.—Spermatheca. Abbreviations: d.b.—dorso-basal hook of femur I. Scale bars 100 μm (A–B) and 50 μm (C).

terior to level of setae *ps*3. *Legs*. Dorso-basal projection of femur I distinctly developed. Legs III and IV 120–125 and 130–140 long, respectively. Solenidia φ of legs III and IV, 9–10 and 2–3 long, respectively.

MATERIAL EXAMINED. Three males and 19 females (BMOC 88-0824-010) ex *Maxomys panglima* (USNM 349021), Palawan Prov., Inagawan Penal Colony, 9°32'56"N, 18°38'50"E, 5 May 1969, coll. K. Barbehenn.

TYPE DEPOSITION. Holotype is deposited in BMNH. Voucher specimens from this study deposited in NMP, UMMZ, USNM.

HOST ASSOCIATIONS AND DISTRIBUTION. The species was originally described from a rat identified as *Maxomys rajah* (Thomas, 1894) from Palawan Island (Fain, 1976b, 1981). This record is actually the result of host misidentification, because *M. rajah* is absent on Palawan. The only described species of the genus *Maxomys* in the Philippine fauna is *Maxomys panglima* (Robinson, 1921) (Musser & Carleton, 2005), which is restricted to Palawan and adjacent islands. *L. (L.) palawanensis* is a monoxenous parasite of this species. The record of two specimens of *L. (L.) palawanensis* from an alcohol preserved *Rattus exulans* (Peale, 1848) from Palawan (Fain, 1981) is probably the result of museum contamination (Bochkov & OConnor, 2005).

TAXONOMIC NOTES. This species belongs to the *rajah* species group and *malayi* subgroup (Bochkov & OConnor, 2005).

***Listrophoroides (Listrophoroides) brachypyx* Fain, 1974**
(Figs 11–12)

Listrophoroides (Listrophoroides) brachypyx Fain, 1974: 21, figs 11–12, 1977: 291, 1981: 36, figs 21–22; Bochkov *et al.*, 2004: 73.

DIAGNOSIS. In both sexes, anterior half of postscapular shield with 3–6 short distinct lines in lateral margins. *Male*. Lobar membrane with median incision and several lateral teeth. Genital organ situated posterior to level of coxae III. Aedeagus relatively short, length (15). Anus situated ventro-terminally. *Female*. Opisthogaster almost completely covered by indistinct shield.

MALE (Fig. 11). Body 365–380 long, 165–170 wide in 10 specimens from *Rattus tanezumi* from Sibuyan Island. Length and width of gnathosoma subequal, 45. *Dorsum*. Postscapular shield 75–85 and 147–155 wide, completely covered by indistinct transverse lines. Anterior half of this shield with 3–6 short, distinct lines in lateral margins. Hysteronotal shield 165–175 long, covered by indistinct transverse lines in anterior third. Distance *e1-e1* 60–65. Setae *e2* situated on hysteronotal shield. Setae *h3* 55–58 long. *Venter*. Striate membranes of coxae II distinctly developed, about 25 wide. Genital organ situated between levels of coxae III and IV, flanked by pair of narrow sclerotized bands extending from level of genital papillae to level of setae *4a*. Aedeagus relatively short, length about 15. Postgenital shield small, only slightly wider than bases of setae *g*. Pair of sclerotized patches situated immediately posterior to setae *4a* present; in some specimens, these patches fused to sclerotized bands flanking genital organ. Coxae III without transverse lines. Sclerotized areas of coxae IV without projections.

Anus situated ventro-terminally. Anal fold not developed. Adanal shields absent. Lobar membrane distinctly developed, with median incision and 3–7 lateral teeth per side. *Legs*. Dorso-apical projection of femur I distinctly developed. Femur IV about 26 wide, 1.7 times wider than femur III (15). Legs III and IV 110–120 and 125–130 long, respectively. Tibiotarsi III and IV 35–42 and 45–47 long, respectively. Length ratio of femur: genu: tibiotarsus IV 1.2 : 1 : 1.2. Solenidia φ of legs III and IV 10 and 40–42, respectively.

FEMALE (Fig. 12). Body 420–440 long, 175–180 wide in 10 specimens. Length and width of gnathosoma subequal, about 50. *Dorsum*. Postscapular shield 88–95 long, 155–160 wide, completely covered by 6 rows of short transverse lines, indistinct in some specimens. Anterior half of this shield with 3–6 short distinct lines in lateral margins. Hysteronotal shield 145–160 long, completely covered by 8–11 transverse lines, interrupted in posterior half of shield. Distances *d1-d1* and *e1-e1* 65–75 and 45–55 long, respectively. Distance *e1-e1* 3–4 times longer than distance *e1*-posterior margin of hysteronotal shield, 9–18. Soft cuticle of hysteronotum with numerous lateral scales situated immediately posterior to level of setae *e2*. Basal cap of spermatheca sacculiform. Bursa copulatrix opening on terminal papilla. *Venter*. Striated membranes of coxae II slightly narrow, about 25 wide. Coxae III without transverse line. Opisthosoma with large opisthogastric shield. Lateral parts of opisthosoma covered by scales extending from level of setae *e2* to level of setae *h3*. *Legs*. Dorso-apical projection of femur I distinctly developed. Legs III and IV 110–115 and 115–120 long, respectively. Solenidia φ of legs III and IV, 10–11 and 2–4 long, respectively.

MATERIAL EXAMINED. Ten males and 10 females (BMOC 92-1400-124) ex *Rattus tanezumi* (FMNH 146934), Sibuyan Isl., Romblon Prov., 7.5 km E, 1.75 km W Silum, 12°28'N, 122°35'E, 30 m, 16 March 1992; coll. S.M. Goodman (SMG 5219); 8 males and 9 females (BMOC 92-1400-069) ex *R. tanezumi* (FMNH 146924), same data, 6.75 km S, 4.5 km E, Magdiwang, 12°26'N, 122°33'N, 1500 m, 27 February 1992, coll. S.M. Goodman (SMG 5057); 1 male (BMOC 92-1400-078) ex *R. tanezumi* (FMNH 146942), same data, 19 February 1992, coll. S.M. Goodman (SMG 4976); 1 female (BMOC 83-1600-003) ex *R. tanezumi* (UMMZ 163650), Negros Oriental, 6 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N, 123°10'E, 835 m, 1 July 1982, coll. P.D. Heideman (PDH 467); 4 males and 7 females (BMOC 95-0601-010) ex *Rattus mindorensis* (FMNH 142621), Mindoro Oriental, Mt. Halcon Range, Mt. Baco, Baco Munic., along Aligatic River, 1005 m, 4 July 1991, coll. R.I. Crombie.

TYPE DEPOSITION. Holotype is deposited in IRSNB. Voucher specimens from this study in FMNH, NMP, OSAL, UMMZ, USNM.

HOST ASSOCIATIONS AND DISTRIBUTION. This species was described originally from a single male collected from an alcohol-preserved specimen of *Melomys platyops* (Thomas, 1906) collected in New Guinea (Fain, 1974). It has been subsequently recorded from several species of the genus *Rattus*, *R. tanezumi*

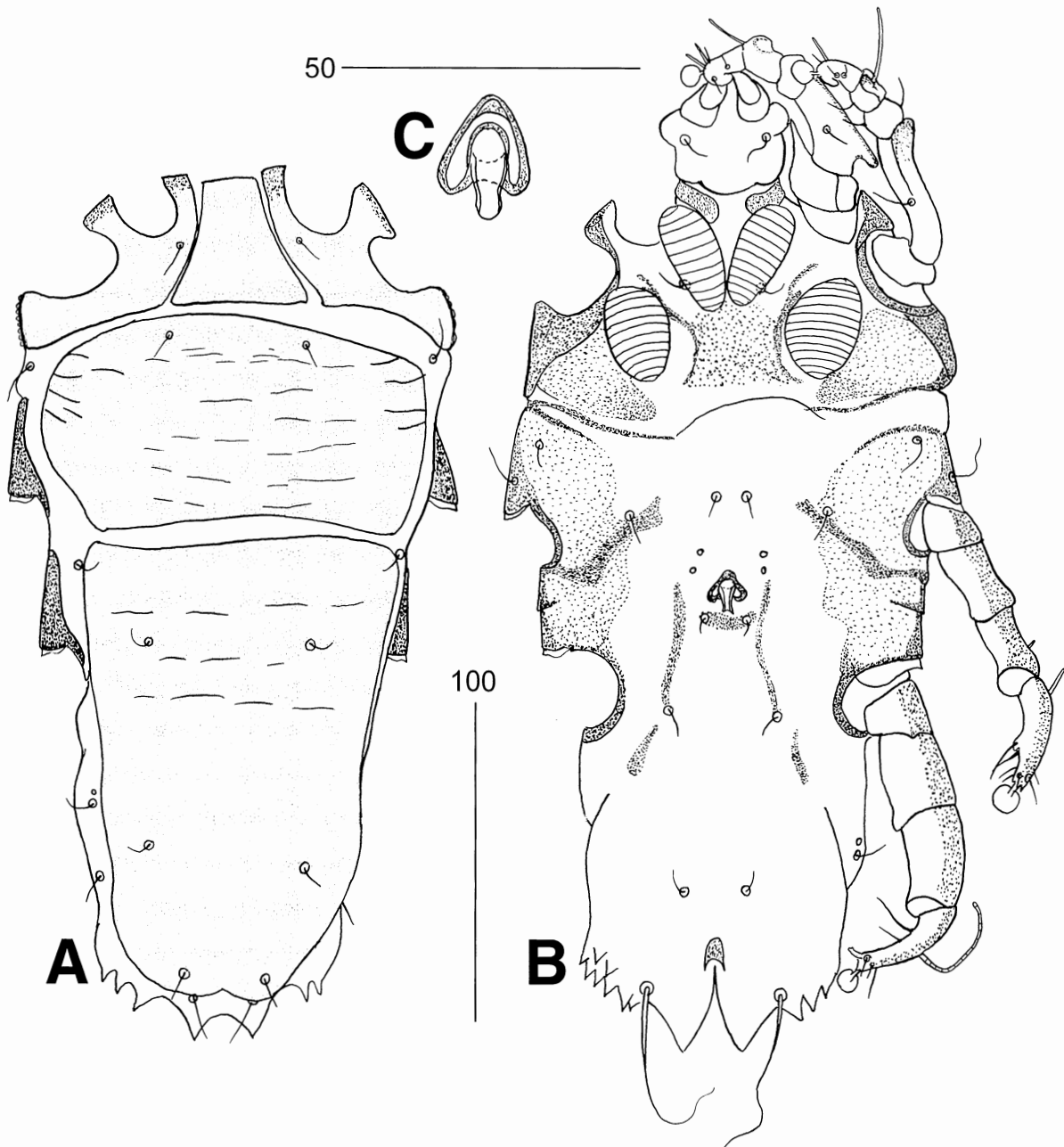


Fig. 11. (A–C). *Listrophoroides brachypyx* Fain, 1974, male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. Scale bars 100 μm (A–B) and 50 μm (C).

Temminck, 1844 (= *mindanensis*) and *R. mindorensis* (Thomas, 1898) from the Philippines (Leyte Isl.), and *R. tiomanicus* (Miller, 1900) from Malaysia (Selangor) (Fain, 1981; Bochkov *et al.*, 2004). The record of *L. brachypyx* from *Melomys platyops* was likely the result of museum contamination, because this species has never been recollected from rats of the genus *Melomys*, despite the thorough investigation of atopomelid mites from New Guinea conducted by Fain (1977). This species is probably specific to oriental *Rattus* species.

TAXONOMIC NOTES. This species belongs to the *borneoensis* group (Bochkov & OConnor, 2005).

***Listrophoroides (Listrophoroides) crunomys* New Species**
(Figs 13–16)

DIAGNOSIS. *Male.* Genital organ situated posterior to level of coxae III and flanked by pair of narrow bands. Aedeagus thin and 22–24 long, supporting sclerite of aedeagus strongly reduced. Anus situated ventro-terminally. *Female.* Opisthogaster almost completely covered by indistinct shield, basal cap of spermatheca ampuliform.

MALE (Fig. 13). Body 330–345 long (330), 135–150 wide (145) in 10 paratypes. Length and width of gnathosoma sub-

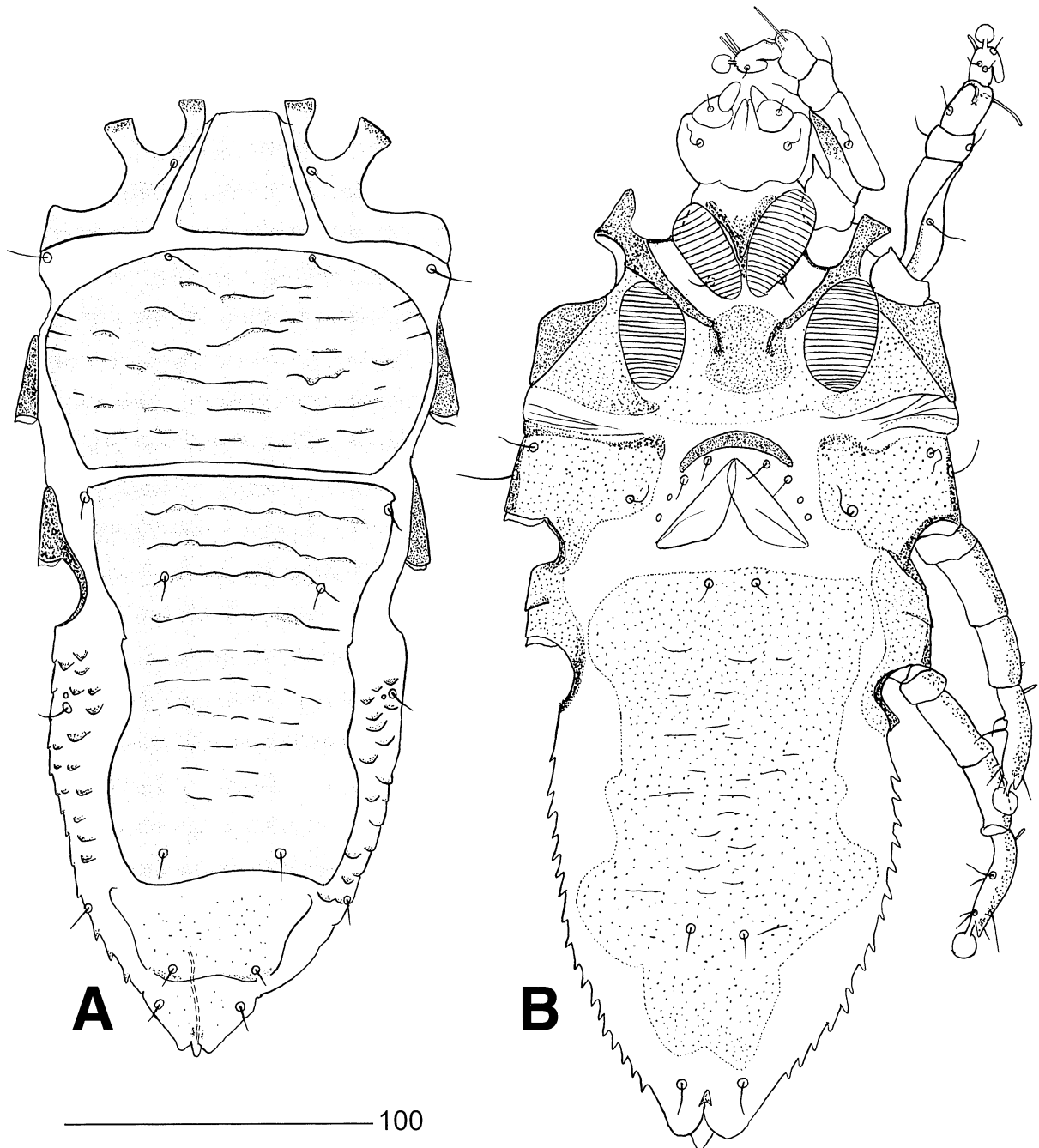


Fig. 12. (A-B). *Listrophoroides brachypyx* Fain, 1974, female. A.—Dorsal view. B.—Ventral view.

equal, about 35. *Dorsum*. Postscapular shield 65–77 long (70), 120–147 wide (135), completely covered by 6 transverse rows of short curved lines, lines of 3 anterior rows well discernible and relatively straight, 3 posterior rows indistinct, some their lines short and curved. Hysteronotal shield 145–160 long (155), covered by interrupted transverse lines in anterior half, 2–3 anterior lines well discernible, curved laterally, posterior lines indistinct. Distance *e1-e1* 40–50 (45). Setae *e2* situated on hysteronotal shield. Setae *h3* 50–55 long (55). *Venter*. Striate membranes of coxae II enlarged, about 35 wide. Genital organ

situated between levels of coxae III and IV, flanked by pair of narrow sclerotized bands ranged from level of genital papillae to level of setae *4a*, 60–75 long (70). Aedeagus very thin, 22–24 long (22). Supporting sclerite of aedeagus strongly reduced. Postgenital shield absent. Pair of narrow sclerotized bands situated immediately posterior to setae *4a*, these bands partly or completely fused to bands flanking genital organ. Coxae III with indistinct transverse lines. Sclerotized areas of coxae IV without projections. Anus situated ventro-terminally. Anal fold not developed. Adanal shields absent. Lobar membrane weakly

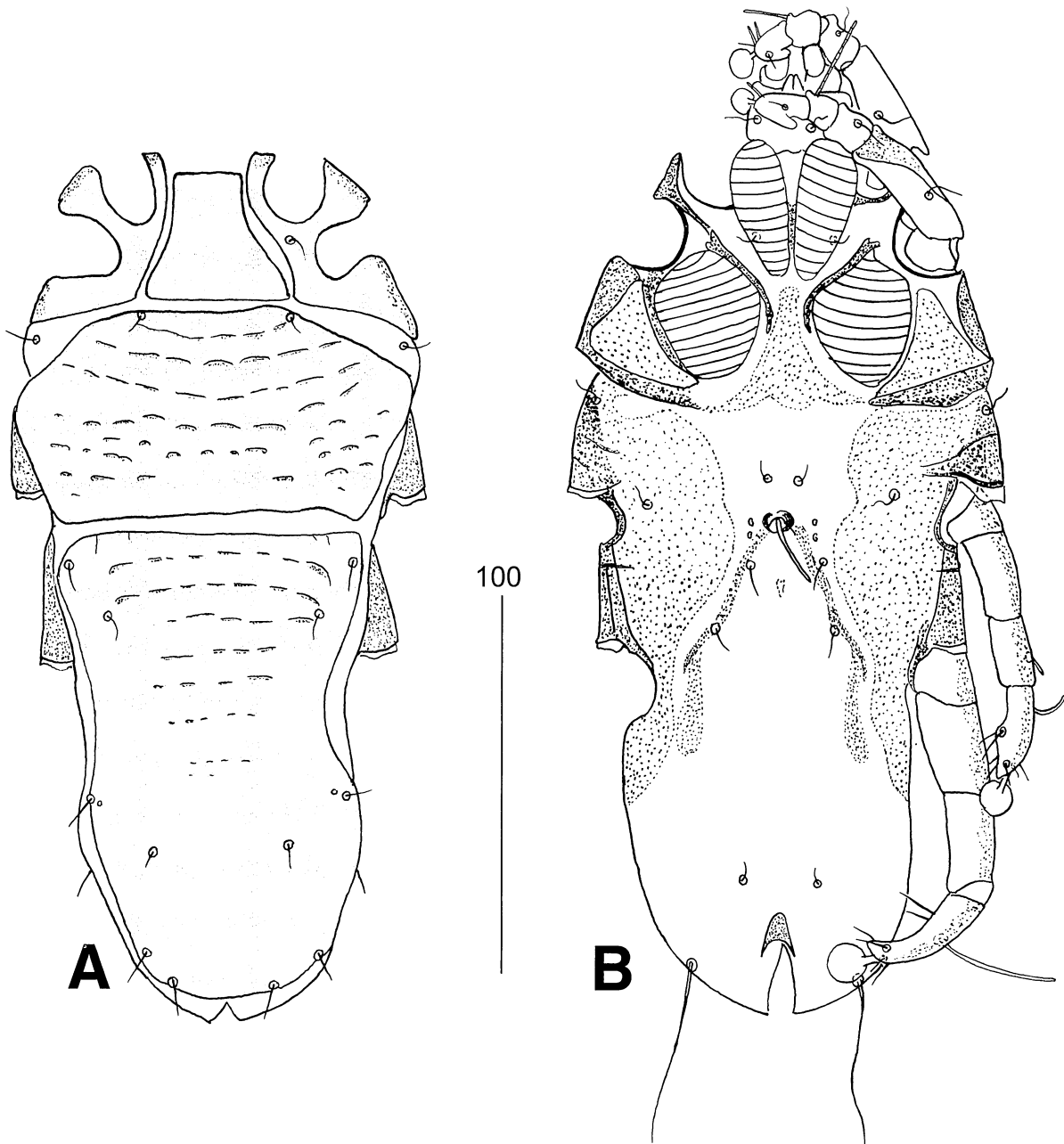


Fig. 13. (A-B). *Listrophoroides crunomys* sp.n. from *Crunomys suncooides*, male. A.—Dorsal view. B.—Ventral view.

developed, with median incision. *Legs*. Dorso-apical projection of femur I distinctly developed. Femur IV about 22 wide, 1.7 times wider than femur III (13). Legs III and IV 110–115 and 125–135 long, respectively. Tibiotarsi III and IV 38–43 and 43–45 long, respectively. Length ratio of femur: genu: tibiotarsus IV 1.3: 1: 1.3. Solenidia φ of legs III and IV 12–13 and 43–45, respectively.

FEMALE (Fig. 14). Body 390–410 long, 145–155 wide in 10 paratypes. Length and width of gnathosoma subequal, 35–38. *Dorsum*. Postscapular shield 70–77 long, 130–147 wide, completely covered by 6 rows of interrupted transverse lines, lat-

eral lines of 3 posterior rows curved, median lines of these rows indistinct in some specimens. Hysteronotal shield 160–180 long, completely covered by 11–13 transverse lines. Lines situated in anterior part of hysteronotal shield curved laterally. Distances $d1-d1$ and $e1-e1$ 77–80 and 55–60 long, respectively. Distance $e1-e1$ 4–6 times longer than distance $e1$ -posterior margin of hysteronotal shield, 9–15. Basal cap of spermatheca ampiliform. *Venter*. Striated membranes of coxae II enlarged, about 37 wide. Coxae III with transverse line. Opistogastric shield distinctly developed. Lateral opisthosoma covered by scales in posterior third. *Legs*. Dorso-basal

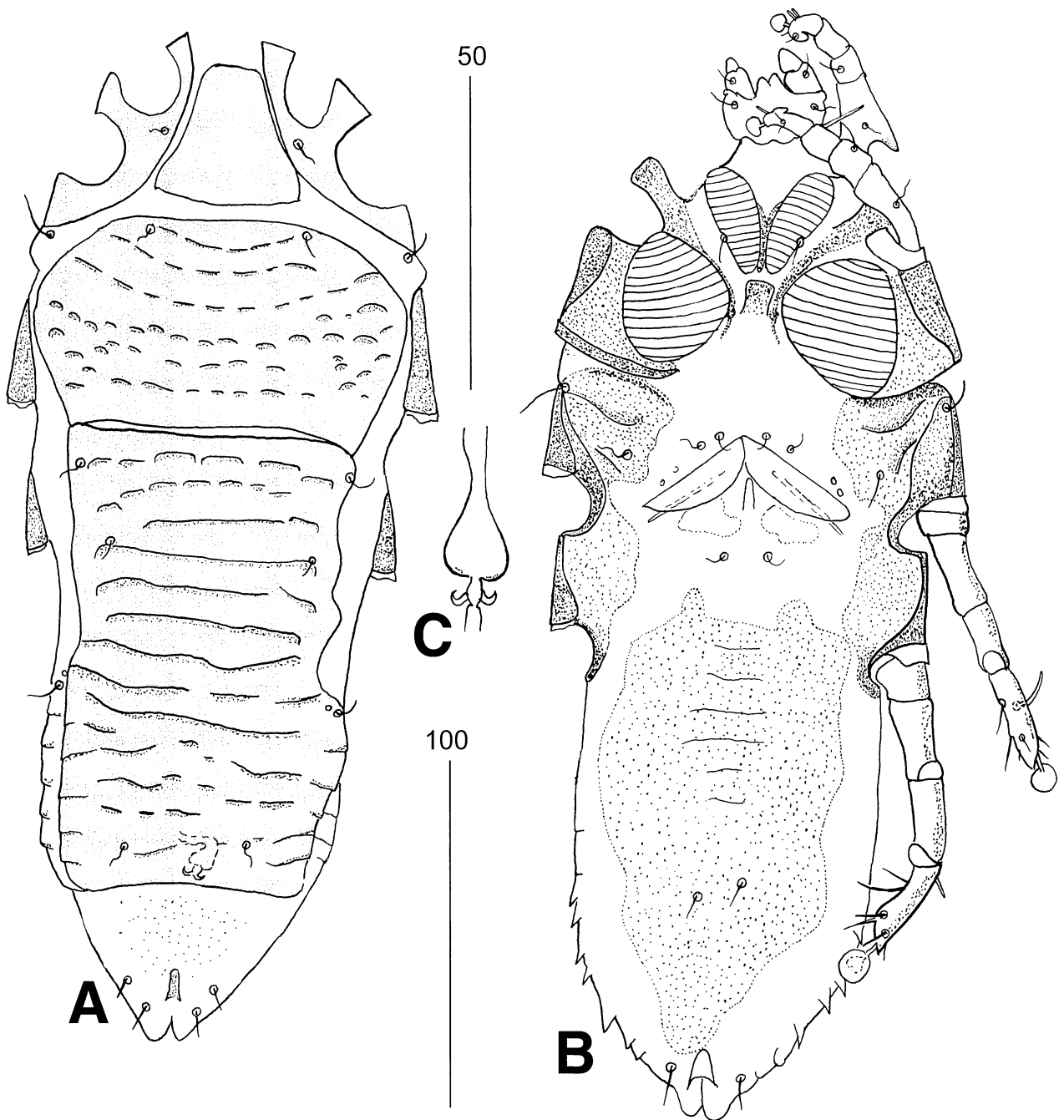


Fig. 14. (A–C). *Listrophoroides crunomys* sp.n. from *Crunomys suncoides*, female. A.—Dorsal view. B.—Ventral view. C.—Spermatheca. Scale bars 100 μm (A–B) and 50 μm (C).

projection of femur I distinctly developed. Legs III and IV 100–105 and 115–120 long, respectively. Solenidia φ of legs III and IV, 12–13 and 4 long, respectively.

ETYMOLOGY. The species name is derived from the generic name of the hosts and is a noun in apposition.

TYPE MATERIAL. Male holotype (BMOC 93-1300-171.1), 15 male and 25 female paratypes (BMOC 93-1300-171, 2–41) ex *Crunomys suncoides* (FMNH 147942), Mindanao Isl., Bukid-

non Prov., Mt. Katanglad Range, 18.5 km S, 4 km E Camp Phillips, 8°09'30"N, 124°51'E, 2250 m, 10 April 1993, coll. L.R. Heaney (LRH 5330).

OTHER MATERIAL EXAMINED. Ten males and 11 females (BMOC 92-1500-057) ex *Crunomys melanius* (FMNH 147106), Mindanao Isl., Bukidnon Prov., Mt. Kitanglad Range, 17 km S, 7 km E Baungon, 8°11'N, 124°45'E, 1550 m, 8 May 1992, coll. L.R. Heaney (LRH 4813); 10 males and 10 females (BMOC

95-1214-010) ex *C. melanius* (FMNH 154861), Camiguin Prov., Mt. Timpoong, 2 km N, 6.5 km W Mahinog, 9°11'N, 124°43'E, 1275 m, 17 March 1995, coll. L.R. Heaney (LRH 5345).

SPECIMEN DEPOSITION. Holotype is deposited in NMP, paratypes in FMNH, IRSNB, OSAL, UMMZ, USNM, and ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION. This species is a specific parasite of the Old Philippine endemics of the genus *Crunomys*, *C. suncooides* Rickart, Heaney, Tabaranza and Baleta, 1998 (type host) and *C. melanius* Thomas, 1907.

TAXONOMIC NOTES. This species is close to *L. (L.) brachypyx* and *L. (L.) bilineatus* Fain, 1975. In males of these species, the genital organ is flanked by a pair of sclerotized bands and females have a large opisthogastric shield. *Listrophoroides (L.) crunomys* is clearly distinguished from them in both sexes by the form of the ornamentation of the dorsal shields, the wide striated membranes of coxae II, and by coxae III bearing a transverse line; in males by the weakly developed lobar membrane without teeth, and in females by the ampuliform basal cap of the spermatheca. In both sexes of *L. (L.) brachypyx* and *L. (L.) bilineatus*, the striated membranes of coxae II are relatively narrow, coxae III are without a transverse line, in males, the lobar membrane is well developed and bears lateral teeth, and in females, the basal cap of the spermatheca is sacculiform.

INTRASPECIFIC VARIABILITY. The specimens of *L. (L.) crunomys* collected from *Crunomys melanius* slightly differ from those found on the type host. In both sexes of these mites, the dorsal shields are more strongly sclerotized and covered by scalloped ornamentation, and the transverse line of coxae III is distinctly developed (Figs. 15–16).

Listrophoroides (Listrophoroides) insularis New Species (Figs 17–18)

DIAGNOSIS. In both sexes, dorsal shields completely covered by strong transverse lines. *Male.* Setae *e1* 18–24 long. Coxal fields IV with short and narrow projections. Genital organ situated posterior to level of coxae III. Aedeagus very short, length about 4. Postgenital shield very small, only slightly wider than bases of setae *g*. Anus situated ventrally. *Female.* Lateral opisthosoma without scales or tubercles. Basal cap of spermatheca sacculiform.

MALE (Fig. 17). Body 335–360 long (335), 140–155 wide (140) in 10 paratypes. Length and width of gnathosoma subequal, about 45. *Dorsum.* Postscapular shield 75–80 long (80), 140–155 wide (155), completely covered by 7 irregular transverse lines, part of lines bifurcate in anterior half of this shield and interrupted in its median part in most specimens examined. Hysteronotal shield 155–165 long (155), covered by 13–15 irregular transverse lines extending from anterior margin to level of setae *e1*. Posterior lines short, slightly curved, and arranged into 4–6 arch-like rows. Distance *e1-e1* 42–45 (44). Setae *e1* 18–24 long (20), 2 times longer than *e2*. Setae *e2* situated on hysteronotal shield. Setae *h3* 75–80 long (80). *Venter.* Striate membranes of coxae II enlarged, about 35 wide. Genital organ situated between levels of coxae III and IV. Aedeagus

very short, about 4 long. Postgenital shield small, only slightly wider than bases of setae *g*. Coxae III with interrupted transverse line. Coxal fields IV with short and narrow projections, not reaching posteriorly to level of setae *4a*. Pair of sclerotized patches posterior to setae *4a* present. Anus situated ventroterminally. Anal fold not developed. Adanal shields absent. Lobar membrane weakly developed, with median incision and distinctly rounded lateral margins. *Legs.* Dorso-apical projection of femur I indistinct. Femur IV 20–24 wide (20) wide, 1.5 times wider than femur III (13). Legs III and IV 95–110 (100) and 115–130 (120) long, respectively. Tibiotarsi III and IV 33–37 (33) and 37–40 (40) long, respectively. Length ratio of femur: genu: tibiotarsus IV 1.3: 1: 1.3. Solenidia ϕ of legs III and IV 22–24 and 44–46 long, respectively.

FEMALE (Fig. 18). Body 385–410 long, 145–160 wide in 10 paratypes. Length and width of gnathosoma subequal, 40. *Dorsum.* Postscapular shield 80–85 long, 150–160 wide, completely covered by 7 irregular transverse lines. Hysteronotal shield 145–155 long, completely covered by 13–15 distinct transverse lines, anterior lines straight, posterior lines interrupted. Distances *d1-d1* and *e1-e1* 75–85 and 50–70 long, respectively. Distance *e1-e1* about 3 times longer than distance *e1*-posterior margin of hysteronotal shield, 18–25. Basal cap of spermatheca sacculiform. *Venter.* Striated membranes of coxae II enlarged, about 40 wide. Coxae III with interrupted transverse line. Opisthosoma with large opisthogastric shield posterior to coxae IV. Median part of opisthosoma immediately posterior to setae *4a* with few indistinct rounded scales; without scales or tubercles laterally. *Legs.* Dorso-apical projection of femur I indistinct. Legs III and IV 95–100 and 105–120 long, respectively. Solenidia ϕ of legs III and IV, 24–26 and 2 long, respectively.

ETYMOLOGY. The name of this species parasitizing endemic rodents of the Philippine Islands is derived from the Latin word *insula* (island) and is an adjective.

TYPE MATERIAL. Male holotype (BMOC 01-0920-054, 1), 10 male and 6 female paratypes (BMOC 01-0920-054, 2–17) ex *Chrotomys whiteheadi* (FMNH 169143), Luzon Isl., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Mapga, 17°28'30"N, 121°04'30"E, 1050 m, 14 March 2001, coll. L.R. Heaney (LRH 6326); 8 male and 20 female paratypes (BMOC 01-0920-055, 1–28) ex *C. whiteheadi* (FMNH 169144), same data, coll. L.R. Heaney (LRH 6335); 8 male and 11 female paratypes (BMOC 01-0920-049, 1–19) ex *C. whiteheadi* (FMNH 169140), same data, 13 March 2001, coll. E.A. Rickart (EAR 4529); 2 male and 8 female paratypes (BMOC 01-0920-051, 1–10) ex *C. whiteheadi* (FMNH 169140), same data, 17 March 2001, coll. E.A. Rickart (EAR 4565); 8 male and 9 female paratypes (BMOC 01-0920-052, 1–17) ex *C. whiteheadi* (FMNH 169142), same data, coll. E.A. Rickart (EAR 4572).

OTHER MATERIAL EXAMINED. Six males and 5 females (BMOC 01-0920-046) ex *Chrotomys silaceus* (FMNH 169134), Luzon Isl., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Am-licao, 17°26'30"N, 121°04'15"E, 1800 m, 21 March 2001, coll. L.R. Heaney (LRH 6391); 1 female (BMOC 01-0920-

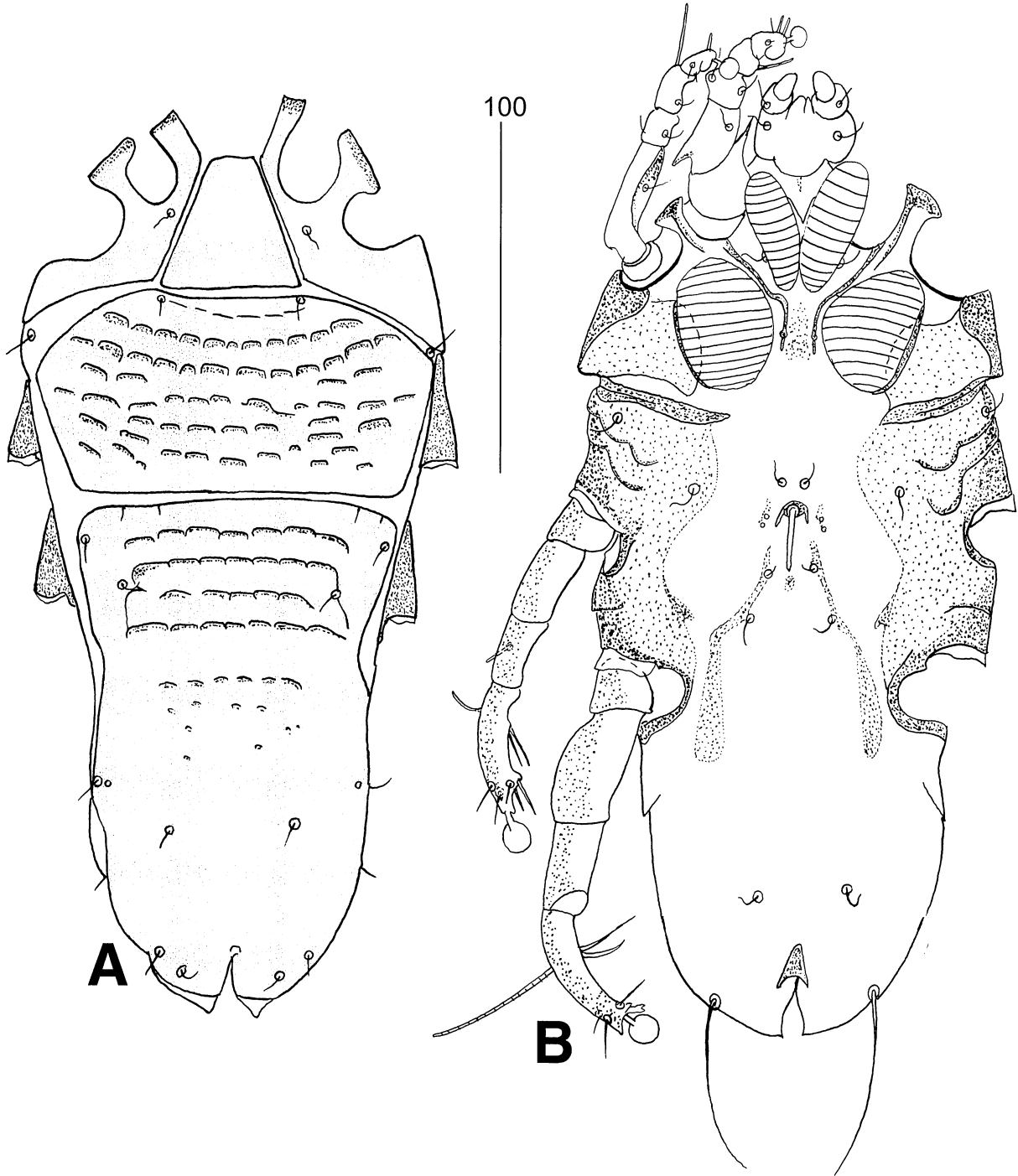


Fig. 15. (A–B). *Listrophoroides crunomys* sp.n. from *Crunomys melanius*, male. A.—Dorsal view. B.—Ventral view.

042) ex *C. silaceus* (FMNH 169130), same data, 20 March 2001, coll. E.A. Rickart (EAR 4576); 1 male and 2 females (BMOC 01-0920-043) ex *C. silaceus* (FMNH 169131), same data, 21 March 2001, coll. E.A. Rickart (EAR 4587); 3 males and 6 females (BMOC 01-0920-044) ex *C. silaceus* (FMNH 169132), same data, 25 March 2001, coll. E.A. Rickart (EAR 4614); 3 males and 1 female (BMOC 06-0201-001) ex *Carpomys phaeurus* (FMNH 175565), Luzon Is., Kalinga Prov.,

Balbalan Munic., Balbalasang Brgy., Mt Bali-it, 2150m., 17°25'41"N, 120°59'48"E, 28 February 2003, coll. L. R. Heaney (LRH 6866).

SPECIMEN DEPOSITION. Holotype is deposited in NMP, paratypes in FMNH, IRSNB, NMP, OSAL, UMMZ, USNM, and ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION. This species is parasite of the Old Philippine endemics of the genera *Chrotomys*, *C.*

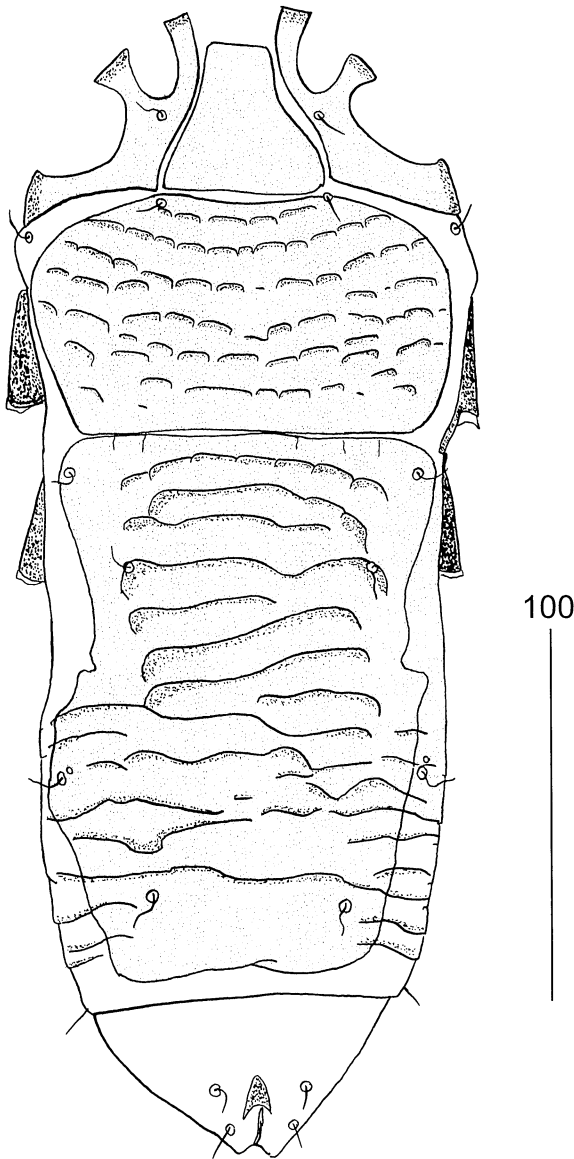


Fig. 16. *Listrophoroides crunomys* sp.n. from *Crunomys melanius*, female.

whiteheadi Thomas, 1895 (type host) and *C. silaceus* (Thomas, 1895) and *Carpomys*, *C. phaeurus* Thomas, 1895.

TAXONOMIC NOTES. This species and *L. (L.) chrotomys* sp.n. possess a unique combination of characters. In both sexes, the dorsal shields are completely covered by irregular striations, the striated membranes of coxae II are enlarged, and coxae III bear an interrupted line; in males, setae *e1* and *h3* are long, 18–24 and 75–80 long, respectively, the postgenital shield is very small, the coxal fields IV have the short and thin projections, the lobar membrane is without teeth; in females, the opisthosoma lacks scales or tubercles laterally, and the basal cap of the spermatheca is sacculiform. In males of *L. (L.) insularis*, the projections of coxal fields IV are narrow and short, do not reach posteriorly to the level of setae *4a*, the lobar membrane is weakly developed and not expanded laterally; in females,

the median scales of the opisthosoma posterior to setae *4a* are indistinct.

***Listrophoroides (Listrophoroides) chrotomys* New Species**
(Fig. 19)

DIAGNOSIS. In both sexes, dorsal shields completely covered by strong transverse lines. *Male.* Setae *e1* 15–22 long. Coxal fields IV with long, wide projections fused to sclerotized patches situated posterior to setae *4a*. Genital organ situated posterior to level of coxae III. Aedeagus short, about 9 long. Postgenital shield very small, only slightly wider than bases of setae *g*. Anus situated ventro-terminally. *Female.* Opisthosoma without scales or tubercles laterally. Basal cap of spermatheca sacculiform.

MALE (Fig. 19A–B). Body 330–365 long (365), 135–155 (150) wide in 10 paratypes. Gnathosoma 35–38 long, 43–47 wide. *Dorsum.* Postscapular shield 77–85 long (80), 130–155 wide (150), completely covered by 7 irregular transverse lines, part of these lines bifurcate in anterior half of postscapular shield. In some specimens, transverse lines of postscapular shield interrupted in median part of this shield. Hysteronotal shield 155–170 long (165), covered by 13–15 distinct transverse lines extending from anterior margin to level of setae *e1*. Posterior lines short, slightly curved, arranged in 4–6 arch-like rows. Distance *e1-e1* 40–45 (40). Setae *e1* 15–22 long (18), twice as long as *e2*. Setae *e2* situated on hysteronotal shield. Setae *h3* 88–100 long (100). *Venter.* Striate membranes of coxae II enlarged, about 35 wide. Genital organ situated between levels of coxae III and IV. Aedeagus short, 9–10 long. Postgenital shield small, only slightly wider than bases of setae *g*. Coxae III with interrupted transverse line. Coxal fields IV with long and wide projections fused or almost fused to sclerotized patches posterior to setae *4a*. Anus situated ventro-terminally. Anal fold not developed. Adanal shields absent. Lobar membrane distinctly developed, with median incision and distinct lateral expansions. *Legs.* Dorso-apical projection of femur I indistinct. Femur IV 20–24 wide (20), 1.5 times wider than femur III (13). Legs III and IV 110–120 (110) and 135–145 (135) long, respectively. Tibiotarsi III and IV 40–45 (42) and 44–48 (45) long, respectively. Length ratio of femur: genu: tibiotarsus IV 1.4: 1: 1.4. Solenidia φ of legs III and IV 20–25 (24) and 48–53 (50) long, respectively.

FEMALE (Fig. 19C). Body 375–405 long, 135–150 wide in 10 paratypes. Length and width of gnathosoma subequal, 45. *Dorsum.* Postscapular shield 80–85 long, 135–150 wide, completely covered by 7 irregular transverse lines. Hysteronotal shield 145–155 long, completely covered by 13–15 irregular transverse lines, anterior lines straight, posterior lines interrupted. Distances *d1-d1* and *e1-e1* 70–75 and 50–60 long, respectively. Distance *e1-e1* about 4 times longer than distance *e1*-posterior margin of hysteronotal shield, 10–12. Basal cap of spermatheca sacculiform. *Venter.* Striated membranes of coxae II enlarged, about 45 wide. Coxae III with interrupted transverse line. Opisthosoma with large opisthogastric shield posterior to coxae IV. Median part of opisthosoma immediately posterior to setae *4a* with sev-

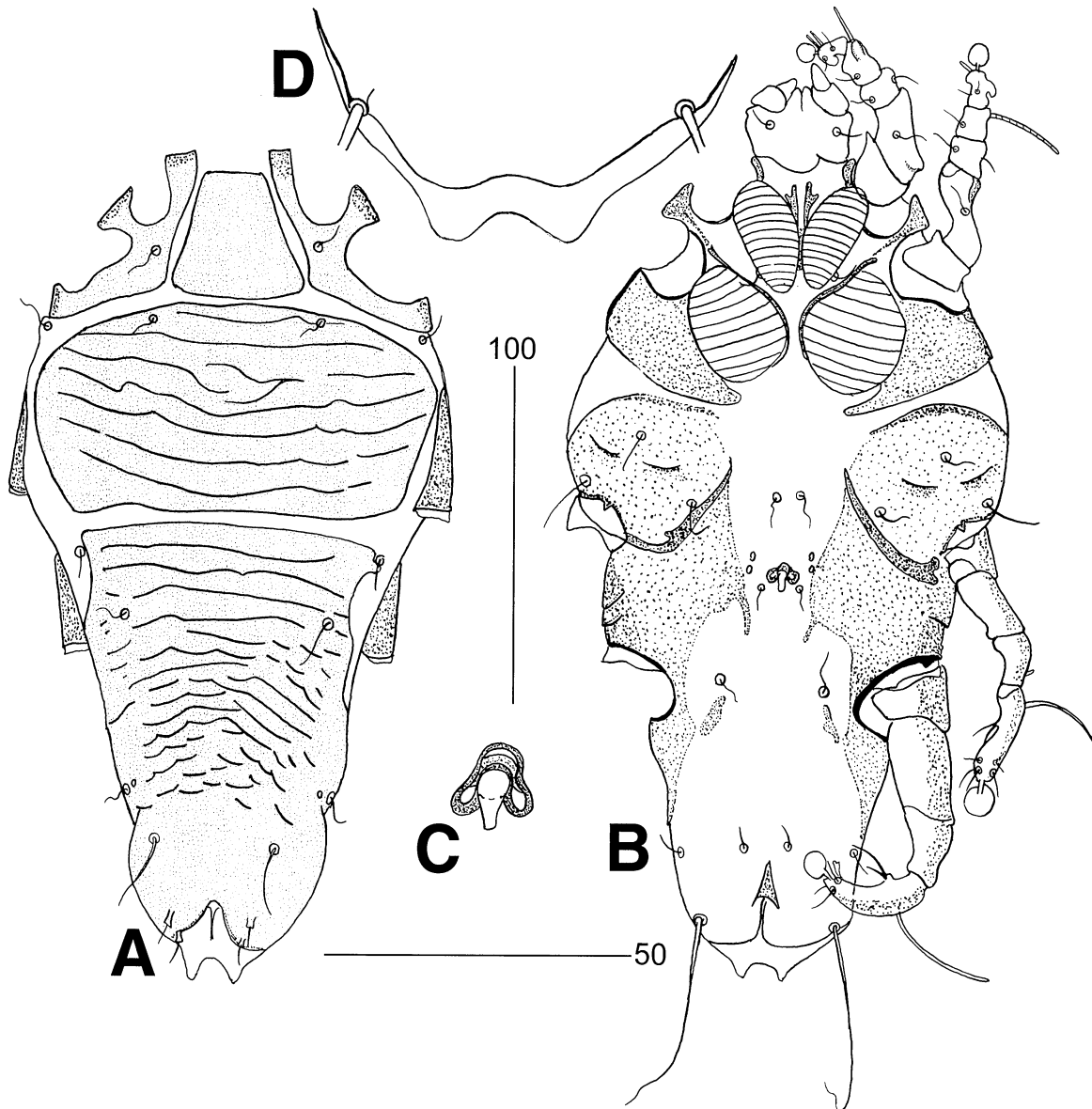


Fig. 17. (A–D). *Listrophoroides insularis* sp.n., male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. D.—Lobar membrane. Scale bars 100 μm (A–B) and 50 μm (C–D).

eral rounded scales; without scales or tubercles laterally. *Legs*. Dorso-apical projection of femur I indistinct. Legs III and IV 95–100 and 105–110 long, respectively. Solenidia ϕ of legs III and IV, 20–23 and 2 long, respectively.

ETYMOLOGY. The species name is derived from the generic name of the host and is a noun in apposition.

TYPE MATERIAL. Male holotype (BMOC 88-1740-005, 1), 1 male and 16 female paratypes (BMOC 88-1740-005, 2–18) ex *Chrotomys gonzalesi* (USNM 458951), Luzon Isl., Camarines Sur Prov., Mt. Isarog, 4 km N, 21 km E Naga, 13°40'N, 123°22'E, 1350 m, 23 March 1988, coll. S.M. Goodman (SMG 2321); 13 male paratypes (BMOC 88-1740-001, 1–13) ex *C. gonzalesi* (USNM 458958), same data, 20 March 1988, coll. R.B. Utzurum (RBU 284).

OTHER MATERIAL EXAMINED. One male and 3 females (BMOC 95-0601-006) ex *Chrotomys mindorensis* (FMNH 142617), Mindoro Oriental, Mt. Halcon Range, Mt. Baco, Baco Munic., Alangsa River, 725m, 8 July 1991, coll. R.I. Crombie; 1 male and 6 females (BMOC 04-0909-006) ex *Bullimus luzonicus* (FMNH 176582), Luzon Isl., Cagayan Prov., Baggao Munic., Brgy. Sta. Margarita, Sitio Matulang, Mt. Twin Peaks, 17°36'48"N, 121° 56'23"E, 300 m, 7 May 2003, coll. M.R. Duya (# 153); 2 females (BMOC 04-0909-001) ex *B. luzonicus* (FMNH 176577), Luzon Isl., Cagayan Prov., Penablanca Munic., Brgy. Mangga, Sitio Lowak, 17°36'48"N, 121°52' 23"E, 110 m, 14 November 2002, coll. M.D. deGula (MDDG 1407); 4 males and 4 females (BMOC 04-0909-009) ex *B. luzonicus* (FMNH 176585), Luzon Isl., Quezon Prov., General Nakar Munic., Brgy. Minahan Norte,

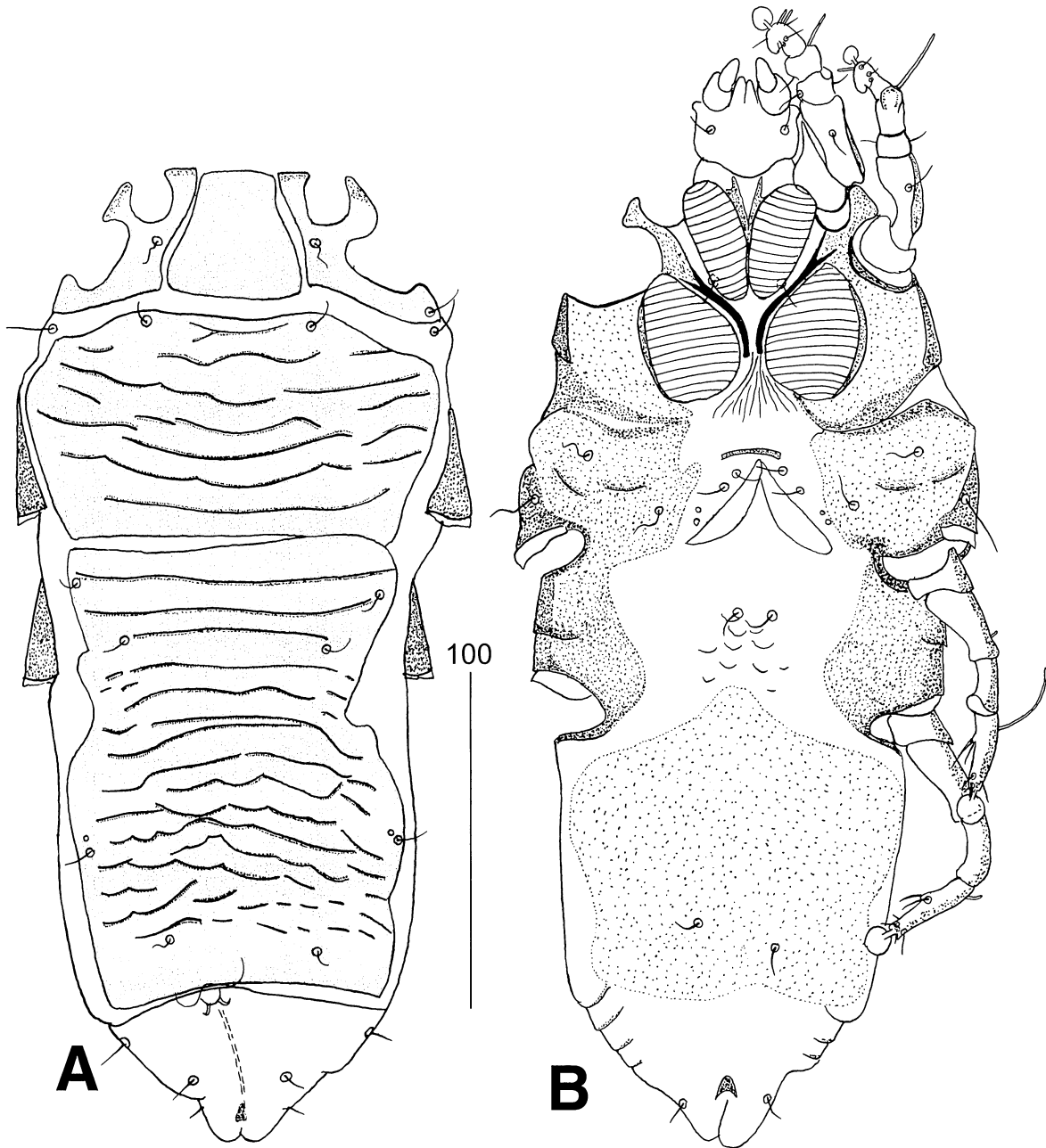


Fig. 18. (A–B). *Listrophoroides insularis* sp.n., female. A.—Dorsal view. B.—Ventral view.

Sitio Pangamitan, Mt. Binuang, 14°46'30"N, 121°33'30"E, 500 m, 27 June 2003, coll. M.R. Duya; 14 males and 9 females (BMOC 04-0909-010) ex *B. luzonicus* (FMNH 176595), Luzon Isl., Quezon Prov., General Nakar Munic., Brgy. Minahan Norte, Sitio Pangamitan, Mt. Binuang, 14°46'30"N, 121°33'30"E, 500 m, 9 August 2003, coll. M.R. Duya (# 218); 4 males and 1 female (BMOC 04-0909-011) ex *B. luzonicus* (FMNH 176597), Luzon Isl., Quezon Prov., General Nakar Munic., Brgy. Minahan Norte, Sitio Pangamitan, Mt. Binuang, 14°46'30"N, 121°33'30"E, 500 m, 11 August 2003, coll. M.R. Duya (# 2129); 3 females (BMOC 04-0909-030) ex *B. luzonicus* (FMNH 178407), Luzon Isl.,

Quezon Prov., Mt. Banahaw, Barangay Lalo, 14°03'06"N, 121°32'22"E, 620 m, 5 May 2004, coll. L.R. Heaney (LRH 7019); 11 males and 18 females (BMOC 04-0909-002) ex *B. luzonicus* (FMNH 176578), Luzon Isl., Quirini Prov., Nagtipunan Munic., Brgy., Disimungal, Sitio Km 18, Mt. Lataan, same locality, 17°36'48"N, 121°56'23"E, 10 March 2003, coll. M.G. deGula (MGDG 1585); 1 female (BMOC 04-0909-003) ex *B. luzonicus* (FMNH 176579), same locality, 8 March 2003, coll. M.G. deGula (MGDG 1596); 4 males and 17 females (BMOC 01-0920-040) ex *B. luzonicus* (FMNH 169128), Luzon Isl., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Am-licao, 17°26'30"N,

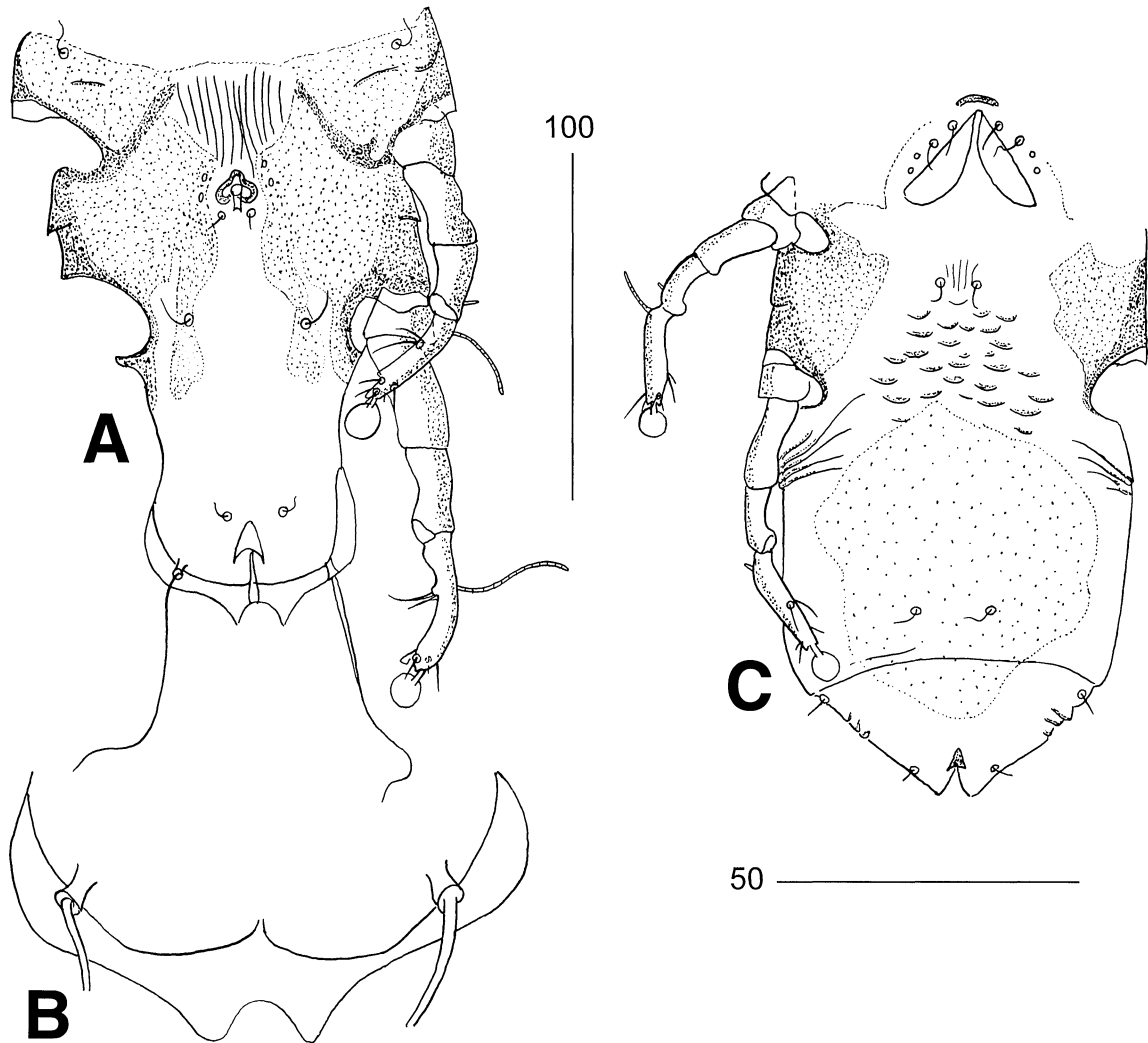


Fig. 19. (A–C). *Listrophoroides chrotomys* sp.n. A.—Male opisthosoma, ventral view. B.—Male lobar membrane, ventral view. C.—Female opisthosoma, ventral view. Scale bars 100 μm (A, C) and 50 μm (B).

121°04'15"E, 1800 m, 23 March 2001, coll. L.R. Heaney (LRH 6413); 4 males and 5 females (BMOC 01-0920-041) ex *B. luzonicus* (FMNH 169129), same data, (LRH 6414).

SPECIMEN DEPOSITION. Holotype is deposited in USNM, paratypes in FMNH, IRSNB, NMP, OSAL, UMMZ, USNM, and ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION. This species is parasite of the Old Philippine endemics *Chrotomys gonzalesi* Rickart and Heaney, 1991 (type host) and *C. mindorensis* Kellogg, 1945. Specific parasites of the genus *Bullimus* are atopomelids of the subgenus *Marquesania*. Numerous collections of this species from the New Philippine endemic *Bullimus luzonicus* (Thomas, 1895), suggest that this species has successfully colonized this host from a species of *Chrotomys*. *Bullimus luzonicus* is sympatric with *C. gonzalesi* in southeastern Luzon and with *C. mindorensis* in central Luzon (Heaney *et al.* 1998).

TAXONOMIC NOTES. This species is very similar to *L. (L.) insularis* sp.n and differs mostly in male characters. In males of *L.*

(*L.*) *chrotomys*, the projections of coxal fields IV are wide and relatively long, extending to the level of setae 4a and are fused with sclerotized patches situated posterior to these setae, the lobar membrane is well developed and bears distinct lateral expansions; in females, median scales of the opisthosoma situated posterior to setae 4a are distinctly developed in most specimens. In males of *L. (L.) insularis*, the projections of coxal fields IV are narrow and short, not reach far to the level of setae 4a, the lobar membrane is weakly developed and without the lateral expansions; in females, the median scales of the opisthosoma situated posterior to setae 4a are indistinct.

Subgenus *Marquesania* Womersley, 1943

Type-species: *Listrophorus expansus* Ferris, 1932

This subgenus has recently been revised by Bochkov & Fain (2003). Three more species were described since this revision

(Bochkov *et al.*, 2004), and with the eight new species described below, it currently includes 24 species.

**Key to Philippine species of the subgenus *Marquesania*
Womersley, 1943**

MALES

1. Postscapular shield covered by distinct ornamentation. Hysteronotal shield covered by distinct ornamentation at least in anterior third. Apical projection of tarsus I indistinct 4
Postscapular and hysteronotal shields without ornamentation or ornamentation indistinct. Apical projection of tarsus I well developed. 2
2. Striated membranes of coxae II reaching lateral margins of body only in their anterior half. 3
Striated membranes of coxae II reaching lateral margins of body along their entire length. *L. (M.) luzonicus* sp.n. (Fig. 36)
3. Posterior ends of postgenital sclerite situated at level of setae *ps3*. Lobar membrane well developed, with distinct median incision. Femur IV 1.8–1.9 times wider than femur III *L. (M.) corpuzarrosae* sp.n. (Fig. 38A)
Posterior ends of postgenital sclerite not extending to level of setae *ps3*. Lobar membrane weakly developed, with short median incision. Femur IV 1.2–1.5 times wider than femur III *L. (M.) bullimus* sp.n. (Fig. 35A)
4. Lateral incisions of hysteronotal shield only moderately developed. Minimum distance between these incisions subequal to or only slightly shorter than width of the incisions. Setae *el* situated on hysteronotal shield. Soft cuticle of opisthonotum without scales or with 1–3 scales 5
Lateral incisions of hysteronotal shield extensive. Minimum distance between these incisions about 1.7 times shorter than width of the incisions. Setae *el* situated off hysteronotal shield. Soft cuticle of opisthonotum with numerous scales *L. (M.) postsquamatus* Fain, 1976 (Fig. 22)
5. Lobar membrane with distinct median incision. Postgenital shield ending well anterior (20–30) to level of setae *ps3* 9
Lobar membrane with indistinct median incision or without incision. Postgenital shield extending to level of setae *ps3* or beyond, sometimes ending slightly anterior (2–8) to this level 7
6. Postscapular shield with distinct lateral bands. Hysteronotal shield completely covered by distinct transverse lines. Coxa III with transverse line 8
Postscapular shield more strongly sclerotized laterally than medially, margins of this sclerotisation unclear. Hysteronotal shield covered by distinct transverse lines anterior to level of setae *e2*. Coxa III without lines
L. (M.) limnomys sp.n. (Fig. 33)
7. Pregenital sclerites absent. Supporting sclerite of aedeagus with free anterior ends, posterior ends of supporting sclerite not hypertrophied. Femur IV about 2 times wider than femur III *L. (M.) apomys* sp.n. (Fig. 27)
Pregenital sclerites present. Supporting sclerite of aedeagus with anterior ends fused to each other, posterior ends of supporting sclerite hypertrophied. Femur IV about 1.6 times wider than femur III
L. (M.) heaneyi sp.n. (Fig. 29)
8. Postgenital shield with median band situated immediately posterior to bases of setae *g*, lateral projections starting at level of setae *4a*, in form of inverted Y 10
Postgenital shield without median band, lateral projections of this shield starting immediately posterior to bases of setae *g*, in form of inverted U *L. (M.) faini* sp.n. (Fig. 31)

9. Small areas of coxal fields IV near genital papillae strongly sclerotized. Anterior ends of aedeagus-supporting sclerite fused to each other. Idiosomal 330–340 long. *L. (M.) paracucullatus* sp.n. (Fig. 21)

Coxal fields IV without sclerotized patches. Anterior ends of aedeagus-supporting sclerite separated. Idiosomal 345–370 long.
L. (M.) cucullatus (Trouessart, 1893). (Fig. 20A, B)

FEMALES

1. Distance *el-el* 1.5–4 times longer than distance *el*-posterior margin of hysteronotal shield. 5
Distances *el-el* and *el*-posterior margin of hysteronotal shield subequal 2
2. Setae *h3* subequal in length to *h1* and *h2*. Soft cuticle of opisthonotum with few lateral scales and without median scales. Opisthogastric shield entire 3
Setae *h3* 2.5 times longer than *h1* and *h2*. Opisthonotum covered by numerous lateral and median scales. Opisthogastric shield represented by pair of small lateral sclerites *L. (M.) postsquamatus* Fain, 1976 (Fig. 23)
3. Postscapular shield more strongly sclerotized laterally than medially. Hysteronotal shield completely covered by distinct transverse lines, 2–3 most posterior lines short 4
Postscapular shield evenly sclerotized. Hysteronotal shield covered by distinct transverse lines in anterior half and indistinct lines in posterior half. *L. faini* sp.n. (Fig. 32)
4. Idiosoma 380–410 long and 125–130 wide.
L. (M.) paracucullatus sp.n.
Idiosoma 385–430 long and 130–150 wide *L. (M.) cucullatus* (Trouessart, 1893) (Fig. 20C)
5. Postscapular shield covered by distinct ornamentation. Lateral part of this shield more strongly sclerotized than median part or bordered with bands. Hysteronotal shield covered by straight or undulating lines. Soft cuticle of opisthonotum without scales posterior to setae *e2*. 8
Postscapular shield covered by indistinct ornamentation or without ornamentation, evenly sclerotized. Hysteronotal shield covered by distinct scales and folds. Soft cuticle of opisthonotum covered by scales immediately posterior to setae *e2* 6
6. Striated membranes of coxae II reaching lateral margin of body only in their anterior half. Setae *ps3* subequal in length or longer than *cp*. 7
Striated membranes of coxae II wide, reaching lateral margin of body along entire length. Setae *ps3* 2 times shorter than *cp*
L. (M.) luzonicus sp.n. (Fig. 37)
7. Coxae IV with distinct transverse fold *L. (M.) corpuzarrosae* sp.n. (Fig. 38A)
Coxae IV without folds or lines *L. (M.) bullimus* sp.n. (Fig. 35A)
8. Postscapular shield with distinct lateral bands. Hysteronotal shield completely covered by distinct transverse lines. Coxa III with transverse line. *L. (M.) apomys* sp.n. and *L. (M.) heaneyi* sp.n. (figs. 28, 30)
Postscapular shield more strongly sclerotized laterally than medially, but medial margins indistinct. Hysteronotal shield covered by distinct transverse lines anterior to level of setae *e2*. Coxa III without lines
L. (M.) limnomys sp.n. (Fig. 34)

Listrophoroides (Marquesania) cucullatus (Trouessart, 1893)
(Fig. 20)

Listrophorus cucullatus Trouessart, 1893: 699.

Listrophoroides cucullatus, Fain, 1970: 281; Domrow, 1992: 1555.

Listrophoroides (Listrophoroides) cucullatus, Fain, 1972a: 10, figs. 1–4, 1974: 17.

Listrophoroides (Marquesania) cucullatus, Fain, 1976a: 17, 1977: 292, 1979: 142, 1981: 105; Bochkov & Fain, 2003: 577, figs. 1–6; Bochkov *et al.*, 2004: 73.

Listrophoroides expansus Ferris, 1932: 120; Domrow, 1958: 49, 1962: 297, 1967: 785; Zumpt, 1961: 306; Barrow *et al.*, 1963: 169.

Marquesania expansa var. *expansa*, Womersley, 1943: 15.

Listrophoroides tragardi Radford, 1940: 101; Domrow, 1958: 50.

DIAGNOSIS. In both sexes postscapular shield more strongly sclerotized laterally than medially. *Male*. Anterior part of post-genital shield forming median sclerotized band immediately posterior to genital organ. Supporting sclerite of aedeagus with free anterior ends. *Female*. Hysteronotal shield completely covered by straight transverse lines, 2–3 short posterior lines, situated at or posterior to level of setae *e*₂.

MALE (Fig. 20A). Body 345–350 long, 129–135 wide in 10 specimens ex *Rattus tiomanicus*. Length and width of gnathosoma subequal, about 35. *Dorsum*. Postscapular shield 75–77 long, 115–125 wide, more strongly sclerotized laterally than medially, bearing 6 transverse lines. Hysteronotal shield 155–

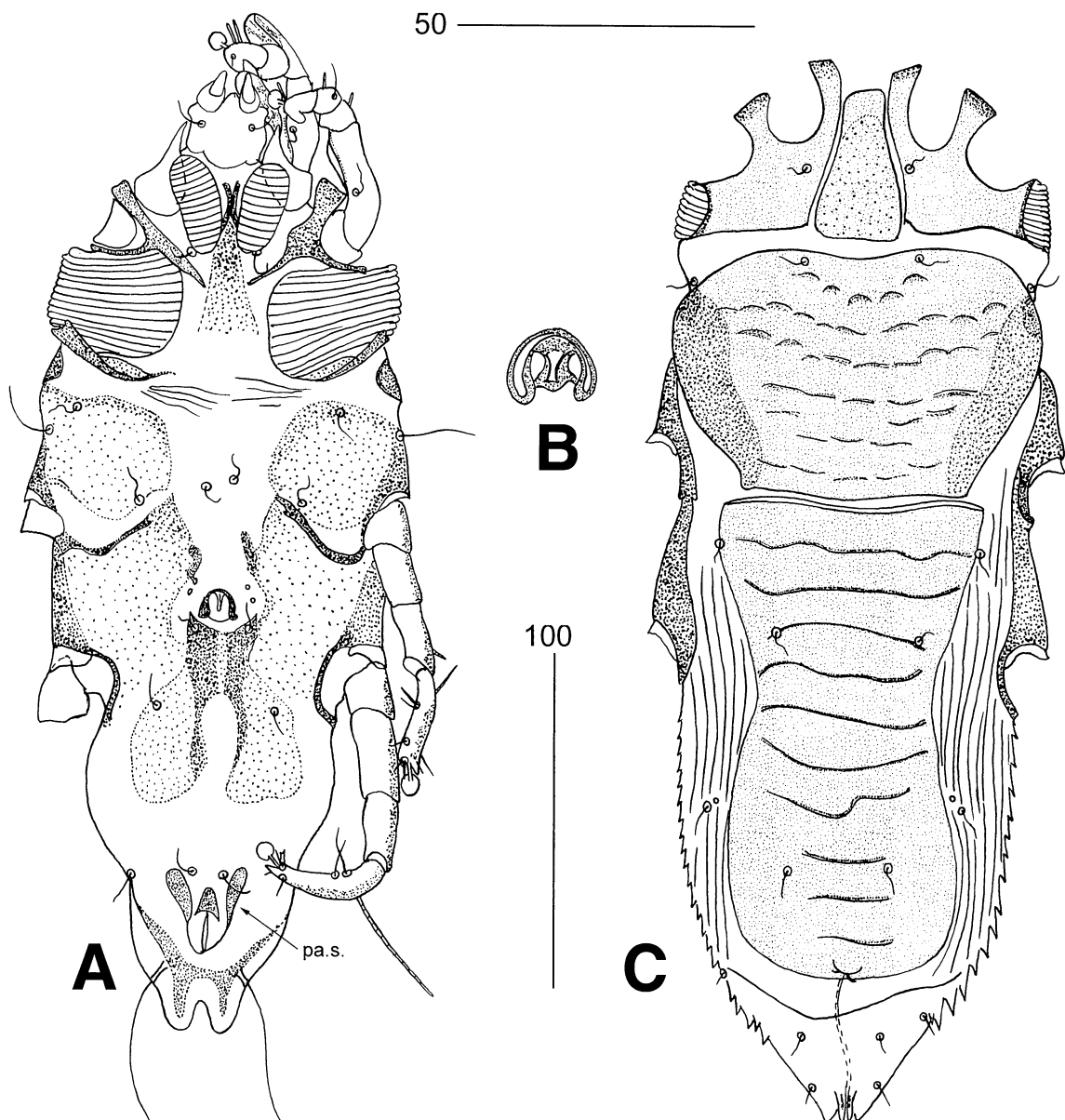


Fig. 20. (A–C). *Listrophoroides cucullatus* Trouessart, 1893. A.—Male, ventral view. B.—Aedeagus. C.—Female, dorsal view. Abbreviations: pa.s.—postanal sclerite. Scale bars 100 μm (A–B) and 50 μm (C).

160 long, covered by transverse lines extending from anterior margin to level of setae *e1*. Incisions of hysteronotal shield well developed, 35–45 long, 25–30 wide, minimum distance between these incisions 35–40. Distance *e1-e1* 22–33. Setae *e2* situated on or off hysteronotal shield, soft cuticle posterior to these setae without scales or with 1–3 scales. Setae *h3* 35–45 long. *Venter*. Striate membranes of coxae II wide, reaching lateral margins of body. Coxae III with indistinct transverse line or without line. Aedeagus very short, length 3–4. Supporting sclerite of aedeagus with free anterior ends. Postgenital shield in form of inverted Y, its anterior part forming median sclerotized band immediately posterior to genital organ, 22–25 long, lateral projections of postgenital shield 65–75 long. Distance between posterior ends of projections of postgenital shield and adanal shields 15–22. Median incision of lobar membrane well developed. *Legs*. Femur IV about 18 wide, 1.2 times wider than femur III (15). Legs III and IV 100–105 and 115–125 long, respectively. Tibiotarsi III and IV 33–37 and 37–45, respectively. Solenidia ϕ of legs III and IV 13–15 and 44–46, respectively.

FEMALE (Fig. 20B). Body 380–400 long, 140–145 wide in 10 specimens. Length and width of gnathosoma subequal, about 50. *Dorsum*. Postscapular shield 80–90 long, 140–150 wide, more strongly sclerotized laterally than medially, completely covered by 5–6 transverse lines. Hysteronotal shield 170–180 long, completely covered by 9–10 straight transverse lines, 2–3 posterior lines short, situated at or posterior to level of setae *e2*. Width of this shield at level of setae *d1* and at level of setae *e1* subequal, 65–77. Distances *e1-e1* and *e1*-posterior margin of hysteronotal shield subequal, 30–35 and 30–40, respectively. Setae *d2* situated on or off shield. *Venter*. Striated membranes of coxae II wide, reaching lateral margins of body. Coxae III with indistinct transverse line. Lateral opisthosoma covered by tubercles in posterior half. Median part of opisthosoma with indistinct ornamentation. *Legs*. Legs III and IV subequal in length, 100–110. Solenidia ϕ of legs III and IV, 13–15 and 3–4 long, respectively.

MATERIAL EXAMINED. Thirteen males and 19 females (BMOC 88-0824-014) ex *Rattus tiomanicus* (USNM 348634), Palawan Prov., Inagawan Penal Colony, 9°32'56"N, 18°38'50"E, 5 May 1969, coll. K. Barbehenn; 8 males and 7 females (BMOC 92-1400-146) ex *Rattus tanezumi* (FMNH 146936), Sibuyan Isl., Romblon Prov., 7.5 km E, 1.75 km W Silum, 12°28'N, 122°35'E, 30 m, 19 March 1992, coll. S.M. Goodman (SMG 5270); 2 males and 3 females (BMOC 92-1400-124) ex *R. tanezumi* (FMNH 146934), same data, 16 March 1992, coll. S.M. Goodman (SMG 5219); 3 females (BMOC 92-1400-069) ex *R. tanezumi* (FMNH 146924), Sibuyan Isl., Romblon Prov., 6.75 km S, 4.5 km E, Magdiwang, 12°26'N, 122°33'E, 1500 m, 27 February 1992, coll. S.M. Goodman (SMG 5057); 7 males and 5 females (BMOC 92-1400-078) ex *R. tanezumi* (FMNH 146942), same data, 5.25 km S, 3.5 km E Magdiwang, 12°27'N, 122°33'E, 725 m, 19 February 1992, coll. S.M. Goodman (146942); 1 male and 9 females (BMOC 88-1710-001) ex *R. tanezumi* (USNM 573359), Catanduanes Prov., 8.5 km W Gig-

moto, 13°47'N, 124°19'E, 250 m, 17 February 1988, coll. E.A. Rickart (EAR 1655); 5 males and 7 females (BMOC 04-0909-034) ex *R. tanezumi* (FMNH 178426), Luzon Isl., Quezon Prov., Mt. Banahaw, Barangay Lalo, 14°03'06"N, 121°32'22"E, 650 m, 15 May 2004, coll. E.A. Rickart (EAR 5326).

TYPE DEPOSITION. The lectotype male and paralectotype female are deposited in MNHN. Voucher specimens from this study are deposited in FMNH, NMP, OSAL, UMMZ, USNM.

HOST ASSOCIATIONS AND DISTRIBUTION. This species was originally described from *Rattus norvegicus* (Berkenhout, 1769) from an undetermined region of Asia (Trouessart, 1893). It occurs on the widespread commensal species *R. norvegicus*, *R. rattus* (L., 1758), and *R. tanezumi* Temminck, 1844, but is apparently restricted to tropical regions. It is also widely distributed on the following native species of the genus *Rattus* in the Oriental region and New Guinea: *R. annandalei* (Bonhote, 1903) and *R. argentiventer* (Robinson and Kloss, 1916) from Malaysia, *R. hoffmanni* (Matschie, 1901) from Indonesia, *R. tanezumi* Temminck, 1844 (= *mindanensis*) from Hong Kong, Borneo, and the Philippines (introduced), *R. tiomanicus* (Miller, 1900) from Malaysia and the Philippines, and *R. xanthurus* (Gray, 1867) from Sulawesi (Fain, 1977, 1981; Bochkov & Fain, 2003, present data). It is also recorded from *Bunomys coelestis* (Thomas, 1896) from Sulawesi (Fain, 1981) and *Stenomys niobe* (Thomas, 1906) in New Guinea. The record of a single male of *L. (M.) cucullatus* from *Apomys insignis* Mearns, 1905 from Mindanao (Bochkov & Fain, 2003) was not confirmed in our collections and probably represents contamination. The records from *Rattus mindorensis* from Leyte (Bochkov & Fain, 2003) represent a host misidentification as this host species does not occur on that island. Specimens reported as this species from *Rattus exulans* (Peale, 1848) from west Malaysia, New Guinea and the Philippines (Mindanao Is.) (Fain, 1977, 1981; Bochkov & Fain, 2003) actually belong to *L. (M.) paracucullatus* sp.n.

TAXONOMIC NOTES. This species is distinguished from other species of the subgenus, except for *L. (M.) paracucullatus* sp.n., by the inverted Y-shape of the postgenital shield in males. In other species, the postgenital shield is in the shape of an inverted V or U.

Listrophoroides (Marquesania) paracucullatus New Species (Fig. 21)

Listrophoroides (Marquesania) cucullatus, Fain, 1977: 292, 1981: 105; Bochkov & Fain, 2003: 577 (in part—misidentification).

DIAGNOSIS. In both sexes, postscapular shield more strongly sclerotized laterally than medially. *Male*. Anterior part of postgenital shield forming a median sclerotized band immediately posterior to genital organ. Supporting sclerite of aedeagus with anterior ends fused to each other. *Female*. Hysteronotal shield completely covered by straight transverse lines, 2–3 short, posterior lines situated at or posterior to level of setae *e2*.

MALE (Fig. 21) Body 335–340 long (340), 130–135 wide (130) in 10 paratypes. Length and width of gnathosoma sub-

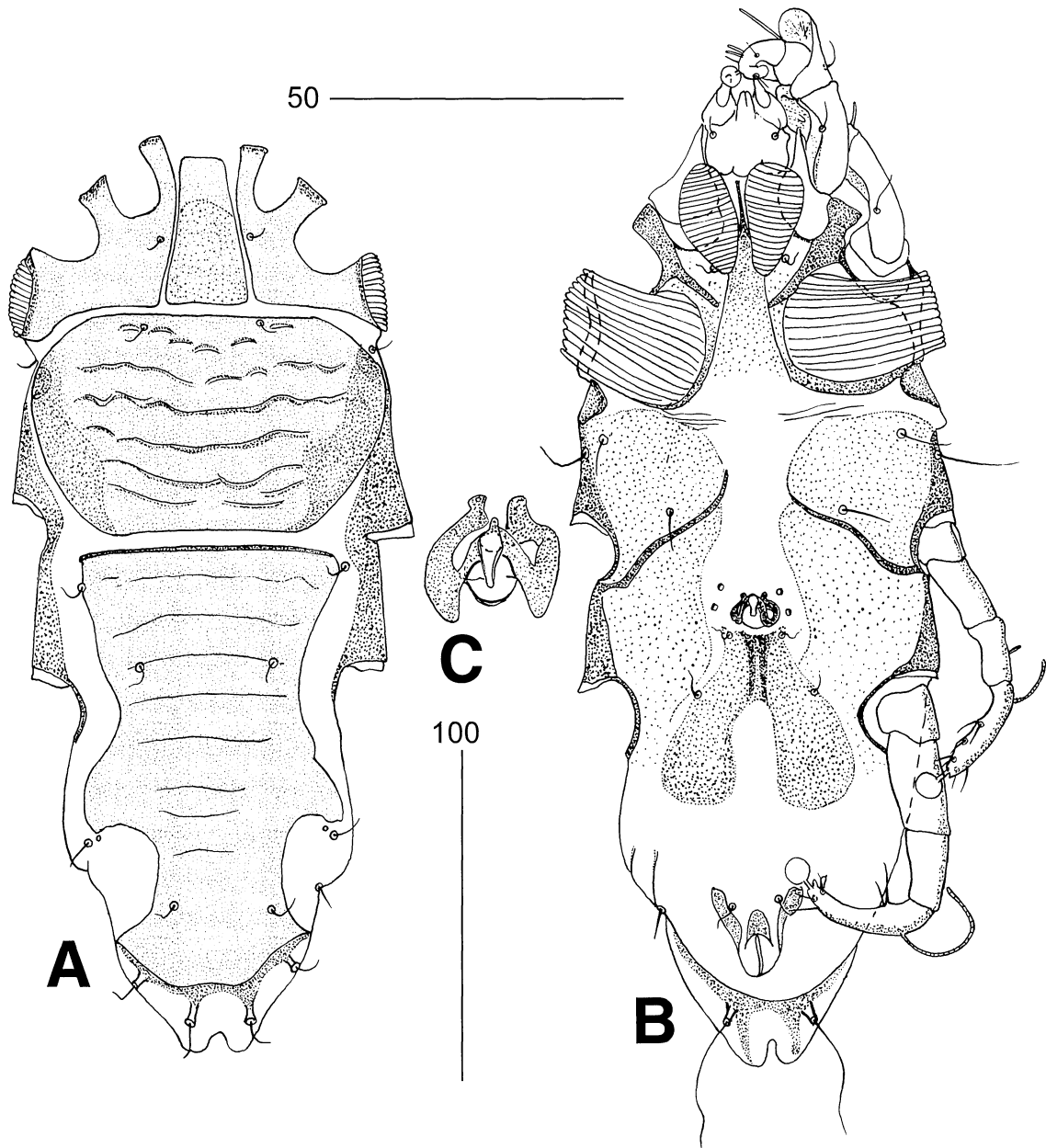


Fig. 21. (A–C). *Listrophoroides paracucullatus* sp.n., male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. Scale bars 100 μm (A–B) and 50 μm (C).

equal, about 35. *Dorsum*. Postscapular shield 75–80 long (77), 115–130 wide (120), more strongly sclerotized laterally than medially, bearing 6 transverse lines. Hysteronotal shield 130–150 long (150), covered by transverse lines extending from anterior margin to level of setae *e1*. Incisions of hysteronotal shield well developed, 22–25 long (25) and 20–23 wide (23), minimum distance between these incisions 30–40 (33). Distance *e1-e1* 25–30 (30). Setae *e2* situated on or off hysteronotal shield, soft cuticle posterior to these setae without scales. Setae *h3* 25–35 (32) long. *Venter*. Striate membranes of coxae II wide, reaching lateral margins of body. Coxae III with transverse line indistinct or absent. Small areas of coxal fields IV strongly sclerotized near genital papillae. Aedeagus short, length

3–5. Supporting sclerite of aedeagus with anterior ends fused to each other. Postgenital shield in form of inverted Y, its anterior part forming a median sclerotized band immediately posterior to genital organ, 22–30 long (30), its lateral projections 65–70 long (70). Distance between posterior ends of projections of postgenital shield and adanal shields 13–15 (15). Median incision of lobar membrane distinctly developed. *Legs*. Femur IV about 18 wide, 1.2 times wider than femur III (15). Legs III and IV 90–100 (90) and 110–115 long (115), respectively. Tibiotarsi III and IV 33–37 and 37–45, respectively. Solenidia φ of legs III and IV 12–15 and 35–42, respectively.

FEMALE. Body 404–410 long, 125–130 wide in 6 paratypes. Length and width of gnathosoma subequal, about 50. *Dorsum*.

Postscapular shield 85–90 long, 125–130 wide, more strongly sclerotized laterally than medially, completely covered by 5–6 transverse lines. Hysteronotal shield 165–170 long, completely covered by 9–10 straight transverse lines, 2–3 posterior lines short, situated at or posterior to level of setae *e2*. Width of this shield at level of setae *d1* and at level of setae *e1* subequal, 70–80. Distances *e1-e1* and *e1*-posterior margin of hysteronotal shield subequal, 30–35 and 30–40, respectively. Setae *d2* situated on or off shield. *Venter*. Striated membranes of coxae II wide, reaching lateral margins of body. Coxae III with an indistinct transverse line. Opisthogaster sclerotized. Opisthogaster covered laterally by tubercles in posterior half. Median part of opisthogaster with indistinct ornamentation. *Legs*. Legs III and IV subequal in length, 100–120. Solenidia ϕ of legs III and IV, 13–15 and 4–5 long, respectively.

ETYMOLOGY. The species name refers to the resemblance of this species to *L. (M.) cucullatus* and is a noun in apposition.

TYPE MATERIAL. Male holotype (BMOC 95-1214-025, 1), 2 male and 3 female paratypes (BMOC 95-1214-025, 2–6) ex *Rattus exulans* (FMNH 154872), Camiguin Prov., Mt. Timpoong, 2 km N, 6.5 km W Mahinog, 9°11'N, 124°43'E, 1275 m, 20 March 1995, coll. L.R. Heaney (LRH 5381); 10 male and 3 female paratypes (BMOC 95-1214-026, 1–13) ex *R. exulans* (FMNH 154872), same data, coll. L.R. Heaney (LRH 5381).

OTHER MATERIAL EXAMINED. Ten male and 8 female paratypes (BMOC 95-1214-012, 1–18) ex *Apomys sp.n. D* (FMNH 154855), Camiguin Prov., Mt. Timpoong, 2 km N, 6.5 km W Mahinog, 9°11'N, 124°43'E, 1275 m, 17 March 1995, coll. L.R. Heaney (LRH 5347); 1 male and 5 females (BMOC 95-1214-011) ex *Apomys sp.n. D* (FMNH 154854), same data, coll. L.R. Heaney (LRH 5346); 8 males and 5 females (BMOC 95-1214-015) ex *Apomys sp.n. D* (FMNH 154857), same data, 18 March 1995, coll. L.R. Heaney (LRH 5353); 4 males and 1 female (BMOC 95-1214-022) ex *Apomys sp.n. D* (FMNH 154858), same data, coll. L.R. Heaney (LRH 5377).

SPECIMEN DEPOSITION. Holotype is deposited in NMP, paratypes in FMNH, OSAL, UMMZ, and ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION. This species has been collected from *Rattus exulans*, a rat widely distributed from Myanmar through New Guinea to many of the Pacific Islands including New Zealand. This mite species has previously been recorded (as *L. cucullatus*) from west Malaysia, a region in the presumed native range of *R. exulans*, as well as from New Guinea and Mindanao Island where the host was presumably introduced by humans (Fain, 1977, 1981, Bochkov & Fain, 2003). Multiple collections of this species from the Old Philippine endemic, *Apomys sp.n. D*, a species endemic to Camiguin Island, are evidence of host switching from *R. exulans* on that island.

TAXONOMIC NOTES. This new species is closest to *L. (M.) cucullatus* but differs consistently in some male characters. In males of *L. (M.) paracucullatus sp.n.*, the small areas of coxal fields IV near to the genital papillae are strongly sclerotized, the anterior ends of the aedeagal-supporting sclerite are fused to each other, and the idiosomal length is 330–340; in females,

the idiosomal length is 380–410, width 125–130. In males of *L. (M.) cucullatus*, coxal fields IV are without any sclerotized patches, the anterior ends of the aedeagal-supporting sclerite are separated, and the idiosomal length is 345–370, width—125–130; in females, the idiosomal length is 385–430, width—130–150.

***Listrophoroides (Marquesania) postsquamatus* Fain, 1976**
(Figs 22–26)

Listrophoroides (Marquesania) postsquamatus Fain, 1976b: 63; 1981: 107, figs 137–140; Bochkov & Fain, 2003: 593, figs 40–43.

DIAGNOSIS. In both sexes, setae *h3* long, 50–58 in males and 35–40 in females. *Male*. Lateral margins of hysteronotal shield hypertrophied, scales posterior to setae *e2* numerous. *Female*. Posterior half of opisthonotum covered by numerous scales.

MALE (Fig. 22). Body 339–392 long, 152–170 wide in 10 specimens. Length and width of gnathosoma subequal, about 37. *Dorsum*. Postscapular shield 62–77 long, 125–154 wide, evenly sclerotized, completely covered by 5–6 transverse rows of short lines. Hysteronotal shield 136–165 long, covered by transverse lines extending from anterior margin to level of setae *e2*. Lateral incisions of hysteronotal shield very large, 44–55 long, 40–44 wide, minimum distance between lateral incisions 13–26. Setae *e2* situated off hysteronotal shield, soft cuticle posterior to these setae with numerous scales. Setae *e1* situated off hysteronotal shield, distance *e1-e1* 22–29. Setae *h3* 51–68 long. *Venter*. Coxae II wide, reaching lateral margins of body. Coxae III with or without a transverse line. Aedeagus short, 7–9 long. Supporting sclerite of aedeagus with anterior ends fused to each other. Postgenital shield in form of inverted U, its projections 62–88 long. Distance between postgenital shield and adanal shields 20–33. Lobar membrane with deep median incision. *Legs*. Femur IV about 33 wide, 2 times wider than femur III (15). Legs III and IV 106–120 and 220–147 long, respectively. Tibiotarsi III and IV 35–42 and 44–55 long, respectively. Solenidia ϕ III and IV 11–13 and 42–53 long, respectively.

FEMALE (Fig. 23). Body 404–439 long, 158–176 wide in 10 specimens. Gnathosoma about 50 long, 40 wide. *Dorsum*. Postscapular shield 73–80 long, 139–154 wide, evenly sclerotized, covered by 5–6 transverse rows of short lines. Hysteronotal shield 154–172 long, covered by 8–10 furrows from anterior margin to level of setae *e2*. Width of this shield at level of setae *d1-d1* 66–84 and at level of setae *e1-e1* 66–77. Setae *d1* situated off shield. Distances *e1-e1* and *e1*-posterior margin of hysteronotal shield subequal, 29–40 and 26–37, respectively. *Venter*. Striated membranes of coxae II wide, reaching lateral margins of body. Coxae III with or without transverse line. Lateral parts of opisthosoma covered by numerous scales. Median part of opisthosoma with rounded scales extending from level of setae *4a* to level of setae *ps3*. Opisthogastric shield represented by pair of small lateral sclerites. Setae *h3* 35–40 long. *Legs*. Legs III and IV 108–114 and 121–132 long, respectively. Solenidia ϕ III and IV 10–13 and 4–7 long, respectively.

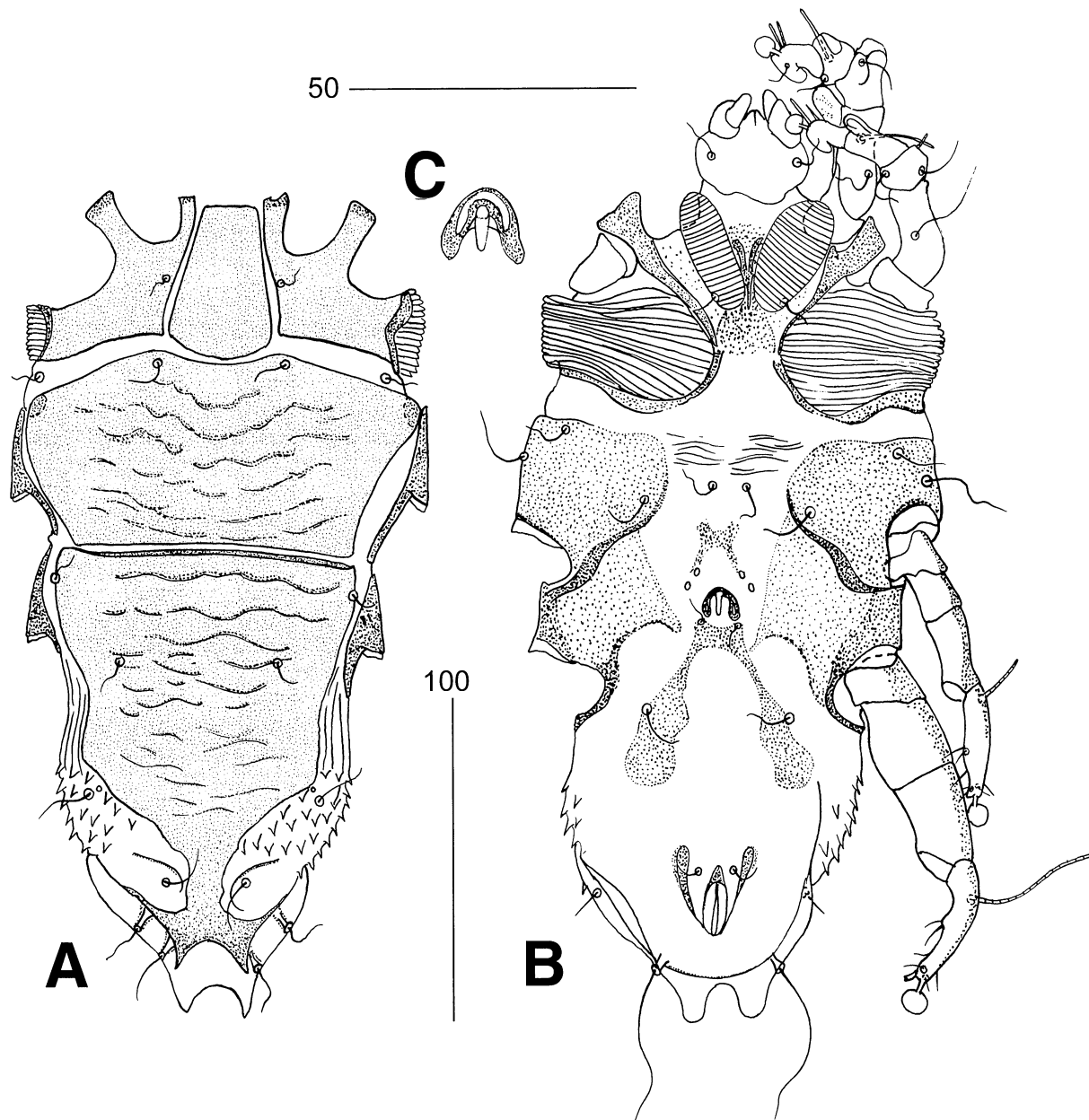


Fig. 22. (A–C). *Listrophoroides postsquamatus* Fain, 1976, male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. Scale bars 100 μm (A–B) and 50 μm (C).

LARVA (Fig. 24). Gnathosoma as in adults. Idiosoma as in female. Idiosomal setation: *scx*, *si*, *se*, *c2*, *c3*, *cp*, *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, *1a*, *3a*. Leg sensilla: I trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*, σ 1), tibia 2 (*gT*, φ), tarsus (setation unclear); II trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*, σ), tibia 2 (*gT*, φ), tarsus (setation unclear); III trochanter 0, femur 0, genu 1 (σ), tibiotarsus 8 (tibia—*kT*, φ , tarsus—*wa*, *ra*, *s*, *d*, *e*, *f*).

PROTONYMPH (Fig. 25). Setae *f2*, *h3*, *ps3*, and *g* added. One pair of remnant genital papillae present between coxae IV. Leg IV added with setae *d*, *ra*, and *wa* of tarsus IV added.

TRITONYMPH (Fig. 26). Setae *4a* and *4b* added on idiosoma, setae *kT* and solenidion φ added on tibia IV, and setae *e*, *f* added

on tarsus IV. Two pairs of remnant genital papillae between coxae IV.

MATERIAL EXAMINED. Twenty-nine males and 16 females (BMOC 01-0920-058) ex *Rattus everetti* (FMNH 169155), Luzon Isl., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Mappa, 17°28'30"N, 121°04'30"E, 1050 m. 17 March 2001, coll. E.A. Rickart (EAR 4564); 7 males and 7 females (BMOC 01-0920-056) ex *R. everetti* (FMNH 169152), same data, 14 March 2001, coll. E.A. Rickart (EAR 4545); 8 males and 7 females (BMOC 04-0909-012) ex *R. everetti* (FMNH 176605), Luzon Isl., Cagayan Prov., Baggao Munic., Brgy. Sta. Margarita, Sitio Matulang, Mt. Twin Peaks, 17°43'57"N, 121°57'09"E,

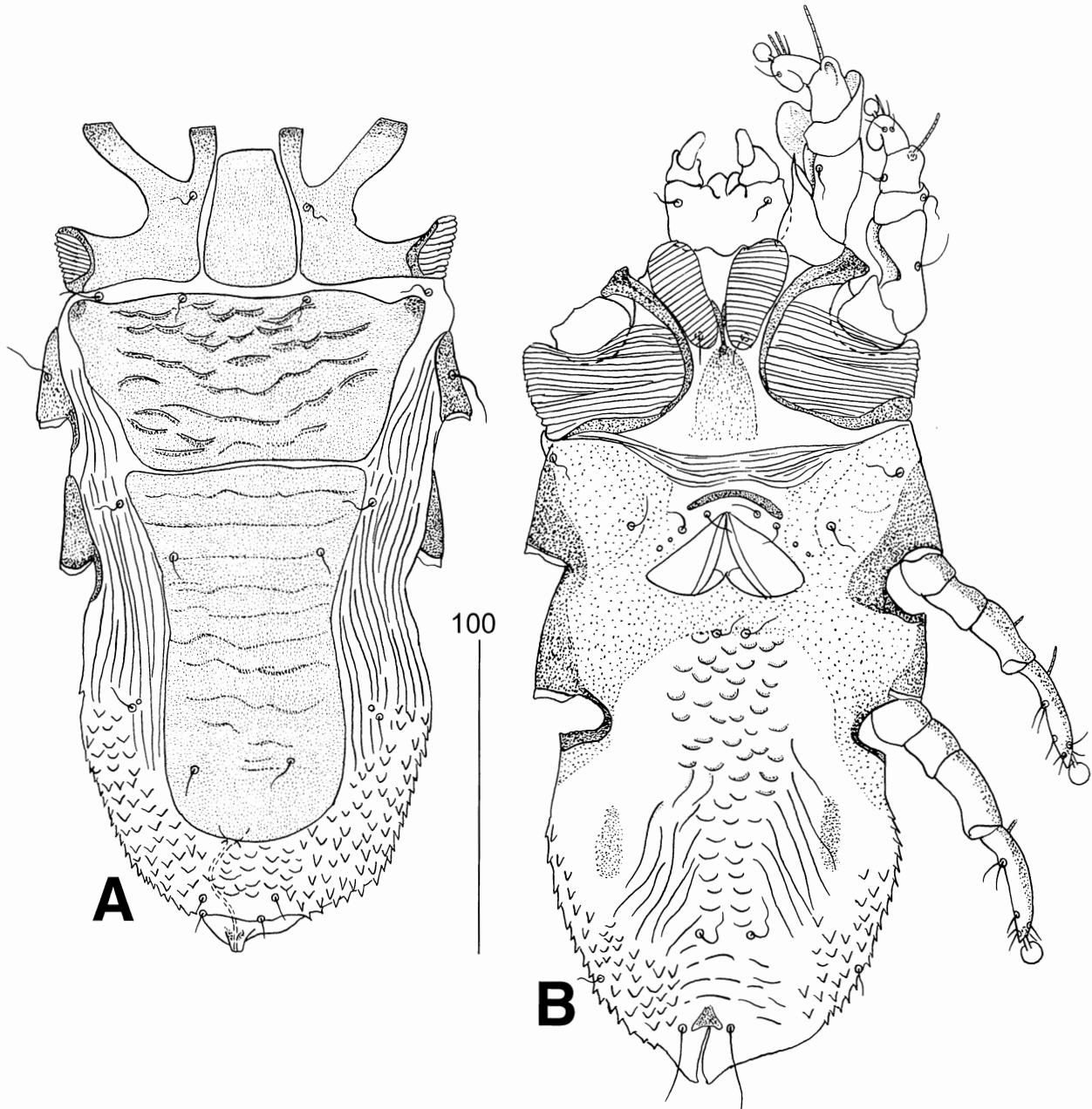


Fig. 23. (A–B). *Listrophoroides postsquamatus* Fain, 1976, female. A.—Dorsal view. B.—Ventral view.

300 m, 6 May 2003, coll. M.R. Duya (# 117); 2 males and 8 females (BMOC 04-0909-013) ex *R. everetti* (FMNH 176606), same data, 8 May 2003, coll. M.R. Duya (# 173); 12 males and 11 females (BMOC 04-0909-014) ex *R. everetti* (FMNH 176607), same data, 8 May 2003, coll. M.R. Duya (# 184); 6 males and 19 females (BMOC 04-0909-015) ex *R. everetti* (FMNH 176608), Luzon Isl., Quezon Prov., General Nakar Munic., Brgy. Minahan Norte, Sitio Pangamitan, Mt Binuang, 14°46'30"N, 121°33'30"E, 500 m, 27 June 2003, coll. M.R. Duya (# 30); 5 males (HK 87-0417-001) ex *R. everetti*, Maripipi Isl., Leyte Prov., 1.8 km N, 3 km W Maripipi, 11°47'N, 124°19'E, 740 m., 14 April 1987, coll. P.D. Heideman (PDH

3321); 2 males and 7 females (HK 87-0310-001) ex *R. everetti* (USNM 458811), Leyte Isl., Leyte Prov., 10.2 km N, 2.2 km E. Baybay, 10°46'N, 124° 49'E, 320 m, 10 March 1987, coll. P.D. Heideman (PDH 3109); 3 males and 3 females from *R. everetti* (USNM 459919), same data, 10.5 km N, 4 km E. Baybay, 10°47'N, 124°50'E, 700 m, 22 March 1987, coll. P.D. Heideman (PDH 3222); 8 males and 12 females (BMOC 89-1111-006) ex *Rattus sp. A.* (FMNH 135719), Sibuyan Isl., Romblon Prov., NW slope Mt. Guitinguitin, 5.25 km S, 3.5 km E Magdiwang, 12°27'N, 122°33'E, 725 m, 22 May 1989, coll. S.M. Goodman (SMG 3006); 10 males and 8 females (BMOC 89-1111-008) ex *Rattus sp. A.* (FMNH 135720), same data, 24

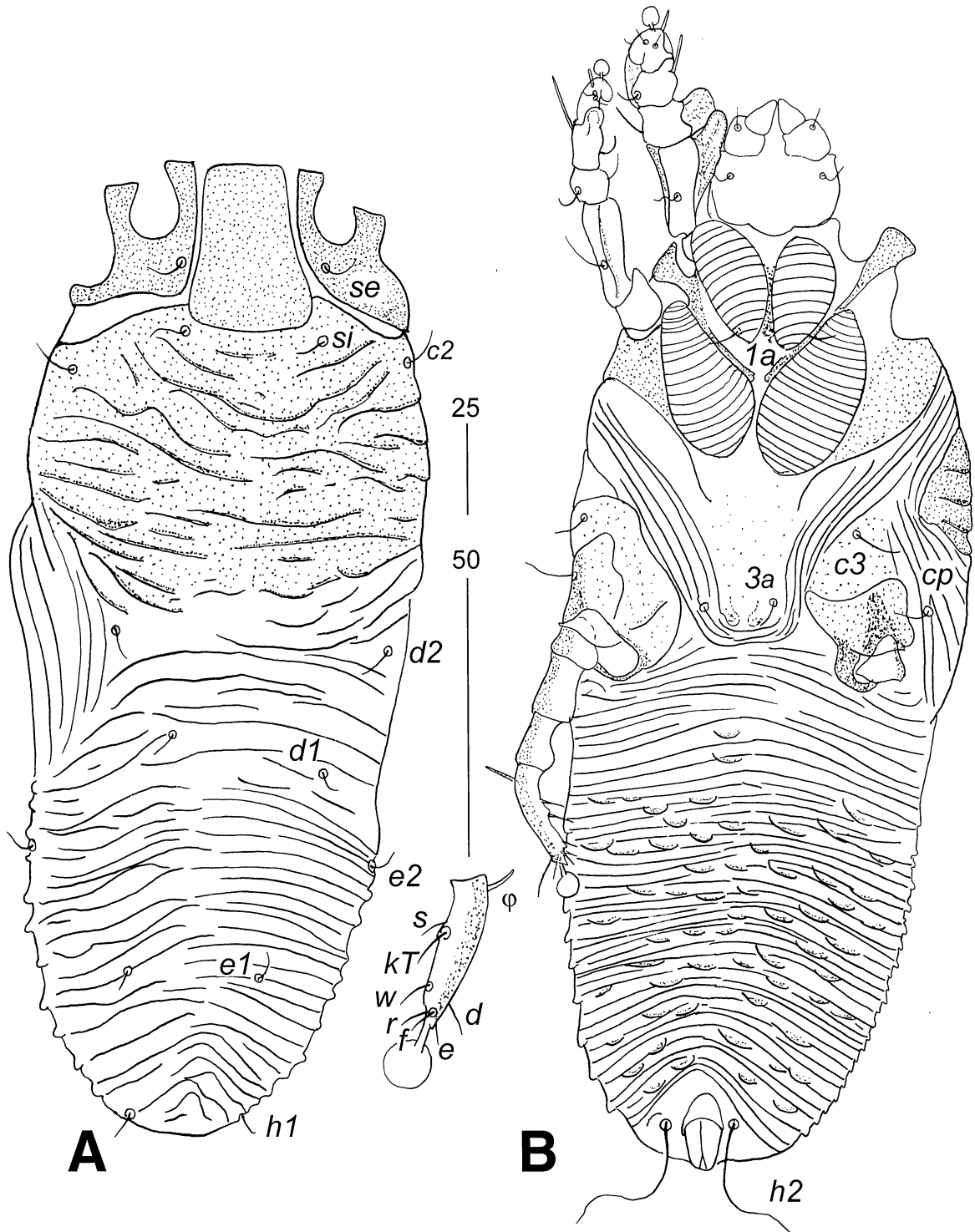


Fig. 24. (A–C). *Listrophoroides postsquamatus* Fain, 1976, larva. A.—Dorsal view. B.—Ventral view. C.—Tibioarsus III, lateral view. Scale bars 100 μm (A–B) and 50 μm (C).

May 1989, coll. S.M. Goodman (SMG 3042); 10 males and 10 females (BMOC 89-1111-003) ex *Rattus* sp. A. (FMNH 135718), same data, 325 m, 7 May 1989, coll. S.M. Goodman (SMG 2957); 7 males and 4 females (BMOC 95-1214-011) ex *Apomys* sp.n. D (FMNH 154854), Camiguin Prov., Mt. Tim-

poong, 2 km N, 6.5 km W Mahinog, 9°11'N, 124°43'E, 1275 m, 17 March 1995, coll. L.R. Heaney (LRH 5346).

TYPE DEPOSITION. Holotype is deposited in BMNH. Voucher specimens from this study are deposited in FMNH, NMP, OSAL, UMMZ and USNM.

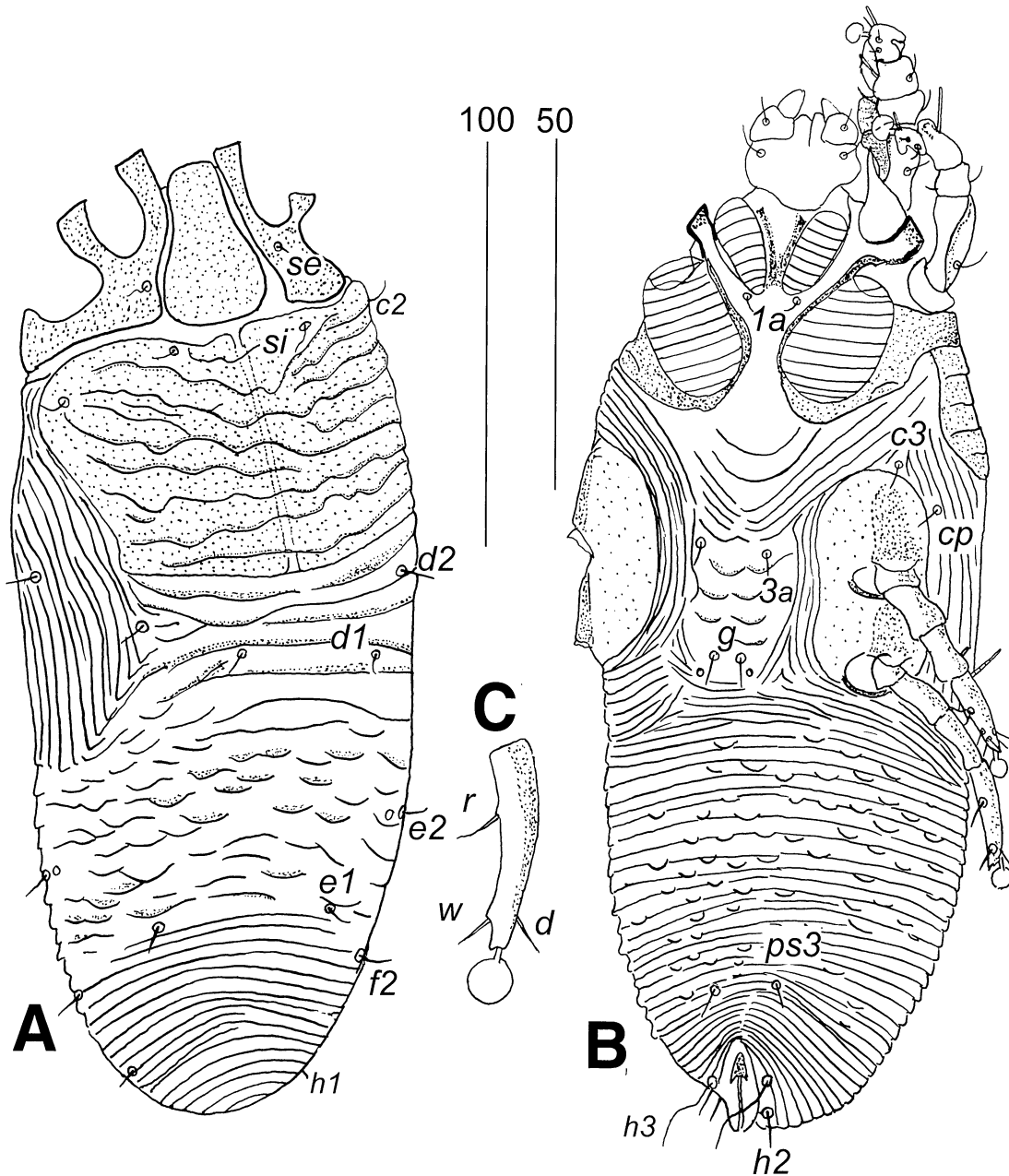


Fig. 25. (A–C). *Listrophoroides postsquamatus* Fain, 1976, protonymph. A.—Dorsal view. B.—Ventral view. C.—Tibiotarsus IV, lateral view. Scale bars 100 μm (A–B) and 50 μm (C).

HOST ASSOCIATIONS AND DISTRIBUTION. This species was described by Fain (1976b) from *Rattus everetti* (Günther, 1879), a New Philippine endemic, occurring on many islands of the Philippine archipelago (Heaney *et al.*, 1998). We also collected this species from several individuals of an undescribed species, *Rattus* sp. A., closely related to *R. everetti* (Heaney *et al.*, 2002) from Sibuyan Island and from a single individual of *Apomys* sp.n. D (Heaney *et al.*, 1998) from Camiguin Island. This species was previously recorded outside the Philippines on *Rattus hoffmanni* (Matshie, 1901) (1 specimen) and *Maxomys hellwaldii* (Jentink, 1878) (4 specimens) from Sulawesi Utara, Indonesia (Whitaker & Dur-

den, 1987). The specific identity of the Sulawesi specimens needs confirmation. It is most likely that *L. postsquamatus* was initially associated with the ancestor of *R. everetti* and *R. sp. A.*, and its association with *Apomys* sp. D. on Camiguin Island is the result of a host shift.

TAXONOMIC NOTES. This species is quite distinct from others in the subgenus and can be distinguished by the following characters. In both sexes, the opisthosoma is covered by numerous scales, setae *h3* are long, 50–58 in males and 35–40 in females; in males, the incisions of the hysteronotal shield are very large, the minimal distance between these incisions is 13–26; in

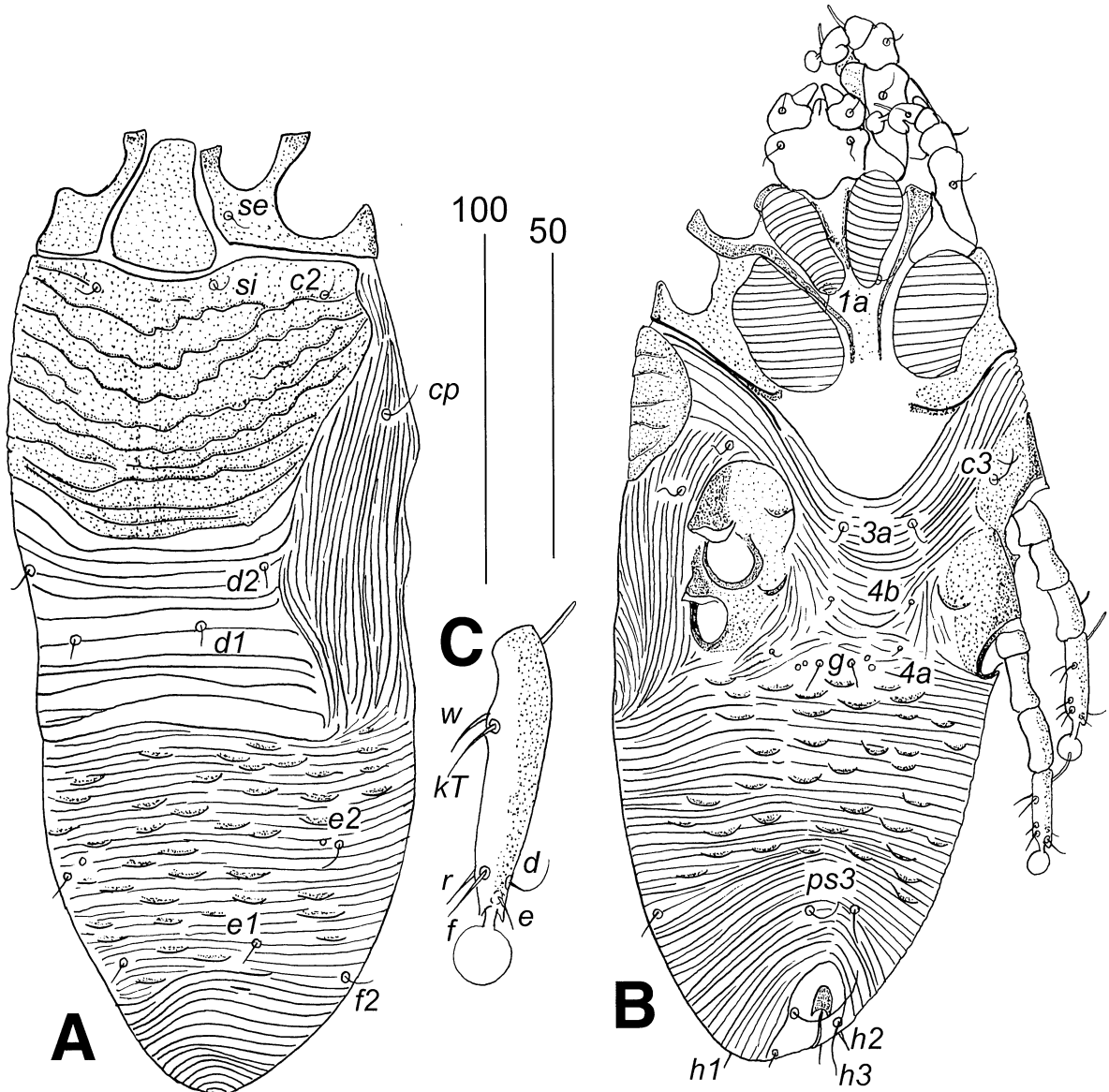


Fig. 26. (A-C). *Listrophoroides postsquamatus* Fain, 1976, tritonymph. A.—Dorsal view. B.—Ventral view. C.—Tarsus IV, lateral view. Scale bars 100 μm (A-B) and 50 μm (C).

females, the opisthogastric shield is represented by a pair of small lateral sclerites.

Listrophoroides (Marquesania) apomys New Species
(Figs 27–28)

DIAGNOSIS. In both sexes, lateral margins of postscapular shield with distinct sclerotized bands. *Male*. Lobar membrane well developed, almost triangular in shape, with widely rounded posterior extremity, without median incision.

MALE (Fig. 27). Body 316–328 long (322), 123–129 wide (129) in 7 paratypes. Length and width of gnathosoma subequal, about 30. *Dorsum*. Postscapular shield 65–70 long (66), 95–110 wide (97), completely covered by 5–6 transverse rows

of short lines. Lateral margins of shield with strongly sclerotized bands. Hysteronotal shield 140–155 long (143), covered by transverse lines extending from anterior margin to level of setae *e2*. Lateral incisions of hysteronotal shield well developed, 30–35 long (30) and 18–25 wide (25), minimum distance between these incisions 20–26 (20). Setae *e2* situated off hysteronotal shield; soft cuticle posterior to these setae without scales or tubercles. Setae *e1* situated on hysteronotal shield, distance *e1-e1* 26–29 (26). Setae *h3* 25–26 long (26). *Venter*. Coxae II wide, reaching lateral margins of body. Coxae III with short transverse line. Aedeagus very short, length 3–4. Anterior ends of aedeagal-supporting sclerite free. Postgenital shield in form of inverted U, its projections 77–88 long (77). Posterior ends of these projections reaching level of setae *ps3* or slightly

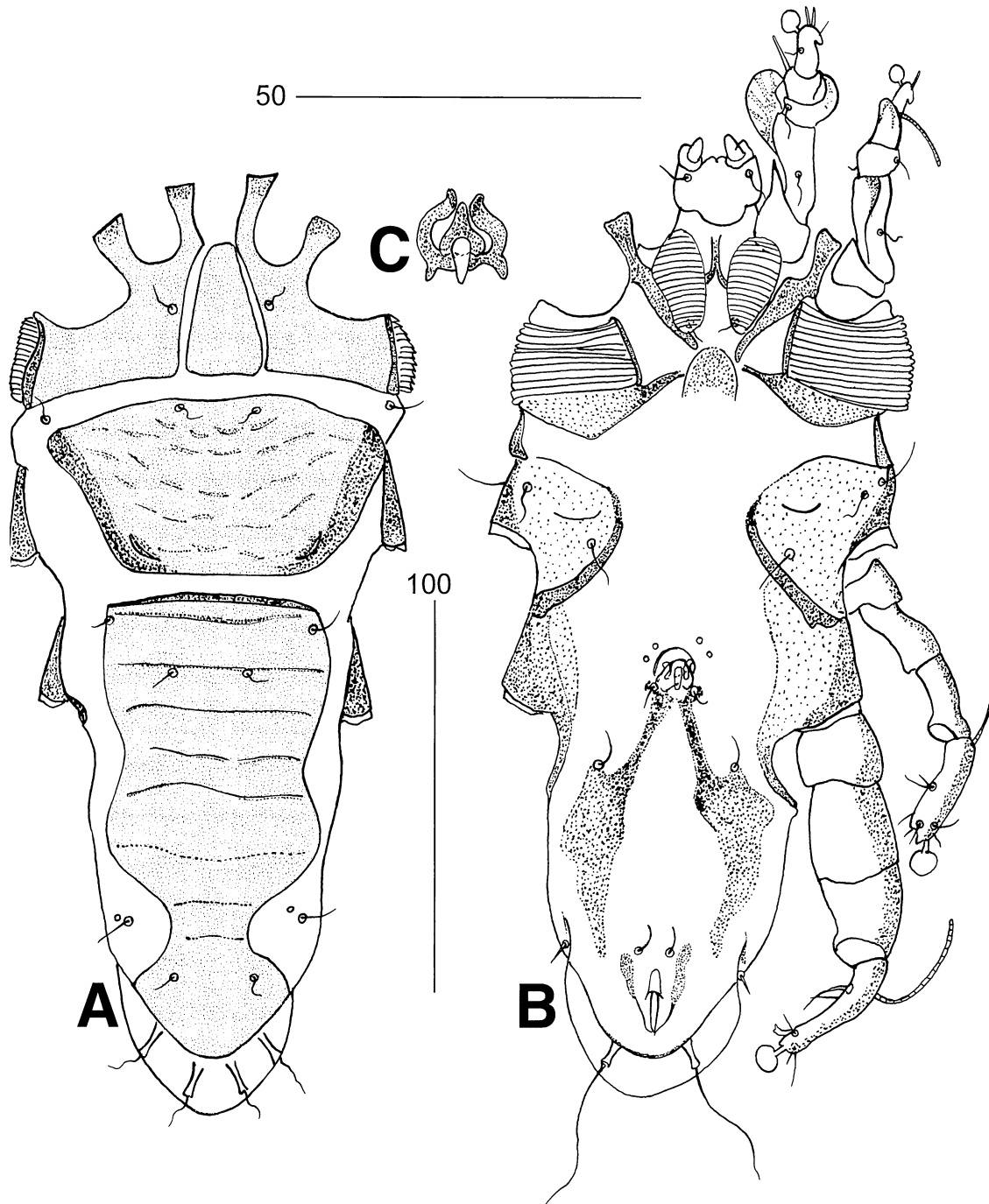


Fig. 27. (A-C). *Listrophoroides apomys* sp.n., male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. Scale bars 100 μm (A-B) and 50 μm (C).

anterior by about 2–10. Lobar membrane well developed, almost triangular in shape, with widely rounded posterior extremity, without median incision. *Legs*. Femur IV about 30 wide, twice as wide as femur III (15). Legs III and IV 100–105 (100) and 117–125 long (120), respectively. Tibiotarsi III and IV 33–35 (35) and 40–45 long (45), respectively. Solenidia φ III and IV 11–13 (13) and 35–37 long (35), respectively.

FEMALE (Fig. 28). Body 339–374 long, 120–135 wide in 10 paratypes. Gnathosoma about 33 long, 28 wide. *Dorsum*.

Postscapular shield 70–81 long, 110–119 wide, covered by 5–6 transverse rows of short lines. Lateral margins of this shield with strongly sclerotized bands. Hysteronotal shield 134–147 long, completely covered by 8–10 furrows. Width of this shield at level of setae *dl-dl* 57–66 and at level of setae *el-el* 62–77. Setae *dl* situated off or on shield. Distance *el-el* 33–37, 2–3 times longer than distance *el*-posterior margin of hysteronotal shield, 9–18. *Venter*. Striated membranes of coxae II wide, reaching lateral margins of body. Coxae III with short

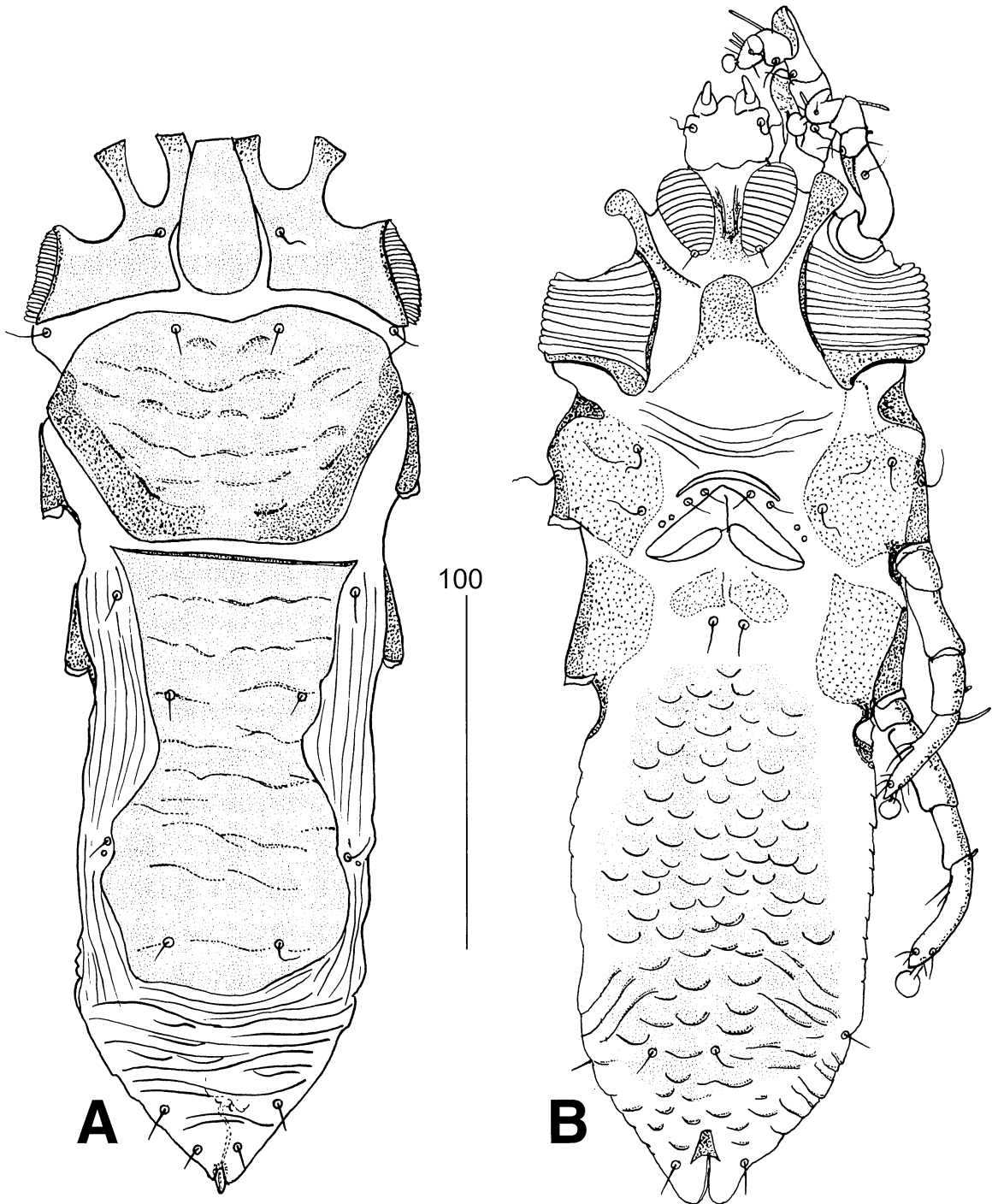


Fig. 28. (A–B). *Listrophoroides apomys* sp.n., female. A.—Dorsal view. B.—Ventral view.

transverse line. Opisthosoma without or with few lateral scales posterior to level of setae *h1*. Median part of opisthosoma with widely rounded scales extending from level of setae *4a* to level of setae *h3*, these scales more numerous posterior to level of setae *f2*. *Legs*. Legs III and IV 80–90 and 90–100 long, respectively. Solenidia ϕ III and IV 11–13 and 4–7 long, respectively.

ETYMOLOGY. The species name is derived from the generic name of the hosts and is a noun in apposition.

TYPE MATERIAL. Male holotype (BMOC 01-0920-031, 1) and 3 female paratypes (BMOC 01-0920-031, 2–4) ex *Apomys datae* (FMNH 169111), Luzon Isl., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Am-Iicao, 17°26'30"N, 121°04'15"E, 1800 m, 24 March 2001, coll. E.A. Rickart (EAR 4607); 3

male and 3 female paratypes (BMOC 01-0920-030, 1–6) ex *A. datae* (FMNH 169110), same data, coll. E.A. Rickart (EAR 4606); 3 male and 2 female paratypes (BMOC 01-0920-033, 1–5) ex *A. datae* (FMNH 169113), same data, 25 March 2001, coll. L.R. Heaney (LRH 6429); 4 female paratypes (BMOC 01-0920-032) ex *A. datae* (FMNH 169112), same data, coll. L.R. Heaney (LRH 6428); 4 male and 8 female paratypes (BMOC 01-0920-028, 1–12) ex *A. datae* (FMNH 169107), same data, 24 March 2001, coll. L.R. Heaney (LRH 6425).

OTHER MATERIAL EXAMINED: Two males and 14 females (BMOC 88-1730-006) ex *Apomys microdon* (USNM 458915), Luzon Isl., Camarines Sur Prov., Mt. Isarog, 4.5 km N, 20.5 km E Naga, 13°40'N, 123°21'E, 1125 m, 24 March 1988, coll. S.M. Goodman (SMG 2334); 4 males and 13 females (BMOC 04-0909-028) ex *A. microdon* (FMNH 178398), Luzon Isl., Quezon Prov., Mt. Banahaw, 14°03'58"N, 121°30'30"E, 3 May 2004, coll. L.R. Heaney (LRH 6985); 4 males and 4 females (BMOC 88-1730-004) ex *Apomys musculus* (USNM 458921), Luzon Isl., Camarines Sur Prov., Mt. Isarog, 4 km N, 21 km E Naga, 13°40'N, 123°22'E, 1350 m, 23 March 1988, coll. S.M. Goodman (SMG 2320); 4 males and 15 females (BMOC 88-1700-004) ex *A. musculus* (USNM 458923), same data, 18 March 1988, coll. L.R. Heaney (LRH 4100); 6 males and 14 females (BMOC 88-1700-009) ex *A. musculus* (USNM 458924), same data, 4 km N, 21.5 km E Naga, 1550, 23 April 1988, coll. L.R. Heaney (LRH 4155); 7 males and 14 females (BMOC 89-1111-002) ex *Apomys sp.n. C* (FMNH 135716), Sibuyan Isl., Romblon Prov., 4.5 km S, 4 km E Magdiwang: NW slope, Mt. Guitinguitin, 12°27'N, 122°33'E, 325 m, 7 May 1989, coll. S.M. Goodman (SMG 2956); 7 males and 13 females (BMOC 89-1111-004) ex *Apomys sp.n. C*. (FMNH 135715), same data, 9 May 1989, coll. S.M. Goodman (SMG 2974); 1 male and 7 females (BMOC 03-0611-001) ex *Apomys sp.n. B* (FMNH 145700), Sibuyan Isl., Romblon Prov., 5.25 km S, 3.5 km E Magdiwang, 12°27'N, 122°26'E, 725 m, 26 February 1992, coll. S.M. Goodman (SMG 5028).

SPECIMEN DEPOSITION. Holotype is deposited in NMP, paratypes or voucher specimens in FMNH, IRSNB, OSAL, UMMZ, USNM, and ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION: This species is a specific parasite of the Old Philippine endemics of the genus *Apomys*, *A. datae* (Meyer, 1899) (type host), *A. microdon* Hollister, 1913, *A. musculus* Miller, 1911, *Apomys sp.n. B*, and *Apomys sp.n. C* (Heaney *et al.*, 1998).

TAXONOMIC NOTES. The species differs from all known species of the subgenus, except for *L. (M.) heaneyi* sp.n., by the presence of distinct sclerotized bands bordering the lateral margins of the postscapular shield. Males of *L. (M.) apomys* sp.n. differ from all other species by the shape of the male lobar membrane. In males of this species, the lobar membrane is well developed, almost triangular in shape, without a median incision. In males of other species, this membrane has a median incision or concavity.

INTRASPECIFIC VARIABILITY. In males from *Apomys musculus*, a few scales are present on soft cuticle posterior to setae *e2*.

Listrophoroides (Marquesania) heaneyi New Species (Figs 29–30)

DIAGNOSIS. In both sexes, lateral margins of postscapular shield with distinct sclerotized bands. *Male*. Lobar membrane with widely rounded median concavity. Pair of pregenital sclerites present. Supporting sclerite of aedeagus with enlarged posterior ends.

MALE (Fig. 29). Body 293–304 long (295), 110–123 wide (110) in 10 paratypes. Length and width of gnathosoma subequal, 25. *Dorsum*. Postscapular shield 59–66 long (62), 100–106 wide (100), completely covered by 5–6 transverse rows of short lines. Lateral margins of this shield with strongly sclerotized bands. Hysteronotal shield 132–143 long (135), covered by transverse lines extending from anterior margin to level of setae *e2*. Lateral incisions of hysteronotal shield well developed, 24–35 long (33) and 18–22 wide (18), minimum distance between these incisions 24–33 (26). Setae *e2* situated off hysteronotal shield, soft cuticle posterior to these setae without scales. Setae *e1* situated on hysteronotal shield, distance *e1-e1* 22–24 (22). Setae *h3* 30–37 long (33). *Venter*. Coxae II wide, reaching lateral margins of body. Coxae III with short transverse line. Aedeagus short, length 5–6 (5). Pair of pregenital sclerites present. Supporting sclerite of aedeagus with fused anterior ends and enlarged posterior ends. Postgenital shield in form of inverted U, its projections 66–70 long (66). These projections reaching adanal shields or ending slightly anterior to them. *Legs*. Genu III with well developed process. Femur IV about 18 wide, 1.6 times wider than femur III (11). Legs III and IV 95–100 (100) and 117–125 long (122), respectively. Tibiotarsi III and IV 35–40 (35) and 40–45 long (44), respectively. Solenidia φ III and IV 10–13 (10) and 37–45 long (44), respectively.

FEMALE (Fig. 30). Body 333–363 long, 117–130 wide in 10 specimens. Gnathosoma about 30 long, 25 wide. *Dorsum*. Postscapular shield 73–77 long, 108–117 wide, covered by 5–6 transverse rows of short lines. Lateral margins of this shield with strongly sclerotized bands. Hysteronotal shield 139–145 long, completely covered by 8–10 furrows. Width of this shield at level of setae *d1-d1* 62–77 and at level of setae *e1-e1* 66–79. Setae *d1* situated off or on shield. Distance *e1-e1* 29–35, 2.3–2.6 times longer than distance *e1*-posterior margin of hysteronotal shield, 11–15. *Venter*. Striated membranes of coxae II wide, reaching lateral margins of body. Coxae III with short transverse line. Opisthosoma with or without few lateral scales posterior to level of setae *h1*. Median part of opisthosoma with widely rounded scales extending from level of setae *4a* to level of setae *h3*, these scales more numerous posterior to level of setae *f2*. *Legs*. Legs III and IV 86–92 and 90–100 long, respectively. Solenidia φ III and IV 9–11 and 4–5 long, respectively.

ETYMOLOGY. This species is dedicated to Dr. Lawrence Heaney of the Field Museum Natural History, in recognition of his contributions to the systematics, ecology and conservation of the Philippine mammal fauna.

TYPE MATERIAL. Male holotype (BMOC 93-1300-126, 1), 10 male and 15 female paratypes (BMOC 93-1300-126, 2–26) ex

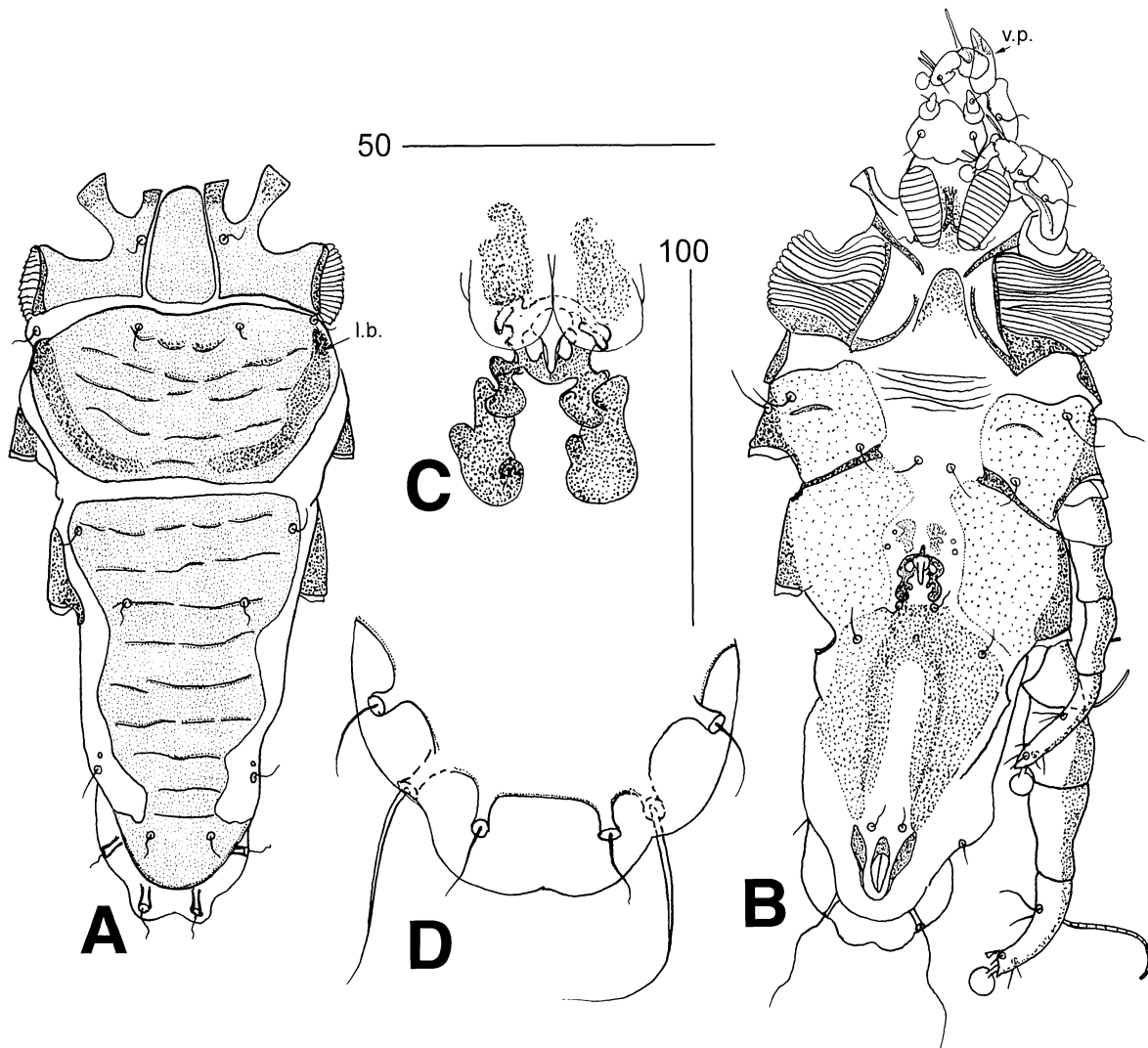


Fig. 29. (A–D). *Listrophoroides heaneyi* sp.n., male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. D.—Lobar membrane, dorsal view. Abbreviations: l.b.—lateral band of postscapular shield, v.p.—ventral process of femur I. Scale bars 100 μm (A–B) and 50 μm (C–D).

Apomys hylocetes (FMNH 147893), Mindanao Isl., Bukidnon Prov., Mt. Katanglad Range, 18.5 km S, 4 km E Camp Phillips, 8°09'30"N, 124°51'E, 2250 m, 4 April 1993, coll. L.R. Heaney (LRH 5238); 6 male and 6 female paratypes (BMOC 93-1300-113, 1–12) ex *A. hylocetes* (FMNH 147891), same data, coll. L.R. Heaney (LRH 5205).

OTHER MATERIAL EXAMINED. One male and 8 females (BMOC 93-1300-009, 1–9) ex *Apomys insignis* (FMNH 147911), Mindanao Isl., Bukidnon Prov., Mt. Katanglad Range, 16.5 km S, 4 km E, Camp Phillips, 8°10'30"N, 124°51'E, 1900 m, 12 March 1993, coll. E.A. Rickart (EAR 2497).

SPECIMEN DEPOSITION. Holotype is deposited in NMP, paratypes in FMNH, NMP, OSAL, UMMZ, and ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION: This species is a specific parasite of the Old Philippine endemics of the genus *Apomys*, *A. hylocetes* Mearns, 1905 (type host) and *A. insignis* Mearns, 1905.

TAXONOMIC NOTES. *Listrophoroides* (*M.*) *heaneyi* sp.n. differs from all other species of the subgenus, except for *L. (M.) apomys* sp.n., by the presence in both sexes of sclerotized bands bordering the lateral margins of the postscapular shield. Males of this species differ from all other species by the presence of a pair of pregenital sclerites, and by the hypertrophied posterior ends of the supporting sclerite of the aedeagus. This species is closest to *L. (M.) apomys* sp.n. and differs by the following characters. In *L. (M.) heaneyi*, pregenital sclerites are present, the posterior ends of the aedeagal-supporting sclerite are hypertrophied, and femur IV is about 1.6 times wider than femur III. In males of *L. (M.) apomys*, pregenital sclerites are absent, the posterior ends of the aedeagal-supporting sclerite are not hypertrophied, and femur IV is about 2 times wider than femur III. Females of these species cannot be unambiguously distinguished from each other. Females of *L. (M.) apomys* from the type host differ slightly from *L. (M.) heaneyi* by the shape of

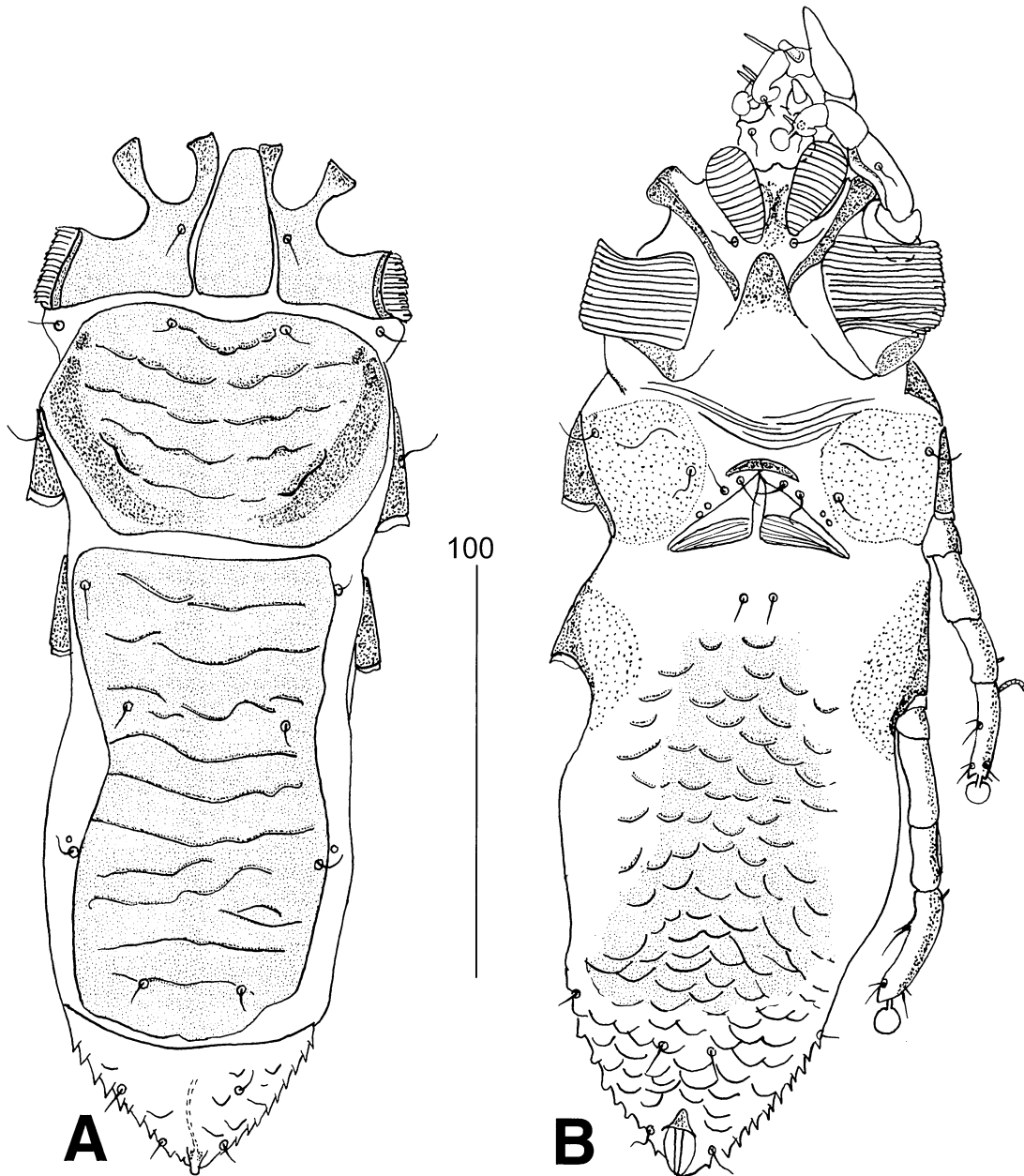


Fig. 30. (A-B). *Listrophoroides heaneyi* sp.n., female. A.—Dorsal view. B.—Ventral view.

the hysteronotal shield. In females of *L. (M.) apomys*, the width of the hysteronotal shield at the level of setae *e2-e2* is 1.3–1.5 times longer than the width of this shield at the level of setae *d1-d1*. In females of *L. (M.) heaneyi*, these distances are subequal.

***Listrophoroides (Marquesania) faini* New Species**
(Figs 31–32)

DIAGNOSIS. *Male*. Incisions of hysteronotal shield distinctly developed, 1–3 scales postero-lateral to setae *e2* present. *Female*. Postscapular shield with 6 rows of interrupted lines, hysteronotal

shield covered by distinct ornamentation in anterior half and indistinct ornamentation in posterior half, distances *e1-e1* and *e1*-posterior margin of hysteronotal shield subequal.

MALE (Fig. 31) Body 328–340 long (333), 130–140 wide (130) in 10 paratypes. Length and width of gnathosoma subequal, about 30. *Dorsum*. Postscapular shield 68–73 long (73), 110–135 wide (115), evenly sclerotized, with 6 interrupted transverse lines, anterior row represented by short curved lines in form of inverted U, 2 most posterior lines indistinct. Hysteronotal shield 143–150 long (150), with transverse lines extending from anterior margin to level of setae *e1*, these lines indistinct in posterior half of this shield. Incisions of hysteronotal shield

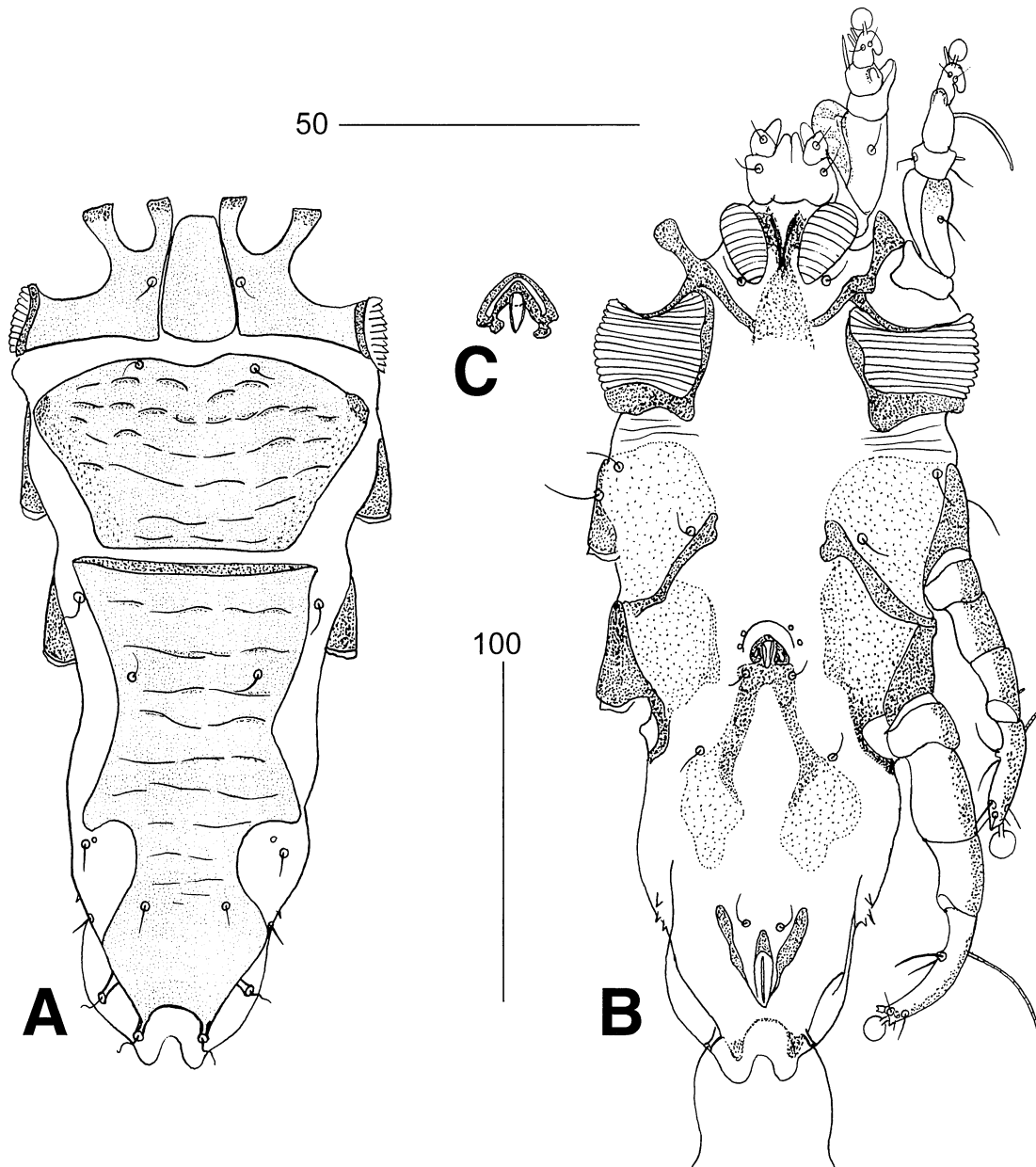


Fig. 31. (A–C). *Listrophoroides faini* sp.n., male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. Scale bars 100 μm (A–B) and 50 μm (C).

33–42 long (40) and 22–26 wide (25), minimum distance between these incisions 33–37 (33). Distance *e1-e1* 24–31 (29). Setae *e2* situated off hysteronotal shield, soft cuticle posterolateral to these setae with 1–3 scales. Setae *h3* 29–35 long (35). *Venter*. Striate membranes of coxae II wide, reaching lateral margins of body. Coxae III without transverse line. Aedeagus short, 4–5 long. Supporting sclerite of aedeagus with fused anterior ends. Postgenital shield in form of inverted V, its projections weakly sclerotized in posterior half, 55–66 long (60). Distance between posterior ends of projections of postgenital shield and adanal shields 20–30 (22). Lobar membrane with median incision. *Legs*. Femur IV 15–20, 1.3–1.5 times wider than femur III (11–12). Legs III and IV 95–100 (100) and

115–120 long (115), respectively. Tibiotarsi III and IV 33–40 (35) and 40–44 long (40), respectively. Solenidia φ of legs III and IV 9–11 (11) and 40–45 long (45), respectively.

FEMALE (Fig. 32). Body 375–395 long, 130–135 wide in 10 paratypes. Gnathosoma about 30 wide and 27 long. *Dorsum*. Postscapular shield 77–85 long, 115–120 wide, evenly sclerotized, completely covered by 6 interrupted transverse lines, anterior row represented by short curved lines in form of inverted U, 2 most posterior lines indistinct. Hysteronotal shield 150–160 long, covered by 9–10 transverse lines extending from anterior margin to level of setae *e1*. Width of this shield at level of setae *d1* 62–77 and at level of setae *e1* 65–80. Distances *e1-e1* and *e1*-posterior margin of hysteronotal shield subequal,

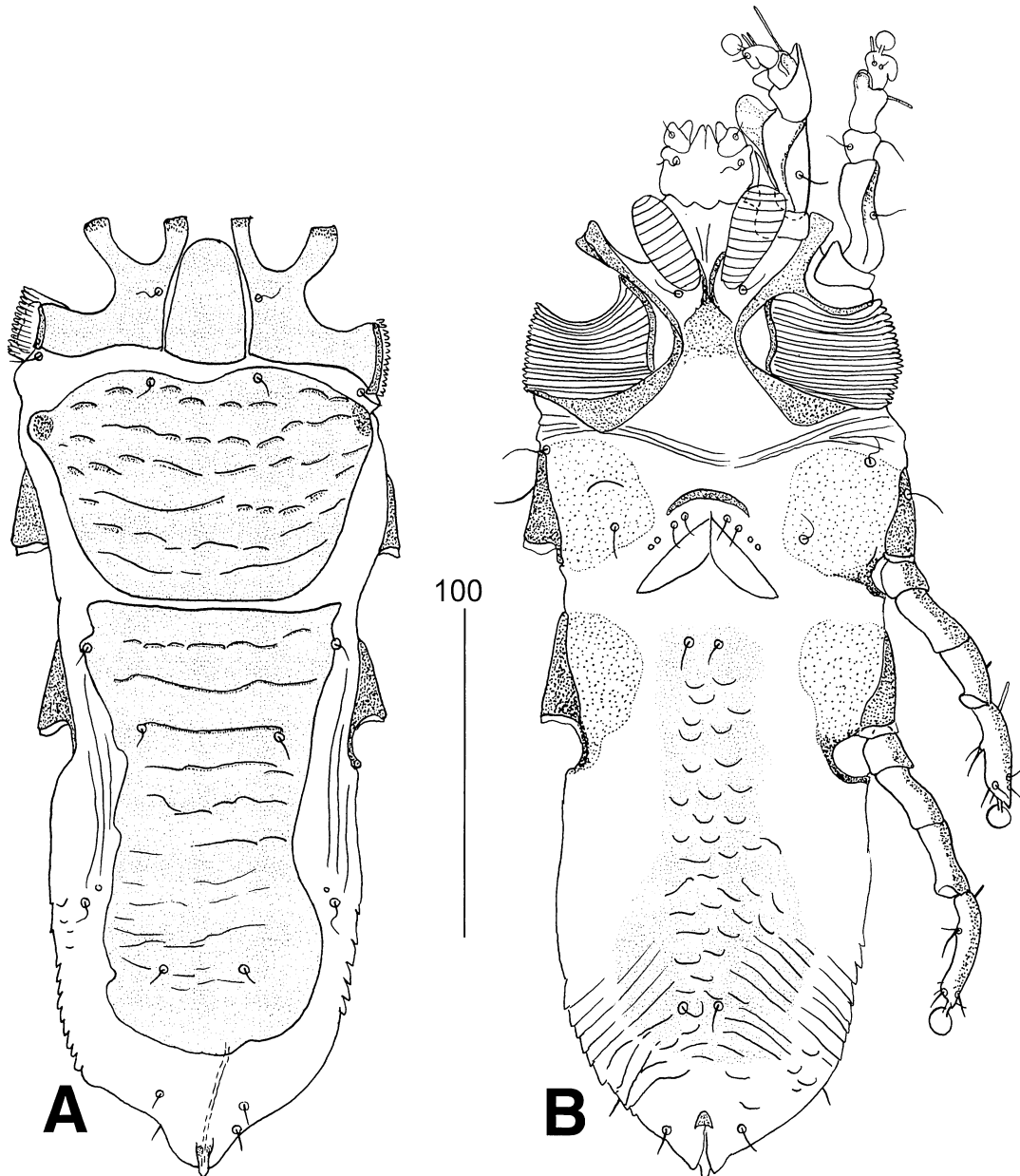


Fig. 32. (A–B). *Listrophoroides faini* sp.n., female. A.—Dorsal view. B.—Ventral view.

25–30 and 25–35, respectively. Setae *d2* situated on or off shield. *Venter*. Striated membranes of coxae II wide, reaching lateral margins of body. Coxae III with or without short transverse line. Opisthogaster with large sclerite. Lateral parts of opisthogaster covered by furrows in posterior third. Median part of opisthogaster with widely rounded scales extending from level of setae *4a* to level of setae *f2*. *Legs*. Legs III and IV subequal in length, 90–100. Solenidia φ of legs III and IV, 11–12 and 3–4 long, respectively.

ETYMOLOGY. This species is dedicated to our colleague, Prof. Alex Fain, of the Royal Institute of Natural Sciences, Brussels, in recognition of his pioneering and extensive contributions to the study of parasitic mites, including the Atopomelidae.

TYPE MATERIAL. Male holotype (BMOC 01-0920-021, 1), 6 male and 6 female paratypes (BMOC 01-0920-021, 2–13) ex *Apomys datae* (FMNH 169065), Luzon Isl., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Mapga, 17°28'30"N, 121°04'30"E, 1050 m, 15 March 2001, coll. E.A. Rickart (EAR 4553); 1 male and 5 female paratypes (BMOC 01-0920-017, 1–6) ex *A. datae* (FMNH 169056), same data, 14 March 2001, coll. E.A. Rickart (EAR 4539); 5 male and 15 female paratypes (BMOC 01-0920-012, 1–20) ex *A. datae* (FMNH 169047), same data, 13 March 2001, coll. L.R. Heaney (LRH 6315); 2 males and 6 female paratypes (BMOC 01-0920-019, 1–8) ex *A. datae* (FMNH 169062), same data, 15 March 2001, coll. L.R. Heaney (LRH 6349).

OTHER MATERIAL EXAMINED. 5 males and 9 females (BMOC 04-0909-036) ex *Apomys* sp.n. (FMNH 178456), Luzon Isl., Quezon Prov., Mt. Banahaw, Barangay Lalo, 14°03'58"N, 121°30'30"E, 1465 m, 2 May 2004, coll. R.A. Rickart (EAR 5210); 1 male and 5 females (BMOC 04-0909-037) ex *A. sp.n.* (FMNH 178459), same data, coll. E.A. Rickart (EAR 5213); 1 males and 6 females (BMOC 04-0909-038) ex *A. sp.n.* (FMNH 178461), same locality, 3 May 2004, coll. L.R. Heaney (LRH 6991); 1 female (BMOC 03-0611-003) ex *Carpomys phaeurus* (FMNH 62291), Ifagao Prov., Mt. Kapiligan, 16°50'45"N, 120°56'28"E, 2121 m, 2 May 1946, coll. H. Hoogstral et al; 1 female (BMOC 06-0201-001) ex *C. phaeurus*, (FMNH 175565), Luzon Is., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Mt Bali-it, 2150m., 17°25'41"N, 120°59'48"E, 28 February 2003, coll. L. R. Heaney (LRH 6866).

SPECIMEN DEPOSITION. Holotype is deposited in NMP, paratypes or voucher specimens in FMNH, IRSNB, NMP, OSAL, UMMZ, USNM, and ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION. This species is a parasite of the Old Philippine endemics of Luzon Island, *Apomys datae* (type host) and an undescribed, large-bodied species of *Apomys* recently collected in Quezon Prov. The single individuals recovered from two specimens of *Carpomys phaeurus* probably represent contamination.

TAXONOMIC NOTES. The new species appears most similar to *L. (M.) interpolatus* Fain, 1975, described from native murids in New Guinea. In both sexes of these species, the body is small and ornamentation of the dorsal shields is similar. *L. (M.) faini* sp.n. differs from this species by the following characters. In females of *L. (M.) faini*, the hysteronotal shield is covered by distinct lines in the anterior half and by indistinct lines in the posterior half, the distances *e1-e1* and *e1*-posterior margin of hysteronotal shield are subequal; in males, coxae III are without any transverse lines. In females of *L. (M.) interpolatus*, the hysteronotal shield is completely covered by distinct lines, the distance *e1-e1* is about 1.8–2.5 times longer than the distance between *e1* and posterior margin of the hysteronotal shield; in males, coxae III have a transverse line.

INTRASPECIFIC VARIABILITY. Most males of *L. (M.) faini* collected from *Apomys* sp.n. (Quezon Prov.) differ slightly from those found on the type host in having the projections of the postgenital shield fused to the adanal shields and by thicker femora IV.

Listrophoroides (Marquesania) limnomys New Species
(Figs 33–34)

DIAGNOSIS. In both sexes, postscapular shield more strongly sclerotized laterally than medially. *Male*. Opisthosomal scales absent posterior to setae *e2*, lobar membrane with indistinct median incision. *Female*. Hysteronotal shield covered by distinct transverse lines extending from anterior margin to level of setae *e2*.

MALE (Fig. 33) Body 310–340 long (340), 110–130 wide (130) in 10 paratypes. Gnathosoma about 45 long, 35 wide.

Dorsum. Postscapular shield 75–80 long (77), 115–125 (123), more strongly sclerotized laterally than medially, covered by 6 transverse rows of short lines, anterior row represented by curved U-shaped lines, other lines indistinct. Hysteronotal shield 140–150 long (145), covered by 6–7 distinct transverse lines extending from anterior margin to level of anterior margin of lateral incision, lines situated posterior to this level indistinct or absent. Incisions of hysteronotal shield 24–33 long (30) and 18–25 wide (20), minimum distance between these incisions 40–44 (40). Distance *e1-e1* 30–37 (33). Setae *e2* situated off hysteronotal shield, soft cuticle posterior to these setae without scales. Setae *h3* 30–35 long (31). *Venter*. Striate membranes of coxae II wide, reaching lateral margins of body. Coxae III with or without transverse line. Aedeagus short, length 4–5 (4). Supporting sclerite of aedeagus with free anterior ends. Postgenital shield in form of inverted U, its projections weakly sclerotized in posterior half, 65–77 long (75), fused to adanal shields in some specimens. Lobar membrane with weakly developed median incision. *Legs*. Femur IV about 18 long, 1.3 times wider than femur III (13). Legs III and IV 88–100 (90) and 100–115 long (115), respectively. Tibiotarsi III and IV 31–35 (35) and 35–37 (37), respectively. Solenidia φ of legs III and IV 13–15 (13) and 33–35 (35), respectively.

FEMALE (Fig. 34). Body 380–400 long, 125–135 wide in 10 paratypes. Gnathosoma about 45 long, 37 wide. *Dorsum*. Postscapular shield 80–85 long, 120–135 wide, more strongly sclerotized laterally than medially, covered by 6 rows of short transverse lines, anterior row represented by curved lines U-shaped lines, 2 most posterior lines indistinct. Hysteronotal shield 165–172 long, covered by 5–7 distinct transverse lines extending from anterior margin to level of setae *e2*, lines situated posterior to this level indistinct or absent. Width of this shield at level of setae *d1* 72–80 and at level of setae *e1* 80–85. Distance *e1-e1* 1.5–2 times longer than distance *e1*-posterior margin of hysteronotal shield, 45–55 and 25–35, respectively. Setae *d2* situated on or off shield. *Venter*. Striated membranes of coxae II wide, reaching lateral margins of body. Coxae III without transverse line. Opisthogaster with large sclerite. Opisthosoma covered by furrows laterally in posterior third. Median part of opisthogaster with broadly rounded scales extending from level of setae *4a* to level of setae *f2*. *Legs*. Legs III and IV subequal in length, 90–100. Solenidia φ of legs III and IV, 11–13 and 2–4 long, respectively.

ETYMOLOGY. The species name is derived from the generic name of the host and is a noun in apposition.

TYPE MATERIAL. Male holotype (BMOC 93-1300-068, 1), 44 male and 44 female paratypes (BMOC 93-1300-068, 2–88) ex *Limnomys bryophilus* (FMNH 147976), Mindanao Isl., Bukidnon Prov., Mt. Katanglad Range, 18.5 km S, 4 km E, Camp Phillips, 8°09'30"N, 124°51'E, 2250 m, 9 April 1993, coll. E.A. Rickart (EAR 2595); 25 male and 44 female paratypes (BMOC 93-1300-136, 1–69) ex *L. bryophilus* (FMNH 147978), same data, 6 April 1993, coll. R.L. Heaney (LRH 5256).

OTHER MATERIAL EXAMINED. Three males and 10 females (BMOC 93-1300-150, 1–13) ex *Tarsomys apoensis* (FMNH

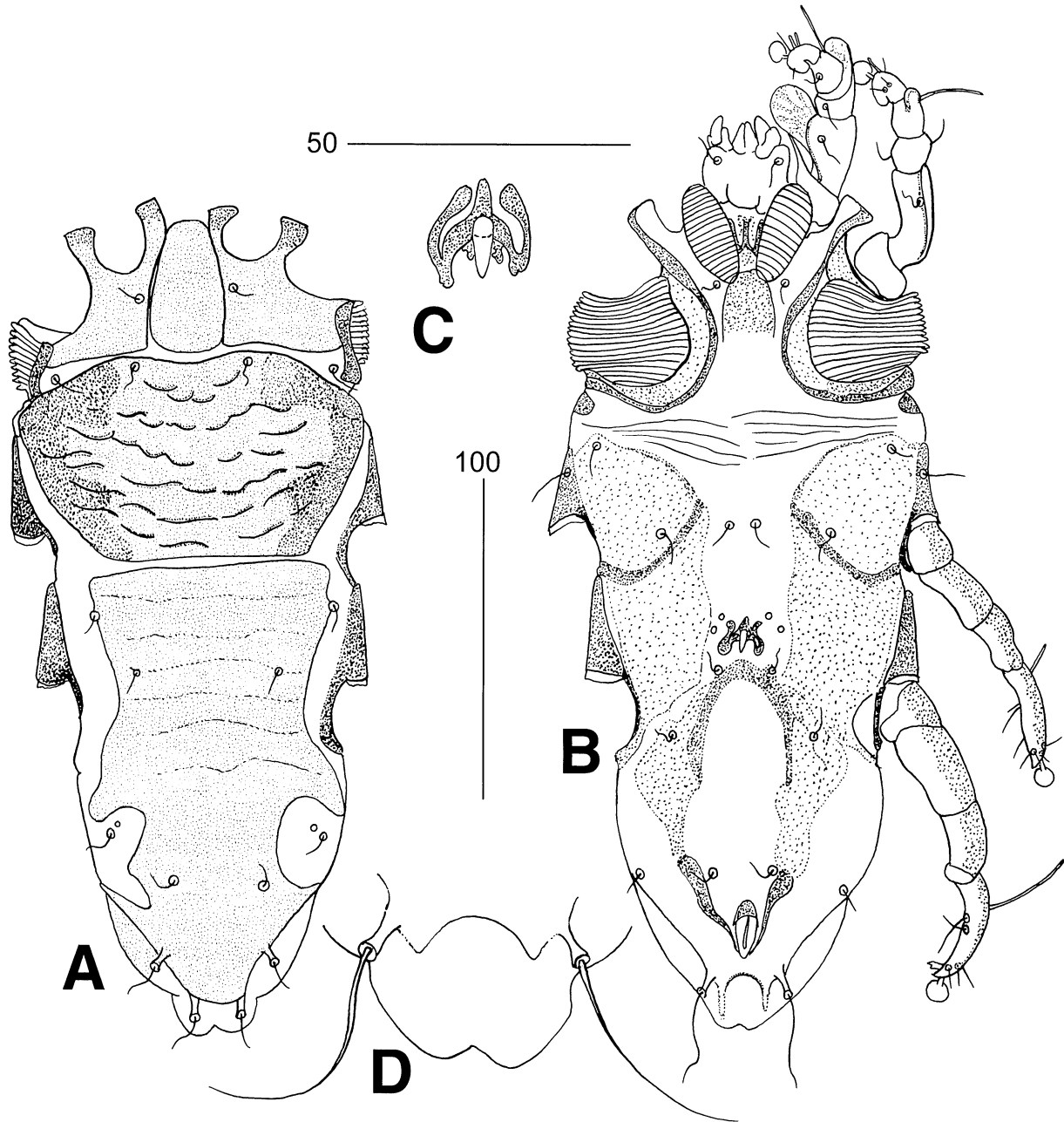


Fig. 33. (A–D). *Listrophoroides limnomys* sp.n., male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. D.—Lobar membrane, ventral view. Scale bars 100 μm (A–B) and 50 μm (C–D).

147969), Mindanao Isl., Bukidnon Prov., Mt. Katanglad Range, 18.5 km S, 4 km E, Camp Phillips, 8°09'30"N, 124°51'E, 2250 m, 8 April 1993, coll. R.L. Heaney (LRH 5290); 18 males and 28 females (BMOC 93-1300-049) ex *T. apoensis* (FMNH 2560), same data, 1 April 1993, coll. E.A. Rickart (EAR 2560); 7 males and 9 females (BMOC 93-1300-007) ex *T. apoensis* (FMNH 147954), same data, 1900 m, 12 March 1993, coll. E.A. Rickart (EAR 2495); 2 males and 3 females (BMOC 93-1300-038) ex *T. apoensis* (FMNH 147956), same data, 1900 m, 23 March 1993, coll. E.A. Rickart (EAR 2543);

SPECIMEN DEPOSITION. Holotype is deposited in NMP, paratypes in FMNH, IRSNB, OSAL, UMMZ, USNM, and ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION. This species is a parasite of the New Philippine endemics of the genera *Limnomys* and *Tarsomys*, *L. bryophilus* Rickart, Heaney and Tabaranza, 2003 and *T. apoensis* Mearns, 1905.

TAXONOMIC NOTES. The new species is closest to *L. (M.) faini* sp.n. and *L. (M.) interpolatus*. It differs from these two species in both sexes by the presence of strongly sclerotized lateral areas of the postscapular shield. In males of *L. (M.)*

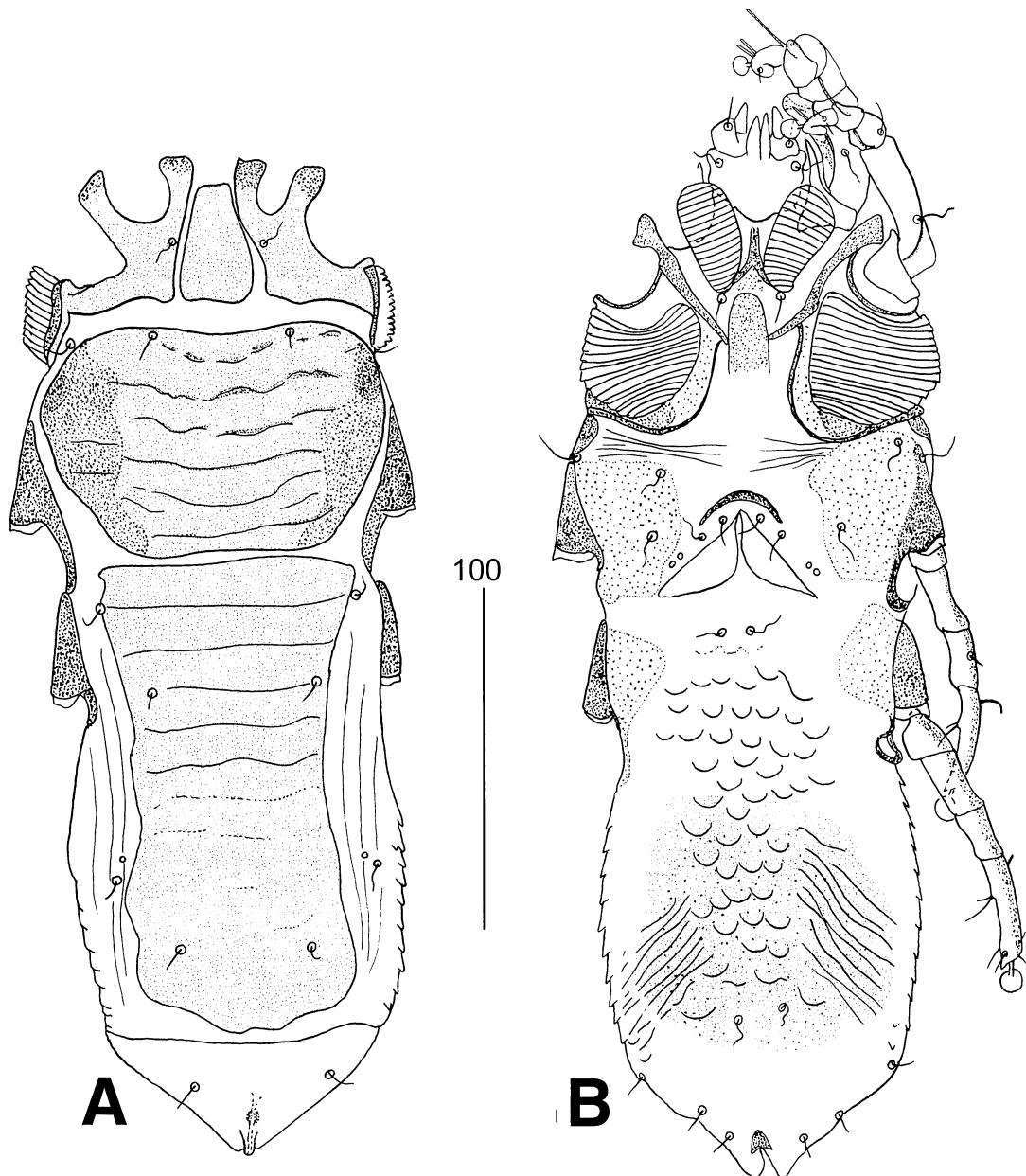


Fig. 34. (A-B). *Listrophoroides limnomys* sp.n., female. A.—Dorsal view. B.—Ventral view.

limnomys sp.n., the median incision of the lobar membrane is weakly developed, the supporting sclerite of the aedeagus has free anterior ends; in females, the distance $e1-e1$ is 1.5–2 times longer than the distance $e1$ -posterior margin of the hysteronotal shield, the hysteronotal shield is distinctly ornamented from the anterior margin to the level of setae $e2$, the lines posterior to this level are absent or indistinct. In both sexes of *L. (M.) faini* sp.n and *L. (M.) interpolatus*, the sclerotization of the postscapular shield is even; in males, the median incision of the lobar membrane is well developed, and in males of *L. (M.) interpolatus*, the supporting sclerite of the aedeagus has fused anterior ends; in females, the hysteronotal shield is almost completely covered by the distinct trans-

verse lines, and in females of *L. (M.) faini* sp.n., the distances $e1-e1$ and $e1$ -posterior margin of the hysteronotal shield are subequal.

Listrophoroides (Marquesania) bullimus New Species
(Fig. 35)

DIAGNOSIS. In both sexes, postscapular shield without ornamentation or covered by indistinct transverse lines. Striated membranes of coxae II reaching lateral margins of body only in anterior half. Tarsus I with anterior projection. *Male*. Hysteronotal shield without ornamentation or with indistinct lines in anterior part. Scales posterior to setae $e2$ absent. Lobar mem-

brane with indistinctly developed median incision. *Female*. Setae *ps3* long, subequal in length to *cp*.

MALE (Fig. 35A) Body 380–400 long (385), 150–165 wide (160) in 10 paratypes. Length and width of gnathosoma subequal, about 45. *Dorsum*. Postscapular shield 75–90 long (80), 140–150 wide (145), evenly sclerotized, without ornamentation or with indistinct transverse lines. Hysteronotal shield 170–180 long (175), without ornamentation or with indistinct transverse lines. Incisions of hysteronotal shield well developed, 55–60 long (60) and 25–35 wide (35), minimum distance between these incisions 50–55 (50), subequal to distance

e1-e1. Setae *e2* situated off hysteronotal shield, soft cuticle posterior to these setae without scales. Setae *h3* 85–100 long (85), 2–3 times longer than *cp*. *Venter*. Striated membranes of coxae II reaching lateral margin of body only in their anterior half. Coxae III without transverse line. Aedeagus short, length 5–7 (7). Anterior ends of aedeagal-supporting sclerite fused to each other. Postgenital shield in form of inverted U, its projections 55–77 long (75). Distance between posterior ends of projections of postgenital shield and adanal shields 25–33 (30). Lobar membrane with indistinct median incision, about 5 long. *Legs*. Tarsus I with well developed apical protrusion. Femur IV

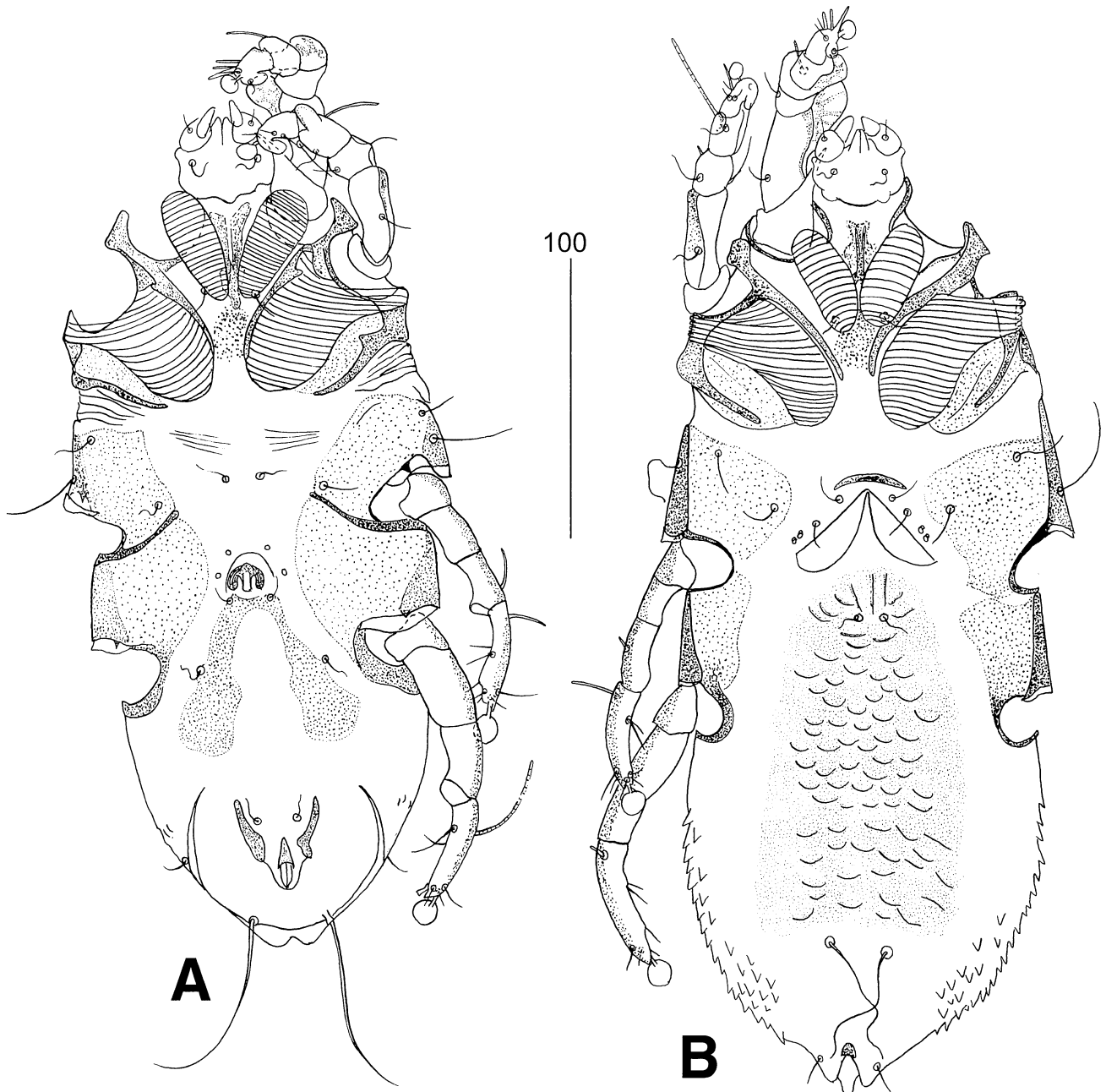


Fig. 35. (A–B). *Listrophoroides bullimus* sp.n. A.—Male, ventral view B.—Female, ventral view.

about 20 wide, 1.5 times wider than femur III (13). Legs III and IV 110–120 (115) and 135–145 long (135), respectively. Tibiotarsi III and IV 45–50 (45) and 45–55 (55), respectively. Solenidia φ of legs III and IV 20–22 (22) and 45–55 (50), respectively.

FEMALE (Fig. 35B). Body 440–450 long, 165–175 wide in 10 paratypes. Length and width of gnathosoma subequal, about 50. *Dorsum*. Postscapular shield 90–97 long, 155–160 wide, evenly sclerotized, without ornamentation or with indistinct transverse lines. Hysteronotal shield 185–195 long, completely covered by 13–15 transverse rows of distinctly developed scales and folds. Width of this shield at level of setae *d1* 75–85 and at level of setae *e1* 60–75. Distance *e1-e1* about 1.5–1.6 times longer than distance *e1*-posterior margin of hysteronotal shield, 45–50 and 25–35, respectively. Setae *d2* situated off shield. *Venter*. Striated membranes of coxae II reaching lateral margin of body only in anterior half. Coxae III and IV without transverse line. Opisthosoma covered laterally by tubercles in posterior half. Median part of opisthosoma with distinct ornamentation. Setae *ps3* 33–45 long, subequal in length to *cp*. *Legs*. Tarsus I with well developed apical protrusion. Legs III and IV 115–120 and 125–130 long, respectively. Solenidia φ of legs III and IV, 15–22 and 4–7 long, respectively.

ETYMOLOGY. The species name is derived from the generic name of the host and is a noun in apposition.

TYPE MATERIAL. Male holotype (BMOC 95-1214-018, 1), 8 male and 10 female paratypes (BMOC 95-1214-018, 2–19) ex *Bullimus gamay* (FMNH 154878), Camiguin Isl., Mt. Timpoong, 2 km N, 6.5 km W Mahinog, 9°11'N, 124°43'E, 18 March 1995, coll. L.R. Heaney (LRH 5358); 6 male and 14 female paratypes (BMOC 95-1214-017, 1–20) ex *B. gamay* (FMNH 154877), same data, coll. L.R. Heaney (LRH 5357); 9 male and 15 female paratypes (BMOC 95-1214-021) ex *B. gamay* (FMNH 154881), same data, 19 March 1995, coll. L.R. Heaney (LRH 5365).

SPECIMEN DEPOSITION. Holotype is deposited in NMP, paratypes in FMNH, IRSNB, OSAL, UMMZ, and ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION. This species is a specific parasite of the New Philippine endemic, *Bullimus gamay* Rickart, Heaney and Tabaranza, 2002.

TAXONOMIC NOTES. This species along with *L. (M.) luzonicus* sp.n., and *L. (M.) corpuzrarosae* sp.n. form a complex of closely related species. The most notable differential character of the complex is the presence in its representatives of a well developed apical protrusion on tarsus I. These three species possess the following combination of characters. In both sexes, the postscapular shield is without ornamentation or with indistinct lines; in males, the hysteronotal shield is without ornamentation or with indistinct lines in the anterior part, the scales are absent posterior to setae *e2*, setae *h3* are 75–90 long, the anterior ends of an aedeagal-supporting sclerite are fused to each other; in females, the hysteronotal shield is completely covered by a scale-like pattern and folds, the distance *e1-e1* is about 1.5–2 times longer than the distance *e1*-posterior margin of the

hysteronotal shield; coxae III are without transverse lines. Among other species of the subgenus, the species of this complex are similar to *L. (M.) dominator* Fain 1976, from murids from Sulawesi and *L. (M.) lativentris* Fain, 1981, from *Sundamys muelleri* (Jentink, 1879) from west Malaysia and south-east Borneo. The mites from *Bullimus* spp. differ from them by the distinct ornamentation of the hysteronotal shield in females, and also differ from *L. dominator* in both sexes by the strongly developed expansion of genu I and the more elongated idiosoma.

Listrophoroides (Marquesania) luzonicus New Species (Figs 36–37)

DIAGNOSIS. In both sexes postscapular shield without ornamentation or covered by indistinct transverse lines. Tarsus I with apical protrusion. *Male*. Hysteronotal shield without ornamentation or with indistinct lines in anterior part. Scales posterior to setae *e2* absent, lobar membrane with indistinct median incision.

MALE (Fig. 36) Body 357–363 long (345), 140–145 wide (140) in 5 paratypes. Gnathosoma about 45 long, 37 wide. *Dorsum*. Postscapular shield 75–80 long (75), 130–140 wide (135), evenly sclerotized, without ornamentation or with indistinct transverse lines. Hysteronotal shield 155–175 long (155), without ornamentation or with indistinct transverse lines. Incisions of hysteronotal shield well developed, 55–57 long (55) and 25–35 wide (30), minimum distance between these incisions 45–48 (45). Distance *e1-e1* 40–45 (45). Setae *e2* situated off hysteronotal shield, soft cuticle posterior to these setae without scales. Setae *h3* 75–90 long (80), 2–3 times longer than *cp*. *Venter*. Striate membranes of coxae II wide, reaching lateral margins of body. Coxae III without transverse line. Aedeagus short, length 4–5 (4). Anterior ends of aedeagal-supporting sclerite fused to each other. Postgenital shield in form of inverted U, its projections 60–65 long (62). Distance between posterior ends of projections of postgenital shield and adanal shields 15–30 (18). Lobar membrane with indistinct median incision. *Legs*. Tarsus I with well developed apical protrusion. Femur IV about 18 wide, 1.1–1.2 times wider than femur III (15–16). Legs III and IV 100–110 (105) and 120–125 long (125), respectively. Tibiotarsi III and IV 33–37 (35) and 45–50 (45), respectively. Solenidia φ of legs III and IV 20–22 (22) and 44–48 (45), respectively.

FEMALE (Fig. 37). Body 380–410 long, 145–165 wide in 10 paratypes. Length and width of gnathosoma subequal, about 40. *Dorsum*. Postscapular shield 80–90 long, 140–150 wide, evenly sclerotized, without ornamentation or with indistinct transverse lines. Hysteronotal shield 158–175 long, completely covered by 13–15 transverse rows of distinctly developed scales and folds. Width of this shield at level of setae *d1* 65–75 and at level of setae *e1* 55–70. Distance *e1-e1* about 1.5–2 times longer than distance *e1*-posterior margin of hysteronotal shield, 42–50 and 22–30, respectively. Setae *d2* situated on or off shield. *Venter*. Striated membranes of coxae II wide, reaching lateral margins of body. Coxae III without transverse line. Opistho-

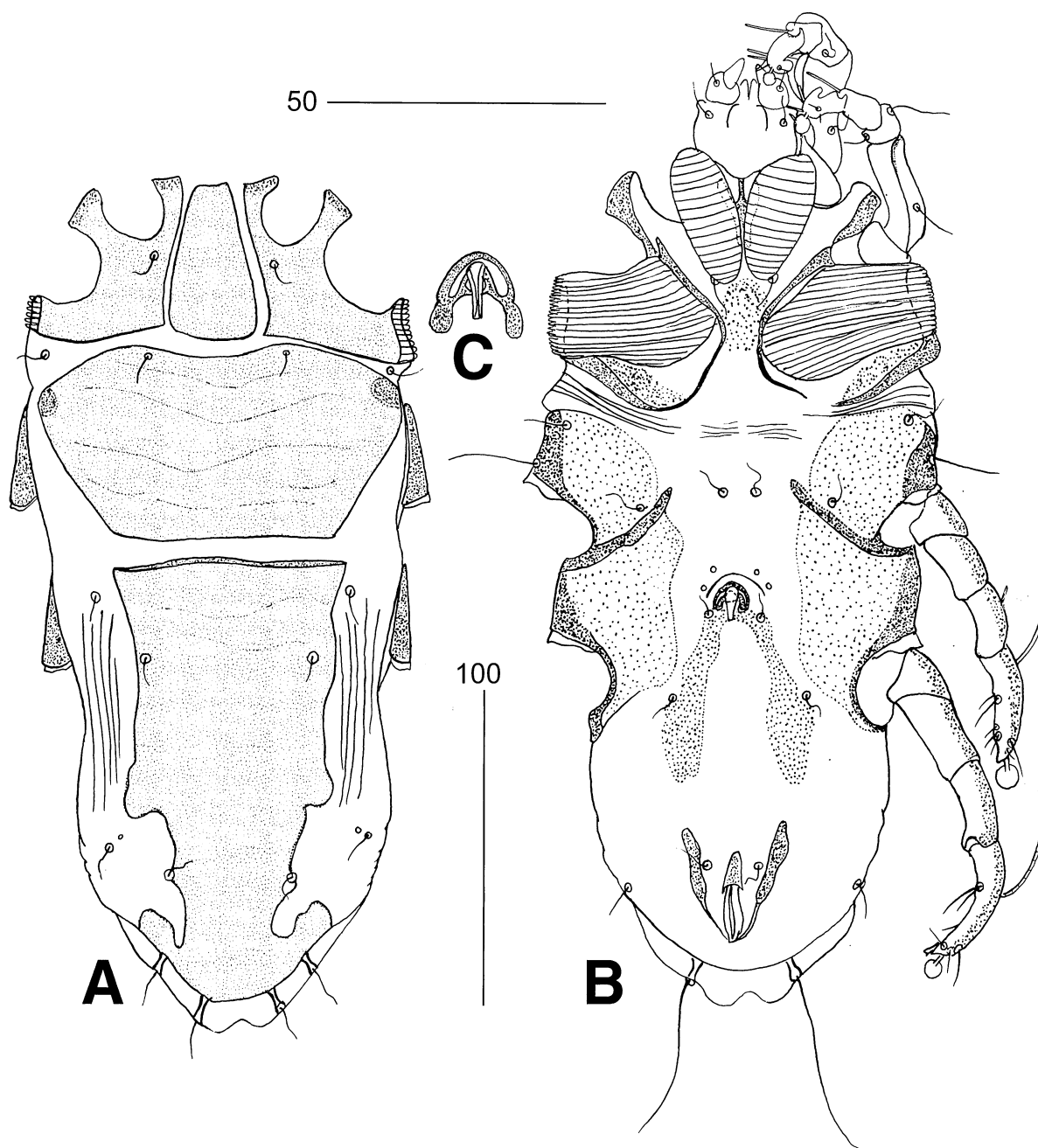


Fig. 36. (A–C). *Listrophoroides luzonicus* sp.n., male. A.—Dorsal view. B.—Ventral view. C.—Aedeagus. Scale bars 100 μm (A, B) and 50 μm (C).

soma covered laterally by tubercles in posterior half. Median part of opisthogaster with indistinct ornamentation. Setae *ps*3 15–20 long, about 2 times shorter than *cp*. Legs. Tarsus I with well developed apical protrusion. Legs III and IV subequal in length, 100–120. Solenidia φ of legs III and IV, 18–22 and 2–3 long, respectively.

ETYMOLOGY. The species name is derived from the species name of the type host and is a noun in apposition.

TYPE MATERIAL. Male holotype (BMOC 01-0920-041, 1), 3 male and 9 female paratypes (BMOC 01-0920-041, 2–16) ex

Bullimus luzonicus (FMNH 169129), Luzon Isl., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Am-licao, 17°26'30"N, 121°04'15"E, 1800 m, 23 March 2001, coll. L.R. Heaney (LRH 6414); 2 male and 2 female paratypes (BMOC 01-0920-040, 1–4) ex *B. luzonicus* (FMNH 169128), same data, coll. L.R. Heaney (LRH 6413); 1 male and 2 female paratypes (BMOC 04-0909-006, 1–3) ex *B. luzonicus* (FMNH 176582), Luzon Isl., Cagayan Prov., Baggao Munic., Brgy. Sta. Margarita, Sitio Matulang, Mt. Twin Peaks, 17°36'48"N, 121° 56'23"E, 300 m, 7 May 2003, coll. M.R. Duya (# 153); 8 male and 12 female

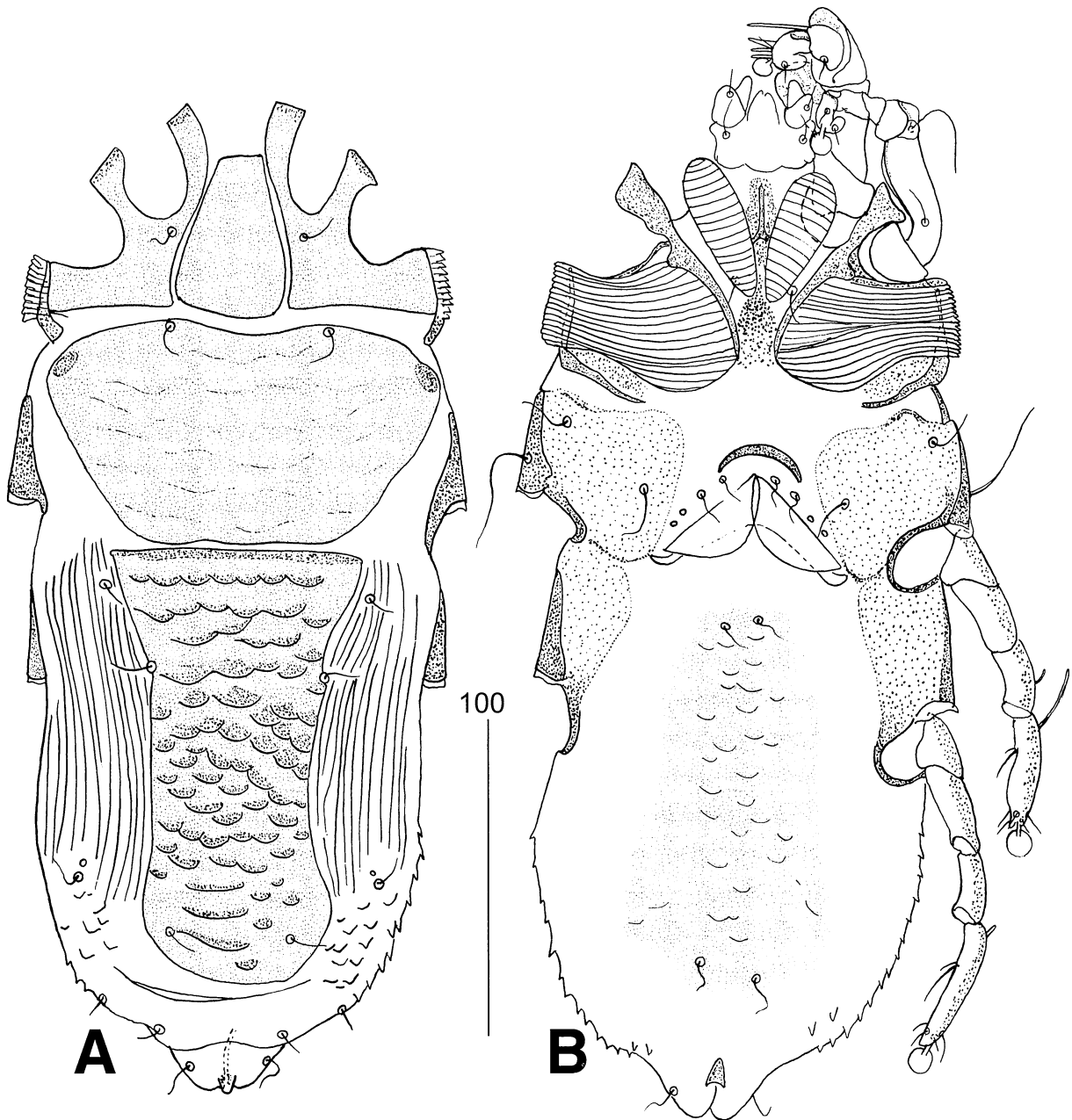


Fig. 37. (A–C). *Listrophoroides luzonicus* sp.n., female. A.—Dorsal view. B.—Ventral view.

paratypes (BMOC 04-0909-007, 1–20) ex *B. luzonicus* (FMNH 176583), Luzon Isl., Cagayan Prov., Baggao Munic., Brgy. Sta. Margarita Botanical Garden, 17°56'26"N, 122°01'E, 2 June 2003, coll. M.R. Duya (# 057); 2 male and 4 female paratypes (BMOC 04-0909-001, 1–6) ex *B. luzonicus* (FMNH 176577), Luzon Isl., Cagayan Prov., Penablanca Munic., Brgy. Mangga, Sitio Lowak, 17° 36'48"N, 121°56'23"E, 1100 m, 14 November 2002, coll. M.G. deGuia (MGDG 1407); 3 male and 12 female paratypes (BMOC 04-0909-002, 1–16) ex *B. luzonicus* (FMNH 176578), Luzon Isl., Quirini Prov., Nagtipunan Munic., Brgy., Disimungal, Sitio Km 18, Mt. Lataan, 17°36'48"N, 121° 56'23"E, 10 March 2003, coll. M.G. deGula (MGDG 1585); 4

male and 4 female paratypes (BMOC 04-0909-003, 1–8) ex *B. luzonicus* (FMNH 176579), same locality, 8 March 2003, coll. M.G. deGula (MGDG 1596); 5 male and 4 female paratypes (BMOC 04-0909-009, 1–9) ex *B. luzonicus* (FMNH 17685), Luzon Isl., Quezon Prov., General Nakar Munic., Brgy. Minahan Norte, Sitio Pangamitan, Mt. Binuang, 14°46'30"N, 121°33'30"E, 500 m, 27 June 2003, coll. M.R. Duya; 5 male and 6 female paratypes (BMOC 04-0909-011) ex *B. luzonicus* (FMNH 176597), same data, 11 August 2003, coll. M.R. Duya (# 2129).

SPECIMEN DEPOSITION. Holotype is deposited in NMP, paratypes in FMNH, IRSNB, NMP, OSAL, UMMZ, and ZISP.

HOST ASSOCIATIONS AND DISTRIBUTION. This species is a monoxenous parasite of the New Philippine endemic *Bullimus luzonicus* (Thomas, 1895).

TAXONOMIC NOTES. The new species is very similar to *L. (M.) bullimus* sp.n. (see taxonomic notes under that species) and differs by the following characters. In both sexes of *L. (M.) luzonicus* sp.n., the striated membranes of coxae II are wide, reaching the lateral margins of the body; in females, setae *ps3* are short, 2 times shorter than *cp*, the opisthosoma is covered ventrally by indistinct ornamentation. In both sexes of *L. (M.) bullimus* sp.n., the striated membranes of coxae II reach the lateral margins of the body only in their anterior half; in females, setae *ps3* are short, subequal in length to *cp*; the opisthosoma is distinctly ornamented ventrally.

Listrophoroides (Marquesania) corpuzarrosae New Species
(Fig. 38)

DIAGNOSIS. In both sexes, postscapular shield without ornamentation or with indistinct transverse lines. Striated membranes of coxae II reaching lateral margin of body only in their

anterior half. Tarsus I with anterior projection. *Male*. Hysteronotal shield without ornamentation or with indistinct lines in anterior part. Scales posterior to setae *e2* absent. *Female*. Setae *ps3* long, subequal in length to *cp*. Coxae IV with a fold.

MALE (Fig. 38A) Body 385–415 long (410), 164–180 wide (180) in 4 paratypes. Length and width of gnathosoma subequal, about 55. *Dorsum*. Postscapular shield 80–90 long (80), 140–155 wide (155), evenly sclerotized, without ornamentation or with indistinct transverse lines. Hysteronotal shield 160–185 long (165), without ornamentation or with indistinct transverse lines. Incisions of hysteronotal shield well developed, 60–65 (65) and 30–40 wide (40), minimum distance between these incisions 33–37 (33). Distance *e1-e1* 33–35 (33). Setae *e2* situated off hysteronotal shield, soft cuticle posterior to these setae without scales. Setae *h3* 65–90 long (70), 2–3 times longer than *cp*. *Venter*. Striated membranes of coxae II reaching lateral margin of body only in their anterior half. Coxae III without transverse line. Aedeagus short, length 8–9 (8). Anterior ends of aedeagal-supporting sclerite fused to each other. Postgenital shield in form of inverted U, its projections 95–105 long (100). Posterior ends of these projections extend

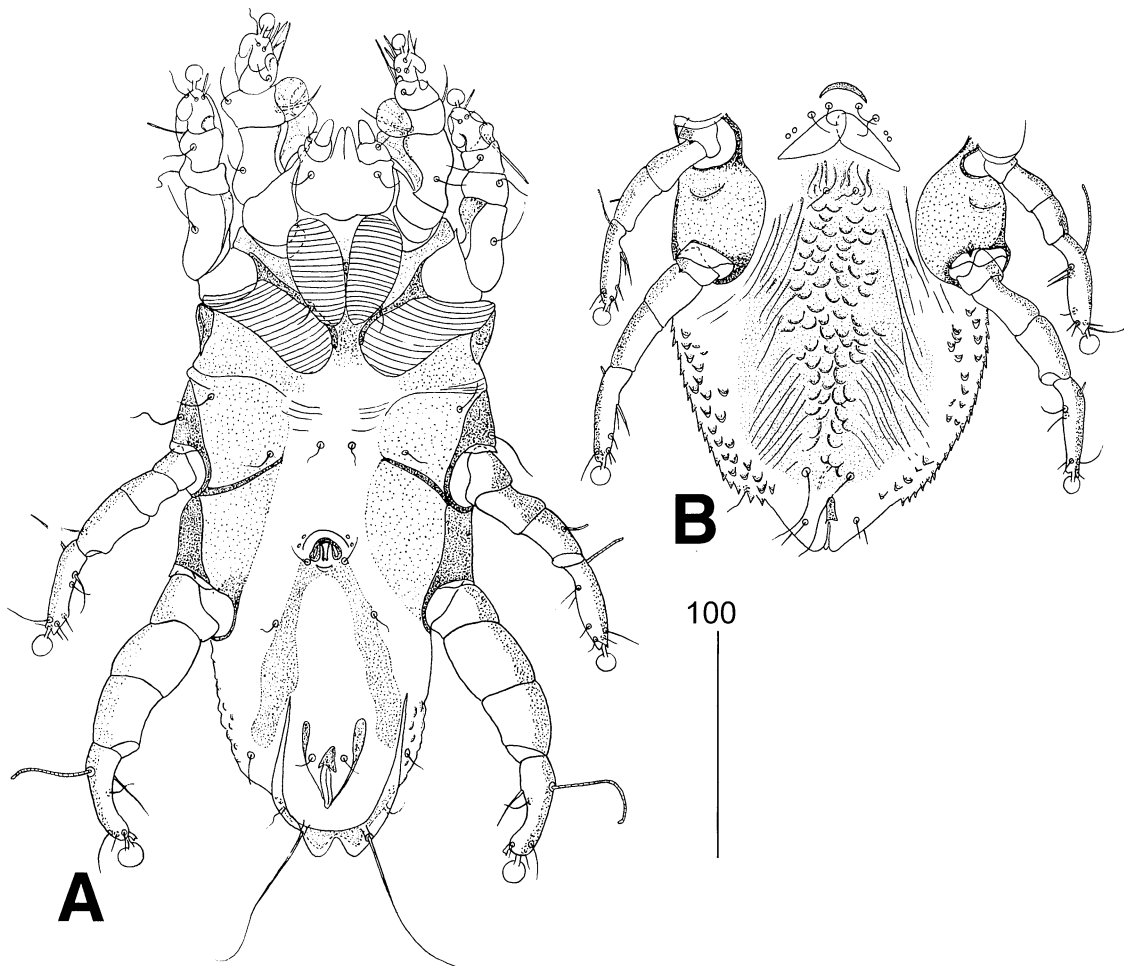


Fig. 38. (A–B). *Listrophoroides corpuzarrosae* sp.n. A.—Male, dorsal view. B.—Female opisthosoma, ventral view.

to level of setae *ps3*, close to adanal shields. Median incision of lobar membrane 22–25 long. *Legs*. Tarsus I with well developed apical protrusion. Femur IV 30–37 wide, 1.8–1.9 times wider than femur III (19–20). Legs III and IV 120–130 (130) and 155–165 long (165), respectively. Tibiotarsi III and IV 45–50 (48) and 50–55 (55), respectively. Solenidia φ of legs III and IV 22–25 (25) and 50–55 (55), respectively.

FEMALE (Fig. 38B). Body 430–435 long, 170–175 wide in 4 paratypes. Length and width of gnathosoma subequal, about 55. *Dorsum*. Postscapular shield 80–85 long, 150–155 wide, evenly sclerotized, without ornamentation or with indistinct transverse lines. Hysteronotal shield 175–180 long, completely covered by 13–15 transverse rows of distinctly developed scales and folds. Width of this shield at level of setae *d1* 65–70 and at level of setae *e1* 55–65. Distance *e1-e1* about 1.5–1.7 times longer than distance *e1*-posterior margin of hysteronotal shield, 42–45 and 25–30, respectively. Setae *d2* situated on or off shield. *Venter*. Striated membranes of coxae II reaching lateral margin of body only in their anterior half. Coxae III without transverse line. Coxae IV with distinct transverse fold. Opisthogaster with distinct sclerite. Opisthogaster covered laterally by tubercles in posterior half. Median part of opisthogaster with indistinct, scale-like ornamentation. Setae *ps3* 33–37 long, subequal in length to *cp* or slightly longer. *Legs*. Tarsus I with well developed apical protrusion. Legs III and IV 110–120 and 140–145 long respectively. Solenidia φ of legs III and IV, 20–25 and 5–7 long, respectively.

ETYMOLOGY. The species name is dedicated to the Philippine acarologist, Dr. Leonila A. Corpuz-Raros (University of the Philippines, Laguna) and is a noun in the genitive case.

TYPE MATERIAL. Male holotype (HK 87-0312-003, 1), 4 male and 4 female paratypes (HK 87-0312-003, 2–9) ex *Bullimus bagobus* (USNM 458789), Leyte Isl., Leyte Prov., 10.2 km N, 2.2 km E Baybay, 10°46'N, 124°49'E, 320 m, 12 March 1987, coll. E.A. Rickart (EAR 1334).

SPECIMEN DEPOSITION. Holotype is deposited in USNM, paratypes in NMP, UMMZ.

HOST ASSOCIATIONS AND DISTRIBUTION. This species is probably a monoxenous parasite of the New Philippine endemic *Bullimus bagobus* Mearns, 1905.

TAXONOMIC NOTES. The new species is very similar to *L. (M.) luzonicus* sp.n. and *L. (M.) bullimus* sp.n. (see taxonomic notes under that species). It differs from these species by the following characters. In males of *L. (M.) corpuzrarosae* sp.n., the posterior ends of the postgenital sclerite extend to the level of setae *ps3*, the lobar membrane has a distinct median incision, femur IV is 1.8–1.9 times wider than femur III; in females, coxae IV bear a distinct fold. In males of *L. (M.) bullimus* sp.n. and *L. (M.) luzonicus* sp.n., the posterior ends of the postgenital sclerite do not reach the level of setae *ps3*, the lobar membrane has a short median incision, femur IV is 1.2–1.5 times wider than femur III; in females, coxae IV are without any folds or lines. In addition, the new species differs from *L. (M.) luzonicus* sp.n. by the following characters. In both sexes of *L. (M.) corpuzrarosae* sp.n., the striated membranes of coxae II

reach the lateral margin of the body only in their anterior half; in females, setae *ps3* are subequal in length to *cp*. In both sexes of *L. (M.) luzonicus* sp.n., the striated membranes of coxae II are wide, reaching the lateral margin of the body as in their anterior as well the posterior half; in females, setae *ps3* are 2 times shorter than *cp*.

PHYLOGENETIC ANALYSIS

Bochkov & OConnor (2005) developed a phylogenetic hypothesis for a hypothetically monophyletic lineage comprising the subgenera *Marquesania*, *Paklistrophoroides* Fain and Hyland, 1980, and *Listrophoroides* (*s.s.*) (the last including the previously recognized species groups, *borneoensis*, *hongkongensis* and *rajah*, and two independent lineages represented by *L. aethiopicus* Hirst, 1923 and *L. mindanensis*, respectively). Results of this analysis indicated that, while the nominal subgenera *Marquesania* and *Paklistrophoroides* were monophyletic, *Listrophoroides* (*s.s.*) was not. The *hongkongensis* group was sister to *Paklistrophoroides*, and the *rajah* and *borneoensis* groups formed a monophyletic group with *L. mindanensis*, with this lineage sister to *Marquesania*. The type species of *Listrophoroides*, *L. aethiopicus* Hirst, 1923, was sister to a clade comprising all other species.

In order to place the newly recognized Philippine species within this complex of *Listrophoroides*, we conducted a new cladistic analysis. In addition to the nine newly described Philippine species, species representing all nominal groups and lineages of the complex were included in the analysis (Table 1). Four Philippine species differ from the most closely related species by only autapomorphic characters and, therefore, we did not include them in the analysis: *L. cucullatus* from *L. paracucullatus* sp.n., *L. chrotomys* sp.n. from *L. insularis* sp.n., *L. bullimus* sp.n. and *L. corpuzrarosae* from *L. luzonicus* sp.n.

Chirodiscoides bolivianus Fain, 1976 (Atopomelidae), a parasite of Neotropical rodents of the family Echimyidae was selected as a distant outgroup within the Atopomelidae.

We include a total of 29 species and 40 morphological characters in the analysis (Table 1). Only qualitative characters, such as the presence/absence of a structure or distinct forms of morphological structures were used. Quantitative characters were included only if non-overlapping states could be defined, and qualitative characters diagnostic only at the species level were excluded. Preparing and editing of the data matrix were done using NEXUS Data Editor 0.5.0 (Page, 2001). All characters were unordered and initially unweighted. Maximum parsimony analysis was used for the estimation of phylogeny. The reconstruction of phylogenetic relationships, analysis of character distributions, drawing, and editing of the trees were performed with PAUP 4.0b.10 for Windows (Swofford, 2001) and WinClada 0.9.99m24 (Nixon, 2000). The exact Branch and Bound search option was used due to the relatively small number of taxa. Support for branches was estimated by Bremer support indices calculated with the program TreeRot for Macintosh (Sorenson, 1999).

Table 1. Data matrix. — character inapplicable; L—subgenus *Listrophoroides*, (b)—*borneoensis* group, (h)—*hongkongensis* group, (r)—*rajah* group; M—subgenus *Marquesania*; P—subgenus *Paklistrophoroides*

Species	Characters				
	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	
L	<i>C. bolivianus</i>	0000000000	00–00000–0	00000000–0	0000001000
L	<i>L. aethiopicus</i>	1000010100	0000000000	00004000–2	0020000000
M	<i>L. apomys</i>	0001110010	0100001000	0110000111	0010100010
L	<i>L. batomys</i>	0000020100	0100001000	00003000–1	0020000011
L(b)	<i>L. bilineatus</i>	0010010100	0110000001	00001120–0	0020000101
L(h)	<i>L. bowersi</i>	0000010100	1200000000	00003010–1	0020000110
L(b)	<i>L. borneoensis</i>	0110010100	1200000001	00001120–0	0020010111
L(b)	<i>L. brachyptyx</i>	0010010100	0100000001	00001120–0	0020000111
L(h)	<i>L. cremoriventer</i>	0000010100	1200000000	00001010–1	0020000000
L	<i>L. crunomys</i>	0000010100	0300000000	1–001100–0	0120010011
L(h)	<i>L. dasyomys</i>	0000010100	1200100000	00001010–2	0020000110
P	<i>L. decoratus</i>	0000010100	1400000010	0000000101	0020000000
M	<i>L. faini</i>	0001011010	0100001000	0010100101	0010100000
L(r)	<i>L. iphiophallus</i>	0010020100	0320110100	00211130–0	1120011001
M	<i>L. heaneyi</i>	0001110010	0100001000	0010100111	0010100010
L(h)	<i>L. hongkongensis</i>	0000010100	1200000000	00002010–1	0020000000
L(h)	<i>L. infraluteus</i>	0100010100	1210000001	00002000–1	0020000100
L	<i>L. insularis</i>	0000010100	0100000000	00001100–0	0020000011
L	<i>L. limnomys</i>	0001010010	0100001000	0110100111	0010100000
L	<i>L. mindanensis</i>	0000020100	0100000000	00003000–1	0020000011
L(h)	<i>L. oenomys</i>	0000010100	1200000000	00003000–1	0020000110
P	<i>L. orbitalis</i>	0001010100	1420000010	0000000101	0020000010
L(h)	<i>L. pahangi</i>	1100010101	0211000000	00003000–1	0121000100
L(h)	<i>L. pakistanicus</i>	0000010000	1100000000	1–000000–1	0020000100
L(r)	<i>L. palawanensis</i>	0010020100	0500010100	00011130–0	1120010001
M	<i>L. paracucullatus</i>	0001010010	0100001000	0110100101	0010100000
M	<i>L. postsquamatus</i>	0001010100	0110001000	0010100101	0010100000
M	<i>L. luzonicus</i>	0001010010	0100001000	0010100101	0010100000
L(h)	<i>L. scutalis</i>	1100010001	1211000010	00003000–1	0121000100

Characters used in phylogenetic analysis

- Length/width of gnathosoma subequal (0); distinctly wider \times 1.4–1.5, CI (here and below, consistency index) 0.5, RI (here and below, retention index) 0.5.
- Idiosoma moderately elongated, δ — \times 2.2–2.6 longer than wide, f — \times 2.3–2.8 (0); stumpy, δ , f — \times 1.8–2 (1), CI 0.5, RI 0.67.
- Prescapular shield rectangular or trapezoidal (0); flask-shaped (1), CI 0.5, RI 0.75.
- Apodemes of postscapular shield absent (0); present (1), CI 0.5, RI 0.86.
- Postscapular shield without lateral bands (0); with lateral bands (1), CI 1, RI 1.
- f : Hysteronotum sclerotized only in anterior half (0); only lateral parts unsclerotized (1); completely sclerotized to level of $\text{f}2$ (2), CI 0.67, RI 0.67.
- δ : Lateral margins of hysteronotum posterior to setae $e2$ without scales (0); with scales (1), CI 1, RI 1.
- f : Opisthonotum posterior to hysteronotal shield not sclerotized (0); sclerotized (1), CI 0.25, RI 0.67.
- δ : Lateral incisions of hysteronotal shield indistinct or absent (0); distinctly developed (1), CI 1, RI 1.
- δ : Lateral margins of opisthosoma without expansions at level of setae $e2$ (0); with expansions (1), CI 1, RI 1.
- f : Scutal organs absent (0); present (1), CI 0.33, RI 0.8.
- Dorsal shields without ornamentation in both sexes (0); completely covered by transverse straight or wave-like lines in both sexes (1); completely covered by short curved lines in both sexes (2); postscapular shield with short curved lines in both sexes, f —hysteronotal shield with distinct transverse lines, δ —hysteronotal shield covered in anterior half by short curved lines, very few in some species (3); shields covered by scalloped impressions in both sexes (4); postscapular shield covered by short curved lines in both sexes, δ —hysteronotal shield covered by short curved lines, f —hysteronotal shield covered by transverse lines (5), CI 0.83, RI 0.9.

13. ♀: Opisthogastric shield median, not dissected (0); paired, strongly reduced (1); unpaired, with 3 posterior extensions, 2 laterals and 1 median (2), CI 0.4, RI 0.4.
14. ♂: Setae *el* present (0); absent (1), CI 1, RI 1.
15. ♀: Setae *ps3* situated below or at level of setae *el* (0); distinctly anterior (1), CI 0.5, RI 0.
16. ♂: Setae *ps3* situated at level of anal opening or slightly anterior (0); distinctly anterior (1), CI 1, RI 1.
17. Striated membranes of coxae I and II subequal or membranes II shorter and narrower (0); membranes of coxae II much wider, reaching lateral body margins (1), CI 0.5, RI 0.86.
18. Crest of coxae II absent (0); present (1), CI 1, RI 1.
19. Sternum between coxae II distinctly sclerotized (0); not sclerotized (1), CI 0.5, RI 0.5.
20. ♂: Aedeagus cone-like or tube-like (0); inflated membranous (1), CI 0.5, RI 0.67.
21. ♂: Aedeagal-supporting sclerite distinctly developed (0); reduced (1), CI 0.5, RI 0.
22. ♂: Anterior ends of aedeagal-supporting sclerite fused (0); free (1), CI 0.5, RI 0.5.
23. ♂: Postgenital shield very small, only about $\times 3$ wider than bases of setae *g* or absent (0); distinctly developed, shaped like inverted U (1); distinctly developed, irregular shape, in some species with indistinct margins (2), CI 1, RI 1.
24. ♂: Median opisthogastric band absent (0); present (1), CI 1, RI 1.
25. ♂: Lobar membrane in median part widely convex (0), with median incision (1); widely concave (2); with nipple-like protrusion (3); almost straight (4), CI 0.5, RI 0.6.
26. ♂: Anus situated ventrally (0); ventro-terminally (1), CI 1, RI 1.
27. ♂: Lobar membrane widely rounded laterally (0); almost straight (1); with several teeth (2); developed only anterior to setae *h3* (3), CI 1, RI 1.
28. ♂: Postanal sclerite absent (0); present (1), CI 0.5, RI 0.87.
29. ♂: Posterior ends of postgenital shield clearly not reaching level of postanal sclerites (0); reaching (1), CI 1, RI 1.
30. ♂: Anal fold absent (0); present, flanking posterior part of anal opening (1); present, flanking anterior part of anal opening (2), CI 0.5, RI 0.75.
31. ♀: Basal cap of spermatheca not sclerotized (0); distinctly sclerotized (1), CI 1, RI 1.
32. ♀: Basal cap of spermatheca irregular in shape (0) (Fig. 8A); regular (1) (Fig. 10C), CI 0.5, RI 0.75.
33. ♀: Spermatheca opening dorsally (0); on dorsal nipple-like protrusion (1); terminally, between lateral lobes of idiosoma or dorso-terminally, before lateral lobes (2), CI 1, RI 1.
34. ♀: Small pocket on opisthonotal surface absent (0); present (1), CI 1, RI 1.
35. Ventral process of femur and genu I absent or indistinct (0); hypertrophied (1), CI 1, RI 1.
36. Dorso-basal hook of femur I absent or indistinct (0); distinctly developed (1), CI 0.5, RI 0.67.
37. ♂: Femur IV about $\times 1.5$ longer than genu IV (0); $\times 1.8$ – 2.5 longer (1), CI 0.5, RI 0.
38. ♂: Femur IV proportionally widened (0); inflated (1), CI 0.33, RI 0.78.
39. Lines of coxae III absent or indistinct (0); present, distinct (1), CI 0.14, RI 0.45.
40. Lateral furrow between coxae III and IV absent (0); present (1), CI 1, RI 1.

Results

Three maximally parsimonious trees (length 92, CI 0.59, RI 0.79) were obtained. Successive weighting (Farris, 1969) based on rescaled consistency indices provided three trees with the same topology as the analysis prepared on unweighted characters. In the strict consensus of these trees, two major clusters and the ungrouped species *L. aethiopicus*, which is sister to the node joining the clusters, are recognizable (Fig. 39). All Philippine species of the subgenus *Listrophoroides* (*s.s.*) belong to cluster I, which has the following structure: the subgenus *Marquesania* (*L. batomys* sp.n. + *L. mindanensis* (the *rajah* and *borneoensis* species groups + *L. insularis*/*L. chrotomys*)). Cluster II includes African, South Asian and some Southeast Asian species comprising the *hongkongensis* species group and the subgenus *Paklistrophoroides*. No Philippine species clustered here. The topology of the strict consensus is congruent with the phylogenetic hypothesis recently proposed for this *Listrophoroides* complex (Bochkov & OConnor, 2005). Bochkov & OConnor (2005) showed that the subgenus *Listrophoroides* (*s.s.*) is a paraphyletic group that includes the subgenera *Marquesania* and *Paklistrophoroides*, and *L. mindanensis* is a sister lineage to the *rajah* + *borneoensis* clade. This pattern was not structurally changed when the new Philippine species were added.

The Philippine lineage *L. batomys* sp.n. + *L. mindanensis* has Bremer support (BS) 2. Two other Philippine endemic *Listrophoroides* (*s.s.*) lineages (*L. insularis* + *L. chrotomys*, and *L. crunomys*) form independent clades situated in the core of cluster I together with *borneoensis* and *rajah* groups (BS 2). The monophyly of the subgenus *Marquesania* is strongly confirmed (Bochkov & Fain, 2003; Bochkov & OConnor, 2005) (BS 7). Because a detailed phylogenetic reconstruction of the subgenus *Marquesania* was not the primary goal of this study, the number of species and, consequently, the number of char-

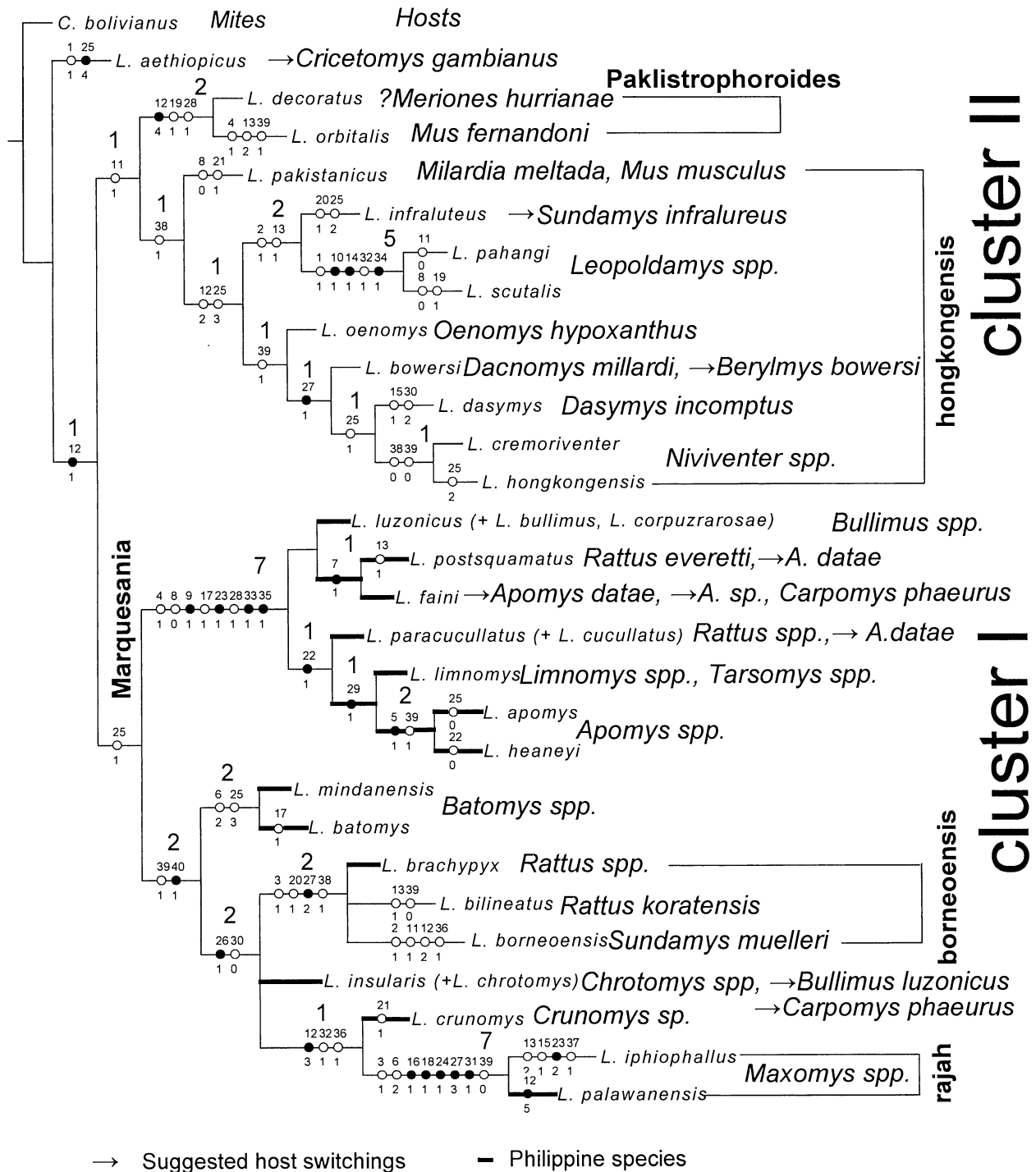


Fig. 39. Phylogenetic relationships between Southeast Asian *Listrophoroides* (subgenera *Listrophoroidea*, *Marquesania*, and *Paklistrophoroides*). Strict consensus of three maximally parsimonious trees obtained with Branch and Bound search option implemented in PAUP for 29 species and 40 unordered and unweighted morphological characters (autapomorphies not included); tree length 92, CI 0.59, RI 0.79. Character numbers are indicated above branches (unambiguous only), their state changes below branches; non homoplasious state changes are in black, homoplasious state changes are in white. Large numbers above the branches are Bremer support indices.

acters were limited for this analysis. Among species of this subgenus, only the node joining *L. apomys* and *L. heaneyi* received Bremer support higher than 1, and these two species form a presumably monophyletic group (BS 2). Because many

potential hosts for these mites in mainland southeast Asia and some insular areas (e.g. Java, Sulawesi) have not been examined for these mites, a complete analysis of relationships among *Marquesiana* species must await further sampling.

HOST-PARASITE RELATIONSHIPS

Based upon associations observed elsewhere, potential hosts of atopomelid mites inhabiting the Philippines belong to the families Muridae, Sciuridae (Rodentia), Soricidae (Soricomorpha), and Erinaceidae (Erinaceomorpha), totalling 83 species in 29 genera (Heaney *et al.*, 2002; Rickart *et al.*, 2005). Because no atopomelids have been reported from Asian Sciuridae, and we did not encounter any on the 136 museum specimens of Philippine squirrels we examined, this host group will not be discussed further. We were able to examine specimens representing 48 of 65 known species of Philippine Muridae, representing 18 of the 22 genera, 5 of the 8 species of shrews

representing both genera, and one of two species of Erinaceidae. In total, we have examined specimens representing over 66% of the known potential hosts of Atopomelidae in the Philippines. We collected a total of 18 species of atopomelid mites from 33 host species in 10 genera (40% of potential hosts species) belonging to the families Muridae (subfamily Murinae) and Soricidae (Table 2). Many of the host species we were unable to examine are very rare and poorly represented in museum collections. For some host species, we were able to examine only one or a few specimens, so the absence of atopomelid mites may represent simple undersampling as well as evolutionary events such as extinction or "missing the boat". Of the two species of the family Erinaceidae (subfamily Galerici-

Table 2. Host ranges and distribution of the Philippine Atopomelidae

Mite species	Host	Locality
Atopomelus Trouessart, 1917		
<i>A. crocidurae</i> Fain and Lukoschus, 1977	<i>Crocidura mindorus</i>	Sibuyan Isl.
<i>A. crocidurae</i> Fain and Lukoschus, 1977	<i>Crocidura grayi</i>	Kalinga Prov. (Luzon Isl.)
<i>A. crocidurae</i> Fain and Lukoschus, 1977	<i>Crocidura beatus</i>	Bohol Isl., Camiguin Isl.
Listrophoroides Hirst, 1923 (subgenus <i>Listrophoroides</i> s.s.)		
<i>L.</i> (s.s.) <i>mindanensis</i> Fain and Lukoschus, 1981	<i>Batomys salomonseni</i>	Mindanao Isl.
<i>L.</i> (s.s.) <i>batomys</i> sp.n.	<i>Batomys granti</i>	Kalinga Prov., Camarines Sur Prov. (Luzon Isl.)
<i>L.</i> (s.s.) <i>palawanensis</i> Fain, 1976	<i>Maxomys panglima</i>	Palawan Isl.
<i>L.</i> (s.s.) <i>brachypyx</i> Fain, 1974	<i>Rattus tanezumi</i>	Sibuyan and Negros Isls.
<i>L.</i> (s.s.) <i>brachypyx</i> Fain, 1974	<i>Rattus mindorensis</i>	Mindoro Isl.
<i>L.</i> (s.s.) <i>crunomys</i> sp.n.	<i>Crunomys suncooides</i>	Mindanao Isl.
<i>L.</i> (s.s.) <i>crunomys</i> sp.n.	<i>Crunomys melanius</i>	Mindanao and Camiguin Isls.
<i>L.</i> (s.s.) <i>insularis</i> sp.n.	<i>Chrotomys whiteheadi</i>	Kalinga Prov. (Luzon Isl.)
<i>L.</i> (s.s.) <i>insularis</i> sp.n.	<i>Chrotomys silaceus</i>	Kalinga Prov. (Luzon Isl.)
<i>L.</i> (s.s.) <i>insularis</i> sp.n.	<i>Carpomys phaeurus</i>	Kalinga Prov. (Luzon Isl.)
<i>L.</i> (s.s.) <i>chrotomys</i> sp.n.	<i>Chrotomys gonzalesi</i>	Camarines Sur Prov. (Luzon Isl.)
<i>L.</i> (s.s.) <i>chrotomys</i> sp.n.	<i>Chrotomys mindorensis</i>	Mindoro Isl.
<i>L.</i> (s.s.) <i>chrotomys</i> sp.n.	<i>Bullimus luzonicus</i>	Kalinga Prov., Cagayan Prov., Quezon Prov. (Luzon Isl.)
Listrophoroides (subgenus <i>Marquesania</i> Womersley, 1943)		
<i>L.</i> (<i>M.</i>) <i>cucullatus</i> (Trouessart, 1893)	<i>Rattus tiomanicus</i>	Palawan Isl.
<i>L.</i> (<i>M.</i>) <i>cucullatus</i> (Trouessart, 1893)	<i>Rattus tanezumi</i>	Sibuyan, Catanduanes, and Leyte Isls.
<i>L.</i> (<i>M.</i>) <i>paracucullatus</i> sp.n.	<i>Rattus exulans</i>	Camiguin Isl.
<i>L.</i> (<i>M.</i>) <i>paracucullatus</i> sp.n.	<i>Apomys</i> sp. D	Camiguin Isl.
<i>L.</i> (<i>M.</i>) <i>postsquamatus</i> sp.n.	<i>Rattus everetti</i>	Kalinga Prov. (Luzon Isl.), Maripipi and Leyte Isls
<i>L.</i> (<i>M.</i>) <i>postsquamatus</i> sp.n.	<i>Rattus</i> sp. A	Sibuyan Isl.
<i>L.</i> (<i>M.</i>) <i>postsquamatus</i> sp.n.	<i>Apomys</i> sp. D	Camiguin Isl.
<i>L.</i> (<i>M.</i>) <i>apomys</i> sp.n.	<i>Apomys datae</i>	Kalinga Prov. (Luzon Isl.)
<i>L.</i> (<i>M.</i>) <i>apomys</i> sp.n.	<i>Apomys microdon</i>	Camarines Sur (Luzon Isl.)
<i>L.</i> (<i>M.</i>) <i>apomys</i> sp.n.	<i>Apomys musculus</i>	Camarines Sur (Luzon Isl.)
<i>L.</i> (<i>M.</i>) <i>apomys</i> sp.n.	<i>Apomys</i> sp. B	Sibuyan Isl.
<i>L.</i> (<i>M.</i>) <i>apomys</i> sp.n.	<i>Apomys</i> sp. C	Sibuyan Isl.
<i>L.</i> (<i>M.</i>) <i>heaneyi</i> sp.n.	<i>Apomys hyloces</i>	Mindanao Isl.
<i>L.</i> (<i>M.</i>) <i>heaneyi</i> sp.n.	<i>Apomys insignis</i>	Mindanao Isl.
<i>L.</i> (<i>M.</i>) <i>heaneyi</i> sp.n.	<i>Apomys microdon</i>	Leyte Is.
<i>L.</i> (<i>M.</i>) <i>faini</i> sp.n.	<i>Apomys datae</i>	Kalinga Prov. (Luzon Isl.)
<i>L.</i> (<i>M.</i>) <i>faini</i> sp.n.	<i>Apomys</i> sp.	Quezon (Luzon Isl.)
<i>L.</i> (<i>M.</i>) <i>faini</i> sp.n.	<i>Carpomys phaeurus</i>	Ifugao (Luzon Isl.)
<i>L.</i> (<i>M.</i>) <i>limnomys</i> sp.n.	<i>Lymnomys bryophilus</i>	Mindanao Isl.
<i>L.</i> (<i>M.</i>) <i>limnomys</i> sp.n.	<i>Tarsomys apoensis</i>	Mindanao Isl.
<i>L.</i> (<i>M.</i>) <i>bullimus</i> sp.n.	<i>Bullimus gamay</i>	Camiguin Isl.
<i>L.</i> (<i>M.</i>) <i>luzonicus</i> sp.n.	<i>Bullimus luzonicus</i>	Cagayan Prov., Kalinga Prov., Quezon Prov., Quirini Prov (Luzon Isl.)
<i>L.</i> (<i>M.</i>) <i>corpuzrarosae</i> sp.n.	<i>Bullimus bagobus</i>	Leyte Isl.

inae) known from the Philippines, atopomelid mites are absent on *Podogymnura truei* Mearns, 1905 (33 specimens examined); *P. aureospinula* Heaney and Morgan, 1982 has not been examined (Table 4). Among Soricidae, atopomelids are absent on *Suncus murinus* (L., 1766) (13 specimens examined), a species presumably introduced into the Philippines and not known to harbor these mites in other parts of its range (Table 4). Finally, among murines, atopomelids are absent on *Rhynchomys isarogensis* Musser and Freeman, 1981 (10 specimens examined), *Phloeomys cumingi* (Waterhouse, 1839) (5 specimens examined), and on the introduced *Mus musculus* L., 1758 (8 specimens examined) (Table 3). *Phloeomys cumingi* has unusual pelage, with very thick, rounded hairs that are not conducive to atopomelid attachment.

The single atopomelid species known from Philippine insectivores is *Atopomelus crocidurae*, which has been collected only from Oriental shrews of the genus *Crocidura* including three species in the Philippines. Atopomelid mites are completely absent on Palearctic and African species of *Crocidura* and other soricid genera. The phylogeny of the Crocidurinae is highly unsettled, but recent work suggests that the genus *Crocidura* probably originated in Africa, migrated to the western Palearctic, and finally reached the Indomalayan region relatively recently (Ruedi & Vogel, 1995). Thus, the absence of *Atopomelus* on African and Palearctic *Crocidura* species suggests that the association with Oriental shrews was the result of a later host shift, possibly from moles or from gymnures, which harbor several species of this genus in Southeast Asia (Bochkov *et al.*, 2005).

The Philippine murines belong to seven hypothetically monophyletic clades or divisions (Musser & Carleton, 2005; see Table 3). Two divisions, *Chrotomys* (genera *Apomys*, *Chrotomys*, *Rhynchomys*) and *Phloeomys* (genera *Batomys*, *Carpomys*, *Crateromys*, *Phloeomys*) include only Old Philippine endemics. The genus *Crunomys*, the only genus of its division is also represented by Old endemics of the Philippines (three species) and Sulawesi (one species, *Crunomys celebensis* Musser, 1982). The speciose *Rattus* division is represented on the Philippines by New Philippine endemics (genera *Abditomys*, *Bullimus*, *Limnomys*, *Palawanomys*, *Tarsomys*, *Tryphomys*, and some endemic species of *Rattus*). In addition, this division includes some more widely distributed species, *Rattus* spp. and *Sundamys muelleri* (Jentink, 1979), known in the Philippines only from Palawan and adjacent islands connected to the mainland during Pleistocene sea level minima (Heaney, 1986; Heaney & Rickart, 1990). The *Micromys* and *Maxomys* divisions are also represented in the Philippines by endemic species inhabiting Palawan and adjacent islands. The *Dacnomys* division is represented in the Philippines only by *Anonymomys mindorensis* Musser, 1981, a monotypic genus endemic to Mindoro Island. The phylogenetic relationship of the genus *Anonymomys* to other Southeast Asian murines is unclear, and it was placed in the *Dacnomys* division provisionally (Musser & Carleton, 2005). Finally, the *Mus* division is represented by the cosmopolitan introduced species *Mus musculus*. The origin of each clade of

Philippine endemics has been considered to be the result of "an independent colonization of the Philippines from the Asian mainland (via Borneo) that has been followed by substantial diversification" (Heaney & Rickart, 1990: 328).

Jansa *et al.* (in press) have analyzed relationships among 13 Philippine rodent genera representing the *Phloeomys*, *Chrotomys*, *Crunomys*, and *Rattus* divisions of Musser and Carleton (2005), along with representatives of many other muroid lineages. Optimally, this would allow statistical comparison of the host and parasite phylogenies through comparison of the cladograms using methods such as Brooks Parsimony Analysis or TreeMap (Dowling, 2002). However the incongruence between the set of rodent taxa used by Jansa *et al.* (in press) and the set of rodents examined for atopomelids precludes using these methods accurately. Visual comparison of the phylogenies of hosts and parasites does suggest some areas of common pattern that do not falsify a hypothesis of cospeciation. Similarly, instances of incongruence suggest host switching or extinction.

Figure 39 recognizes four monophyletic lineages within the *Listrophoroides* complex analyzed: 1) *L. aethiopicus*, 2) *Paklistrophoroides* + the *hongkongensis* group, 3) *Marquesania*, and 4) the *rajah* and *borneoensis* groups along with some Philippine taxa. Atopomelids associated with the Philippine murines all cluster within the last 2 clades. Mites clustering within the second clade (cluster II of Fig. 39) are associated with African, South Asian and some Southeast Asian murines of the genera *Dacnomys*, *Leopoldamys*, and *Niviventer*. The occurrence of *L. infraluteus* Fain, 1976 on *Sundamys infraluteus* (Thomas, 1888) (Fig. 39) can be interpreted as the result of a host switch from rats of the genus *Leopoldamys* (Bochkov & O'Connor, 2005). The lineages included in cluster I of Fig. 39 represent the subgenera *Listrophoroides* (*s.s.*) (*L. mindanensis*, *L. batomys*, the *borneoensis* and *rajah* species groups), and *Marquesania*, which are associated with Southeast Asian murines and their relatives from New Guinea and Australia (Fig. 39).

The Philippine mites of the subgenus *Marquesania* are associated with hosts from the *Rattus* division and the Old Philippine endemics of the genus *Apomys* (*Chrotomys* division) (Fig. 39, Table 3). The relationships among most species of this subgenus are weakly supported, except for the lineage *L. apomys*-*L. heaneyi*. The closely related species *L. cucullatus* and *L. paracucullatus*, probably arrived in the Philippines relatively recently on their introduced hosts of the genus *Rattus*. On the other hand, *L. postsquamatus*, parasitizing the Philippine endemics *Rattus everetti* and *Rattus* sp. A., is very distinct from all other representatives of *Marquesania* associated with *Rattus* hosts. *Rattus everetti* clustered with the Philippine endemic genera *Tarsomys* and *Limnomys*, and not with introduced *Rattus* species in the analysis of Jansa *et al.* (in press), and is considered by some authors as a species that should be generically separated from other *Rattus* species (Musser & Carleton, 2005). Hosts of the sister genera *Limnomys* and *Tarsomys* (Jansa *et al.*, in press) are parasitized by *Listrophoroides limnomys* and the three closest mite species, *L. bullimus*, *L. luzonicus* and *L. corpuzarrosae*, are associated with *Bullimus*

Table 3. Distribution of the Philippine murines (Murinae) and their associations with mites of the genus *Listrophoroides* (Acari: Atopomelidae) (host data based on Musser & Carleton, 2005)

Superspecific host taxa	Host species/ n observed hosts	Host ranges	Mite species
<i>Chrotomys</i> Division (Old Philippine Endemics)			
* <i>Apomys</i>			
	<i>abrae</i> (Sanborn, 1952)/3	C. Luzon	?
	<i>datae</i> (Meyer, 1899)/23	N. Luzon	<i>apomys</i> , → <i>faini</i>
	<i>gracilirostris</i> Ruedas, 1995/0	Mindoro	no hosts examined
	<i>hylocetes</i> Mearns, 1905/24	Mindanao	<i>heaneyi</i>
	<i>insignis</i> Mearns, 1905/34	Dinagat, Mindanao#	<i>heaneyi</i>
	<i>littoralis</i> (Sanborn, 1952)/5	Biliran, Bohol, Leyte, and Mindanao	?
	<i>microdon</i> Hollister, 1913/7	Catanduanes, Luzon	<i>apomys</i> , <i>heaneyi</i>
	<i>musculus</i> Miller, 1911/10	Dinagat, Luzon#, and Mindoro	<i>apomys</i>
	<i>sacobianus</i> Johnson, 1962/0	N. & C. Luzon	no hosts examined
	<i>sp. A/2</i>	Negros and Panay	?
	<i>sp. B/2</i>	Sibuyan	<i>apomys</i>
	<i>sp. C/25</i>	Sibuyan	<i>apomys</i>
	<i>sp. D/6</i>	Camiguin	→ <i>paracucullatus</i> , → <i>postsquamatus</i>
	<i>sp. E/0</i>	Mindoro	
	<i>sp./3</i>	Luzon	<i>faini</i>
* <i>Archboldomys</i>	<i>luzonensis</i> Musser, 1982/4	SE. Luzon	?
	<i>musseri</i> Rickart, Heaney, Tabaranza and Baleta, 1998/3	N. Luzon	?
* <i>Chrotomys</i>	<i>gonzalesi</i> Rickart and Heaney, 1991/7	SE. Luzon	<i>chrotomys</i>
	<i>mindorensis</i> Kellogg, 1945/4	SE. Luzon	<i>chrotomys</i>
	<i>sibuyanensis</i> Rickart, Heaney, Goodman and Jansa, 2005/0	N. Luzon# and Mindoro#	
	<i>silaceus</i> (Thomas, 1895)/4	Sibuyan.	
	<i>whiteheadi</i> Thomas, 1895/9	N. Luzon	<i>insularis</i>
* <i>Rhynchomys</i>	<i>isarogensis</i> Musser and Freeman, 1981/10	N. Luzon	<i>insularis</i>
	<i>soricoides</i> Thomas, 1895/5	SE. Luzon	—
		N. Luzon	?
<i>Crunomys</i> Division (Old Philippine and Sulawesi endemics)			
* <i>Crunomys</i>			
	<i>fallax</i> Thomas, 1897/0	N. Luzon	
	<i>melanius</i> Thomas, 1907/5	Mindanao, Leyte, and Camiguin#	<i>crunomys</i>
	<i>suncoides</i> Rickart, Heaney, Tabaranza and Baleta, 1998/1	Mindanao	<i>crunomys</i>
	<i>mindorensis</i> Musser, 1981/0	Mindoro	no hosts examined
<i>Dacnomys</i> Division			
* <i>Anonymomys</i>			
<i>Maxomys</i> Division			
<i>Maxomys</i>			
	<i>panglima</i> (Robinson, 1921)/2	Balabac, Palawan#, Busuanga, Calauit, and Cullion	<i>palawanensis</i>
<i>Micromys</i> Division			
<i>Chiripodomys</i>			
	<i>calamianensis</i> (Taylor, 1934)/0	Busuanga, Balabac, and Palawan	no hosts examined
<i>Haeromys</i>			
	<i>pusillus</i> (Thomas, 1893)/1	Borneo, Palawan, and Calauit#	?
<i>Mus</i> Division			
<i>Mus</i>			
	<i>musculus</i> L., 1758/8	Cosmopolitan	—

Phloeomys Division (Old Philippine endemics)					
* <i>Batomys</i>	<i>dentatus</i> Miller, 1911/0 <i>granti</i> Thomas, 1895/7 <i>russatus</i> Musser, Heaney and Tabaranza, 1998/0 <i>salomonsemi</i> (Sanborn, 1953)/24 <i>melanurus</i> Thomas, 1895/0 <i>phaeurus</i> Thomas, 1895/2 <i>australis</i> Musser, Heaney and Rabor, 1985/1 <i>heaneyi</i> Gonzales and Kennedy, 1996/0 <i>paulus</i> Musser and Gordon, 1981/0 <i>schadenbergi</i> (Meyer, 1895)/1 <i>cumingi</i> (Waterhouse, 1839)/5 <i>pallidus</i> Nehring, 1890/1	N. Luzon N. Luzon Dinagat Mindanao, Dinagat, Biliran, and Leyte# N. Luzon N. Luzon Dinagat Panay Ilin N. Luzon SE. Luzon, Marinduque, and Catanduanes N. and C. Luzon	no hosts examined <i>batomys</i> no hosts examined <i>mindanensis</i> no hosts examined <i>faini</i> ? no hosts examined no hosts examined ? ? ?		
* <i>Carpomys</i>					
* <i>Crateromys</i>					
* <i>Phloeomys</i>					
Rattus Division (New Philippine endemics)					
* <i>Abditomys</i>	<i>latidens</i> (Sanborn, 1952)/1 <i>bagobus</i> Mearns, 1905/3	N. and C. Luzon Samar, Calicoan, Leyte#, Dinagat, Siargao, Mindanao, Bohol, and Maripipi	? <i>corpuzarrosae</i>		
* <i>Bullimus</i>					
* <i>Limnomys</i>	<i>gamay</i> Rickart, Heaney and Tabaranza, 2002/16 <i>luzonicus</i> (Thomas, 1895)/25 <i>bryophilus</i> Rickart, Heaney and Tabaranza, 2003/10 <i>sibuanus</i> Mearns, 1905/8 <i>furvus</i> Musser and Newcomb, 1983/0 <i>argentiventer</i> (Robinson and Kloss, 1916)/5 <i>everetti</i> (Günther, 1879)/36	Camiguin Luzon Mindanao Mindanao Palawan Thailand to New Guinea. Philippines: Cebu, Luzon, Mindanao, Mindoro, and Negros Philippines excluding Palawan Faunal Region and the Batanes-Babuyan groups Bangladesh to Easter Island and throughout the Philippines Mindoro Nepal to New Guinea. Philippines: N. Luzon	<i>bullimus</i> . → <i>chrotomys</i> <i>luzonicus</i> <i>limnomys</i> ? ? <i>postsquamatus</i> <i>paracucullatus</i> <i>brachyphx</i> ? no hosts examined <i>brachyphx</i> , <i>cucullatus</i>		
* <i>Palawanomys</i>					
<i>Rattus</i>	<i>tawitawiensis</i> Musser and Heaney, 1985/0 <i>tiomanicus</i> (Miller, 1900)/3 <i>sp. A/4</i> <i>muelleri</i> (Jentink, 1879)/0	Tawitawi Malay Peninsula to Borneo and Palawan. Philippines: Arena, Bancalan, Busuanga, Calaut, and Palawan Sibuyan Southern Myanmar to Palawan. Philippines: Balabac, Busuanga, Culion, and Palawan Mindanao Mindanao N. and C. Luzon Is.	no hosts examined <i>cucullatus</i> <i>postsquamatus</i>		
<i>Sundamys</i>					
* <i>Tarsomys</i>	<i>apoensis</i> Mearns, 1905/17 <i>echinatus</i> Musser and Heaney, 1992/0 <i>adustus</i> Miller, 1910/3		<i>limnomys</i> no hosts examined ?		
* <i>Tryphomys</i>					

*genera endemic to the Philippines; # localities where atopomelids recorded; ? not enough host specimens observed; - atopomelids absent on this host; → host switching.

Table 4. Distribution of the Philippine insectivores (Soricomorpha and Erinaceomorpha) and their associations with mites of the genus *Atopomelus* (Acari: Atopomelidae) (host data based on Heaney *et al.*, 1998)

Superspecific host taxa	Host species/ n observed hosts	Host ranges	Mite species
<i>Crocidura</i>	<i>attenuata</i> Milne-Edwards, 1872/0	Asian continent and many associated shallow-water islands.	no hosts examined
	<i>beatus</i> Miller, 1910/6	Philippines: Batan	
	<i>grandis</i> Miller, 1910/0	Biliran, Bohol#, Camiguin#, Leyte, Maripipi, and Mindanao	<i>crocidurae</i>
	<i>grayi</i> Dobson, 1890/20	Mindanao	no hosts examined
	<i>mindorus</i> Miller, 1910/4	Catanduanes, Luzon#, and Mindoro	<i>crocidurae</i>
	<i>negrina</i> Rabor, 1952/1	Mindoro and Sibuyan#	<i>crocidurae</i>
<i>Suncus</i>	<i>palawanensis</i> Taylor, 1934/0	Negros	?
	<i>murinus</i> (L., 1766)/13	Palawan and Balabac	no hosts examined
* <i>Podogymnura</i>	<i>aureospinula</i> Heaney and Morgan, 1982/0	Asia and Indo-Australia; throughout the Philippines	–
	<i>truei</i> Mearns, 1905/33	Dinagat.	no hosts examined
		Mindanao	–

*genera endemic to the Philippines; # localities where atopomelids recorded; ? not enough host specimens observed; – atopomelids absent on this host.

gamay, *B. luzonicus*, and *B. bagobus*, respectively. This pattern of association of *Marquesania* species associated with species in the “*Rattus*” division is disrupted by atopomelids associated with hosts of the genus *Apomys*. Atopomelids from these widely distributed Philippines endemic rats clearly do not form a monophyletic group. Species of the lineage *L. apomys*+*L. heaneyi* are widely distributed on these hosts, being recorded on seven of 14 species known to date (Heaney *et al.*, 1998), and their ancestor was possibly associated with the ancestor of this genus. However, their distribution appears to reflect more the historical biogeography of their hosts rather their phylogenetic relationships. The genus *Apomys* has been divided into two unequal species groups, the *datae* group, including *A. datae* and *A. gracilirostris*, and the *abrae-hylocetes* group, including all other species (Steppan *et al.*, 2003; Musser & Carleton, 2005). *Listrophoroides apomys* parasitizes five *Apomys* species belonging to both groups from Luzon and Sibuyan Islands (*A. datae*, *A. microdon*, *A. musculus*, *A. sp. B*, and *A. sp. C*), whereas *L. heaneyi* parasitizes hosts from Mindanao Island (*A. hylocetes* and *A. insignis*). *Listrophoroides faini* does not belong to the lineage *L. apomys*+*L. heaneyi*. This species has been collected from *A. datae*, *Apomys* sp., and *Carpomys phaeurus* from different localities on Luzon Island. Its occurrence on hosts of the genus *Apomys* is probably the result of host switching from another host, possibly of the genus *Carpomys*. Finally, *Apomys* sp. D inhabiting Camiguin Island is parasitized by *L. paracucullatus* and *L. postsquamatus*. We did not collect native atopomelids (i.e. *L. apomys* or *L. heaneyi*) from it, suggesting that both were originally absent on it through a founder effect (“missing the boat”) or suffered extinction on the island. The small island inhabited by this *Apomys* also harbors *R. exulans* and *R. everetti*, hosts parasitized by *L. paracucullatus* and *L. postsquamatus*, respectively, and given the careful handling of host specimens to prevent parasite contamination, the records of these species on *Apomys* sp. D. are undoubtedly the result of host switching in the absence of a native species on this host.

Seven Philippine atopomelid species belong to the subgenus *Listrophoroides* (*s.s.*) (Tables 2, 3). *Listrophoroides brac-*

hypyx exhibits a host distribution on Oriental *Rattus* species parallel with species of the subgenus *Marquesania*, *L. (M.) cucullatus* and *L. (M.) paracucullatus* (see host associations and distribution). Five other species are represented by three phylogenetic lineages (Fig. 39), which, like their Old Philippine endemic hosts, exhibit phylogenetic relationships that are unclear (Musser & Carleton, 2005). These lineages comprise (i) *L. mindanensis*+*L. batomys* from *Batomys salomonseni* and *B. granti*, respectively (*Phloeomys* division) (ii) *L. insularis* and *L. chrotomys* from *Chrotomys silaceus*/*C. whiteheadi*, and *C. gonzalesi*/*C. mindorensis*, respectively (*Chrotomys* division), and (iii) *L. crunomys* from *Crunomys melanius* and *C. suncoides* (*Crunomys* division). *Listrophoroides palawanensis*, parasitizing *Maxomys panglima* (*Maxomys* division) belongs to the *rajah* species group, all of whose included species are obligate associates of spiny rats of the genus *Maxomys* (Bochkov & OConnor, 2005). The sister relationship between *L. cruomys* and the lineage comprising the *rajah* species group is historically consistent with the relationship between the hosts, *Crunomys* and *Maxomys*, as suggested by Jansa *et al.* (in press). Parasitism of *L. chrotomys* on *Bullimus luzonicus* is probably the result of host switching from *C. gonzalesi*, which is sympatric with *B. luzonicus* on Luzon Island. These hosts are not closely related, and as was mentioned above, rats of the genus *Bullimus* are parasitized by closely related species of the subgenus *Marquesania* (*L. bullimus*, *L. luzonicus*, and *L. corpuzra-rosae*), whereas hosts in the genus *Chrotomys* harbor two sister species of the subgenus *Listrophoroides* (*s.s.*), *L. chrotomys* and *L. insularis*. Similarly, the association of *L. insularis* with *Carpomys phaeurus* is also probably the result of host switching from a species of the genus *Chrotomys*. These mites are common on rats of the latter genus.

In conclusion, the phylogenetic relationships among Philippine atopomelids partially reflect the host phylogeny, with evidence that several groups of closely related species are associated with related rodent groups. However, this coevolutionary pattern is often violated by obvious or presumed host switchings. It is clear that some *Listrophoroides* species that originated on

hosts belonging to different murine lineages were able to colonize hosts from other lineages of this subfamily. Therefore, the clearest evidence for historical co-phylogenetic patterns appears at the level of closely related host and parasite species rather than between *Listrophoroides* (*s.l.*) and the Philippine Murinae as a whole.

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LITERATURE CITED

- Balashov, Yu.S. 1982. [*Host-parasite relationships of arthropods with terrestrial vertebrates.*] Nauka, Leningrad. 320 pp. (In Russian)
- Barrow, G.J., Domrow, R. & E.H. Derrick. 1963. Rocky Creek, an outlying focus of scrub typhus in North Queensland. *Australasian Annals of Medicine*, 12: 166–170.
- Bochkov, A.V. 2001. Parallel evolution of mites of the family Myobiidae (Acari: Prostigmata) and jerboas (Rodentia: Dipodoidea). *Parazitologiya* (St. Petersburg), 35: 9–18. (In Russian with English summary)
- Bochkov, A.V. & A. Fain. 2003. Revision of the subgenus *Marquesania* (Acari, Atopomelidae). *Invertebrate Systematics*, 17: 575–604.
- Bochkov, A.V., Klimov, P.B. & B.M. OConnor, 2005. Fur-mites of the genus *Atopomelus* Trouessart, 1918 (Acari: Atopomelidae): life-cycle, phylogeny, and host parasite-associations. *Acarologia*, 45: 207–241.
- Bochkov, A.V. & B.M. OConnor. 2003. New cheyletid mites (Acari, Cheyletidae) associated with birds. *Acta Parasitologica*, 48: 265–279.
- Bochkov, A.V. & B.M. OConnor. 2005. Phylogeny and host associations of the fur-mite subgenus *Listrophoroides* (*sensu stricto*) Hirst (Acari: Atopomelidae), with an intriguing example of synhospitality on rats of the genus *Maxomys*. *Invertebrate Systematics*, 19: 437–498.
- Bochkov, A.V., OConnor, B.M. & A. Gorog. 2004. New species and records of fur mites (Acari: Astigmata: Atopomelidae) from Southeast Asian rodents (Rodentia: Muridae). *Acarina*, 12: 67–86.
- Brooks, D.R. 1990. Parsimony analysis in historical biogeography and coevolution: methodological and theoretical updates. *Systematic Zoology*, 39: 14–30.
- Brown, W.A. & M.L. Goff. 1988. Chigger mites (Acari: Trombiculidae) of Leyte Island, Philippine Islands with descriptions of five new species and a key to the genera and species. *Journal of Medical Entomology*, 25: 214–223.
- Clayton, D.H. & J. Moore. 1997. Introduction. Pp. 1–6. In D.H. Clayton & J. Moore. (eds), *Host-parasite evolution: general principles and avian models*. Oxford University Press. New York.
- Corpuz-Raros, L.A. 1993. A checklist of Philippine mites and ticks (Acari) associated with vertebrates and their nests. *Asia Life Sciences*, 2: 177–200.
- Dabert, J. 2003. The feather mite family Syringobiidae Trouessart, 1896 (Acari, Astigmata, Pterolichoidea). II. Phylogeny and host-parasite evolutionary relationships. *Acta Parasitologica*, 48 (Supplement): 185–233.
- Dabert, J., Dabert, M. & S.V. Mironov. 2001. Phylogeny of the feather mite subfamily Avenzoariinae (Acari: Analgoidea: Avenzoariidae) inferred from combined analyses of molecular and morphological data. *Molecular Phylogenetics and Evolution*, 20: 124–135.
- Domrow, R. 1958. A summary of the Atopomelidae (Acarina, Listrophoridae). *Proceedings of the Linnean Society of New South Wales*, 83: 40–54.
- Domrow, R. 1992. Acari Astigmata (excluding feather mites) parasitic on Australian vertebrates: an annotated checklist, keys and bibliography. *Invertebrate Taxonomy*, 6: 1459–1606.
- Dowling, A.P.G. 2002. Testing the accuracy of TreeMap and Brooks parsimony analyses of coevolutionary patterns using artificial associations. *Cladistics* 18: 416–485.
- Esselstyn, J.A., Widmann, P. & L.R. Heaney. 2004. The mammals of Palawan Island, Philippines. *Proceedings of the Biological Society of Washington*, 117: 271–302.
- Ehrnsberger, R., Mironov, S.V. & J. Dabert. 2001. A preliminary analysis of phylogenetic relationships of the feather mite family Freyanidae Dubinin, 1953 (Acari: Astigmata). *Biological Bulletin of Poznan*, 38: 181–201
- Fain, A. 1970. Diagnoses de nouveaux listrophoroides de la famille Atopomelidae (Acarina, Sarcoptiformes). *Bulletin et Annales de la Société Royale d'Entomologie de Belgique*, 106: 275–306.
- Fain, A. 1972a. Les listrophorides en Afrique au sud du Sahara (Acarina: Sarcoptiformes). III. Famille Atopomelidae. *Annales Musée royal de Afrique Centrale (8°)*, *Sciences Zoologiques*, 197: 1–200.
- Fain, A. 1972b. Les listrophorides d'Australie and de Nouvelle-Guinee (Acarina: Sarcoptiformes). *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 48: 1–196.
- Fain, A. 1974. Nouveaux acariens parasites pilicoles (Myobiidae and Atopomelidae). *Bulletin et Annales de la Société Royal d'Entomologie de Belgique*, 110: 170–172.
- Fain, A. 1976a. Faune de Madagascar, Arachnides, Acariens, Astigmata, Listrophoroidea. *ORSTOM, CNRS Paris*, 42: 1–131.
- Fain, A. 1976b. Nouveaux acariens parasites de la superfamille Listrophoroidea (Astigmata). *Acta Zoologica and Pathologica Antverpiensia*, 64: 37–67.
- Fain, A. 1977. Notes on the listrophoroid mites of New Guinea (Acarina: Listrophoroidea). *Journal of Medical Entomology*, 14: 279–297.
- Fain, A. 1979. Diagnoses de nouvelles especes du genre *Listrophoroides* Hirst, 1923 (Acari, Astigmata). *Bulletin de la Société royal Belge d'Entomologie*, 115: 190–193.
- Fain, A. 1981. Le genre *Listrophoroides* Hirst, 1923 (Acari, Astigmata, Atopomelidae) dans la region Orientale. *Bulletin de l'Institut royal des Sciences naturelles de Belgique (Entomologie)*, 53: 3–122.
- Fain, A. 1994. Adaptation, specificity and host-parasite coevolution in mites (Acari). *International Journal for Parasitology*, 24:1273–1283
- Fain, A. 2001. Notes on a small collection of mites (Acari) parasitic on bats in the Philippines. *Acarologia*, 42: 67–74.
- Fain, A. & F.S. Lukoschus. 1977. Une nouvelle espèce du genre *Atopomelus* Trouessart, 1917 (Acarina, Astigmata, Listrophoroidea). *Bulletin et Annales de la Société Royal d'Entomologie de Belgique*, 113: 29–31.
- Farris, J.S. 1969. A successive approximations approach to character weighting. *Systematic Zoology*, 18: 374–385.
- Ferris, G.F. 1932. Ectoparasites of marquesan rats. *Bernice P. Bishop Museum Bulletin*, 98: 117–127.
- Grandjean, F. 1939. La chaetotaxie des pattes chez les Acarididae. *Bulletin de la Société Zoologique de France*, 64: 50–60.
- Griffiths, D.A., Atyeo, W.T., Norton, R.A. & C.A. Lynch. 1990. The idiosomal chaetotaxy of astigmatid mites. *Journal of Zoology (London)*, 220: 1–32.
- Heaney, L.R. 1986. Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Biological Journal of the Linnean Society*, 28: 127–165
- Heaney, L.R. 1993. Biodiversity patterns and the conservation of mammals in the Philippines. *Asia Life Sciences* 2: 261–274.

- Heaney, L.R. 2001. A decade of research on Philippine mammals: progress and challenges. *Silliman Journal*, 42: 88–108.
- Heaney, L. R., Balete, D.S., Dolar, L., Alcalá, A.C., Dans, A., Gonzales, P.C., Ingle, N., Lepiten, M., Oliver, W., Rickart, E.A., Tabaranza, B.R. Jr. & R. C. B. Uzzurum. 1998. A synopsis of the mammalian fauna of the Philippine Islands. *Fieldiana Zoology new series*, 88:1–61.
- Heaney, L. R., Balete, D.S., Dolar, L., Alcalá, A.C., Dans, A., Gonzales, P.C., Ingle, N., Lepiten, M., Oliver, W., Rickart, E.A., Tabaranza, B.R. Jr. & R. C. B. Uzzurum. 2002. A synopsis of the mammalian fauna of the Philippine Islands. http://www.fieldmuseum.org/philippine_mammals/Precursor.htm
- Heaney, L.R., Heideman, P.D., Rickart, E.A., Uzzurum, R.B., & J.S.H. Klompen. 1989. Elevational zonation of mammals in the central Philippines. *Journal of Tropical Ecology*, 5: 259–280.
- Heaney, L. R., & E.A. Rickart. 1990. Correlation of clades and clines: geographic, elevational, and phylogenetic distribution patterns among Philippine mammals. Pp. 321–332. In G. Peters & R. Hutterer (eds), *Vertebrates in the Tropics*. Museum Alexander Koenig, Bonn.
- Hutterer, R. 2005. Order Erinaceomorpha. Pp. 212–219. Order Soricomorpha. Pp. 220–311. In D.E. Wilson & D. M. Reeder (eds), *Mammal Species of the World. A Taxonomic and Geographic Reference*. 3rd edition. Johns Hopkins University Press, Baltimore.
- Jansa, S., Barker, K. & L. R. Heaney. (in press) Molecular phylogenetics and divergence time estimates for the endemic rodents of the Philippine Islands: Evidence from mitochondrial and nuclear gene sequences. *Systematic Biology*.
- Klompen, J.S.H. Phylogenetic relationships in the mite family Sarcoptidae (Acari: Astigmata). *Miscellaneous Publications. Museum of Zoology, University of Michigan*, 180: 1–154.
- Mironov, S.V. & J. Dabert. 1999. Phylogeny and co-speciation in feather mites of the subfamily Avenzoariinae (Analgoidea: Avenzoariidae). *Experimental & Applied Acarology*, 23: 525–549.
- Musser, G. G., & M.D. Carleton. 2005. Superfamily Muroidea. Pp. 894–1531. In D.E. Wilson & D. M. Reeder (eds), *Mammal Species of the World. A Taxonomic and Geographic Reference*. 3rd edition. Johns Hopkins University Press, Baltimore.
- Nixon, K.C. 2000. WinClada. Version 0.9. 0.9.99m24. Program and documentation in cladistic.com. Ithaca, New York.
- Norton, R.A. 1998. Morphological evidence for the evolutionary origin of Astigmata (Acari: Acariformes). *Experimental and Applied Acarology*, 22: 559–594.
- O'Connor, B.M. 1982. Astigmata. Pp. 146–169. In S.B. Parker (ed.), *Synopsis and Classification of Living Organisms*, vol. 2. McGraw-Hill, New York.
- O'Connor, B.M. 1987. Host associations and coevolutionary relationships of astigmatid mite parasites of New World primates. 1. Families Psoroptidae and Audycoptidae. *Fieldiana Zoology*, 39: 245–260.
- Oliver, W.L.R. & L.R. Heaney. 1996. Biodiversity and conservation in the Philippines. *IZN (International Zoo News)*, 43: 329–337
- Page, R.D.M. 2001. NDE: NEXUS Data Editor 0.5.0. University of Glasgow, Glasgow.
- Radford, C.D. 1940. Notes on some species of parasitic mites. *Parasitology*, 32: 91–104.
- Ramery, R.R., Kelley, S.T., Boyce, W.M. & B.D. Farrell. 2000. Phylogeny and host specificity of psoroptic mange mites (Acarina: Psoroptidae) as indicated by ITS sequence data. *Journal of Medical Entomology*, 37: 791–796.
- Rickart, E.A., Heaney, L.R., Goodman, S.M. & S. Jansa. 2005. Review of the Philippine genera *Chrotomys* and *Celaenomys* (Murinae) and description of a new species. *Journal of Mammalogy* 86: 415–428.
- Ruedi, M. & P. Vogel. 1995. Chromosomal evolution and zoogeographic origin of Southeast Asian shrews (genus *Crocidura*). *Experientia*, 51: 174–178.
- Sorenson, M.D. 1999. TreeRot. Version 2. University of Boston, Boston.
- Steppan, S., Zawadzki, Ch. & L.R. Heaney. 2003. Molecular phylogeny of the endemic Philippine rodent *Apomys* (Muridae) and the dynamics of diversification in an oceanic archipelago. *Biological Journal of the Linnean Society*, 80: 699–715.
- Swofford, D.L. 2001. PAUP. Phylogenetic Analysis Using Parsimony (* and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Trouessart, E.L. 1893. Notes sur les Sarcoptides pilicoles (Listrophorinae). *Compte Rendu hebdomadaire des séances and mémoires de la Société de Biologie*, 5: 698–700.
- Uchikawa, K., O'Connor, B.M. & H. Klompen. 1991. New Myobiidae (Acarina: Trombidiformes) from Philippine mammals. *Zoological Science (Tokyo)*, 8: 157–168.
- Whitaker, J.O. Jr. & L.A. Durden. 1987. Some ectoparasitic mites from mammals from Sulawesi Utara, Indonesia. *Entomological News*, 98: 26–30.
- Womersley, H. 1943. Australian species of Listrophoridae Canest. (Acarina) with notes on the genera. *Transactions of the Royal Society of South Australia*, 67: 10–19.
- Zumpt, F. 1961. *The Arthropod Parasites of Vertebrates in Africa South of the Sahara (Ethiopian region)*. Vol. I (Chelicerata). South African Institute for Medical Research, Johannesburg. 457 pp.

