

FUR-MITES OF THE GENUS *ATOPOMELUS* TROUESSART, 1918  
(ACARI: ATOPOMELIDAE) LIFE-CYCLE  
PHYLOGENY AND HOST PARASITE-ASSOCIATIONS

BY A.V. BOCHKOV\*<sup>1,2</sup>, P.B. KLIMOV<sup>1</sup>, & B.M. OCONNOR<sup>1</sup>

(Accepted January 2005)

ATOPOMELIDAE  
MAMMALIAN ECTOPARASITES  
HOST-PARASITE ASSOCIATIONS  
PHYLOGENY  
SYSTEMATICS  
MITES

**SUMMARY:** The genus *Atopomelus* TROUESSART, comprising fur mites of eulipotyphlan mammals, is revised, and all postembryonic stages are described for the first time. An emended diagnosis of the genus, descriptions of three previously recognized species and two new species, *A. hylomys* sp.nov. and *A. priapus* sp.nov., and keys to males and females are provided. Phylogenetic relationships among the species are analyzed using cladistic methods. Species of the atopomelid genera *Lemuroptes* LAWRENCE, *Micropotamogalichus* FAIN, and *Didelphoe-cius* FAIN were selected as close outgroups and *Listrophorus leuckarti* (Listrophoridae) was chosen as a distant outgroup. A single, most parsimonious cladogram was obtained (*A. talpae* (*A. crocidurae* (*A. locusta* (*A. hylomys* + *A. priapus*))))). *Atopomelus* species primarily parasitize Oriental insectivores, gymnures of the genus *Hylomys* (Erinaceidae) (3 mite species) and shrews of the genus *Crocidura* (Soricidae) (*A. crocidurae*). A single species, *A. talpae* is known from *Talpa romana* (Talpidae) in Italy. Plesiomorphic characters of this genus suggest that it's the ancestor of the clade was associated with the basal Eulipotyphla and hedgehogs as the earlier derivative of this host clade. The occurrence of *A. talpae* on *T. romana* is probably the result of an ancient host switch from gymnures inhabiting Europe in the Oligocene. The association between atopomelids and Oriental shrews is probably also secondary. Host switching of atopomelids onto Oriental *Crocidura*, probably happened with pioneering shrew species dispersing into this region from the Palaearctic.

INTRODUCTION

Fur-mites of the family Atopomelidae are permanent, mono- or oligoxenous parasites of marsupials, "insectivores", primates, and rodents. These mites are known from both hemispheres but most of the diversity is found in the Neotropical, Afrotropical, Oriental, and Aus-

tralian regions. To date, this family includes 47 genera and more than 370 species (OCONNOR, 1982; BOCHKOV & FAIN, 2003). Most of the atopomelid genera or subgenera are associated with particular host groups and, therefore, are good potential models for analysis of co-phylogenetic evolution between parasites and hosts (FAIN, 1994).

1. Museum of Zoology, University of Michigan, 1109 Geddes Avenue, Ann Arbor, Michigan 48109, USA

\* Corresponding author

2. Zoological Institute, Russian Academy of Sciences, Universitetskaya embankment 1, St. Petersburg 199034, Russia

To date, the only atopomelid taxon to be analyzed phylogenetically is the subgenus *Marquesania* of the genus *Listrophoroides* (BOCHKOV & FAIN, 2003). There are several reasons why phylogenetic and co-phylogenetic studies of this family have been limited. First, the external morphology, especially the leg setation, has not been adequately described for many taxa. Second, the morphology of the immature stages has never been described in detail, and the developmental homology of leg and idiosomal setae has never been established. Third, many genera and species of potential hosts have not been examined for these parasites. And finally, many species were described from one or only a few specimens, rendering some published host associations questionable (BOCHKOV & FAIN, 2003).

The present paper is a systematic revision of the genus *Atopomelus* Trouessart, 1918, including an emended diagnosis of this genus, descriptions of previously recognized and two new species and keys to males and females. Morphology of all postembryonic stages and homology of leg and idiosomal setae with those of other Astigmata are studied in detail for the first time in this family. Finally, the phylogenetic relationships among species of this genus and their host associations are analyzed.

The genus *Atopomelus* was established by TROUSSERT (1918) for a single species *Atopomelus locusta* TROUSSERT, 1918, described from *Hylomys* (= *Neotetracus*) *sinensis* (TROUSSERT, 1909) (Erinaceidae) in China. There has been some confusion regarding the publication date of this work, with prior authors (e.g. RADFORD, 1950; FAIN & LUKOSCHUS, 1977; FAIN *et al.*, 1973) giving the date as 1917. Although the paper was presented at the meeting of the Société Zoologique de France on 11 December 1917, the issue of the society's "Bulletin" containing the published paper is dated 15 March 1918. *Atopomelus locusta* has never been recollected nor fully re-described since the original description. Two additional species have been described more recently. *Atopomelus crociduræ* FAIN & LUKOSCHUS, 1977 was described from two females collected from *Crocidura attenuata aequicauda* ROBINSON & KLOSS, 1918 (= *Crocidura aequicauda* [*sic*]) (Soricidae) from Sumatra (FAIN & LUKOSCHUS, 1977) and *A. talpæ* FAIN, LUKOSCHUS & CAUWENBERGE, 1973, was

described from both sexes collected from *Talpa romana* THOMAS, 1902 (Talpidæ) in Italy (FAIN *et al.*, 1973).

#### MATERIALS AND METHODS

*Materials.* Most specimens examined in this study were collected by the authors from dried or fluid preserved host specimens in various institutions. Particularly, large series of host specimens collected as part of recent surveys of small mammals in the Philippines by Dr. Lawrence HEANEY of the Field Museum of Natural History and on the island of Borneo by Dr. Antonia GOROG of the University of Michigan Museum of Zoology were available. These materials were supplemented by study of type specimens when available. Collection locality information is taken from the original host data. Some place names, particularly early 20<sup>th</sup> century Chinese localities, could not be located in modern references due to original inaccuracies or changes in transliteration. These are reproduced as on the original host specimen labels. In the descriptions below, idiosomal chaetotaxy follows GRIFFITHS *et al.* (1990). The leg chaeto- and solenidiotaxy follow GRANDJEAN (1939). All measurements are given in micrometers ( $\mu\text{m}$ ) 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 pretarsal ambulacrum; length of the tibiotarsus = length from most basal point of this segment to the apex of the tarsus, excluding pretarsal ambulacrum. Names of hosts follow WILSON & REEDER (1992) except that we follow more recent works that support the polyphyly of the traditional mammalian order Insectivora (or Lipotyphla) and recognize two orders, Eulipotyphla (including Erinaceidae, Solenodontidae, Soricidae, and Talpidæ) and Afrosoricida (including Chrysochloridae and Tenrecidae) (STANHOPE *et al.*, 1998). Specimen depositories and reference numbers are cited using the following abbreviations:

BMOG # — B.M. O'CONNOR reference number  
EMEC — Essig Museum of Entomology, University of California, Berkeley, USA  
FMNH — Field Museum of Natural History, Chicago, USA  
IRSNB — Institut royal des Sciences naturelles de Belgique, Brussels, Belgium  
ISZAF — Istituto Sperimentale per la Zoologia Agraria, Florence, Italy  
MBBJ — Museum Zoologicum Bogoriense, Bogor, Indonesia  
MNHN — Muséum National d'Histoire Naturelle, Paris, France  
MRAC — Musée royal de l'Afrique Centrale, Tervuren, Belgium  
MVZ — Museum of Vertebrate Zoology, University of California, Berkeley, USA  
NHMV — Naturhistorisches Museum, Vienna, Austria  
RMNH — Nationaal Natuurhistorische Museum, Leiden, the Netherlands  
UMMZ — Museum of Zoology, University of Michigan, Ann Arbor, USA  
UPPC — Philippine National Acarological Collection, Los Baños, Philippines  
USNM — National Museum of Natural History, Smithsonian Institution, Washington, USA  
ZISP — Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia

*Cladistics.* Three species representing genera of Atopomelidae that are morphologically similar to *Atopomelus* were used as close outgroups: *Didelphoeceus surinamensis* FAIN, 1976, from *Caluromys philander* (L., 1758) (Didelphimorphia: Didelphidae), *Lemuroptes potto* FAIN, 1972, **stat. nov.** (*L. primarius potto*) from *Perodicticus potto* (MÜLLER, 1766) (Primates: Loridae), and *Micropotamogalichus congoensis* FAIN, 1970 from *Micropotamogale ruwenzorii* (DE WITTE & FRECHKOP, 1955) (Afrosoricida: Tenrecidae). The original descriptions of *Lemuroptes* spp., and *Micropotamogalichus* (monotypic) contain some inaccuracies. Therefore we also give here emended diagnoses based on re-examination of the type materials (see Appendix). The genus *Didelphoeceus* is in need of a separate taxonomic review, therefore, we simply selected a species showing many ancestral cha-

acter states for this genus. *Listrophorus leuckarti* PAGENSTECHEER, 1861 (Listrophoridae), whose morphology has been recently re-described in detail (WURST, 1993), was chosen as a more distant outgroup, because the family Listrophoridae has been considered as closely related to the Atopomelidae (O'CONNOR, 1982).

Preparing and editing of the data matrix were done using NEXUS Data Editor 0.5.0 (PAGE, 2001). In total, 9 taxa and 46 characters were included in the analysis (TABLES 1 and 2). Reconstruction of phylogenetic relationships was performed with PAUP 4.0\* b10 for Macintosh (SWOFFORD, 2001). Maximum parsimony analysis was used for the estimation of phylogeny. All characters were unordered. The exact search option (Branch and Bound) was used due to the relatively small number of taxa. Bremer branch support values were calculated in PAUP with a command file generated in TreeRot.v2 (SORENSEN, 1999). For analysis of character distribution, we used DELTRAN (slow) optimization. Drawing and editing of trees were done with WINCLADA (NIXON, 1999).

#### TAXONOMY

Family Atopomelidae GÜNTHER, 1942

Genus *Atopomelus* TROUESSART, 1918

*Atopomelus* TROUESSART, 1918: 155.

Type species: *Atopomelus locusta* TROUESSART, 1918, by monotypy

*Diagnosis.* Adults: Postscapular shield undivided, hair clasping organs of coxae I not developed, anterior apodemes of coxae I and II fused, clasping organs of coxae II represented by pair of well developed valves, paraproctal setae *ps1* absent, pretarsal ambulacra of legs II-III strongly flattened dorsoventrally. Male: hysteronotal shield well developed, adanal suckers present, legs IV hypertrophied, trochanters IV with ventral spur, femur and genu IV fused, tibiotarsus saber-like, without pretarsal ambulacrum or sucker-like setae, subequal in length to femurogenu. Female: idiosoma strongly elongated, hysteronotal shield absent, hysterosoma completely covered by triangular cuticular microtrichae.

1. Gnathosoma length and width subequal (0), distinctly elongated (1); CI 0.5
2. Attachment organs of coxae I present (0), absent (1); CI 1
3. Attachment organs of coxae II represented by striated membranes (0), by valves with complicated system of sclerites (1); CI 1
4. Postscapular shield in female divided medially (0), not divided (1); CI 1
- 5\*. Undivided postscapular shield in female with posterior median incision (0), without (1); CI 1
6. Postscapular shield in male divided medially (0), entire, strongly reduced (1), entire, covering most part of propodonotum (2); CI 1
7. Undivided postscapular shield in male unornamented (0), ornamented (1); CI 1
8. Hysteronotal shield in male divided medially (0), entire (1); CI 1
9. Undivided hysteronotal shield in male unornamented (0), ornamented (1); CI 0.5
10. Genital valves fused anteriorly (0), widely separated (1); CI 1
11. Genital papillae in female separated (0), contiguous (1); CI 1
- 12\*. Opisthosomal copulatory papilla in female absent (0), present (1); CI 1
13. Distal part of spermatheca narrow (0), broadened or inflated (1); CI 1
14. Scales of median part of female hysteronotum longer than wide (0), wide than longer (1); CI 0.5
15. Opisthonotum in male behind hysteronotal shield smooth (0), covered by scales or protuberances (1); CI 0.5
16. Aedeagus short (0), hypertrophied (1); CI 0.5
17. Opisthosomal lobes in male present (0), absent (1); CI 0.5
- 18\*. Setae *vi* present (0), absent (1); CI 1
19. Setae *f2* and *h3* in female short (0), macrosetae (1); CI 1
20. Setae *ps2-3* in female present (0), absent (1); CI 0.33
21. Setae *e1* in male subequal to *c2* (0), distinctly longer (1); CI 1
22. Setae *e2* shorter than *e1* (0), subequal or longer (1); CI 0.33
23. Setae *ps2* in male present (0), absent (1); CI 1
24. Setae *ps3* in male present (0), absent (1); CI 1
25. Adanal suckers in male present (0), absent (1); CI 1
26. Coxae IV in female widely separated (0), fused (1); CI 1
27. Dorsal spur of trochanter IV in male absent (0), present (1); CI 0.5
28. Ventral spur of trochanter IV in male absent (0), present (1); CI 1
29. Ventral spur of trochanter IV in homeomorph male with single apex (0), bifurcate (1); CI 1
30. Setae *pR* II absent (0), present (1); CI 1
31. Setae *sR* III present (0), absent (1); CI 1
32. Genu and femur I-II smooth ventrally (0), striated (1); CI 1
33. Femur and genu IV in male separated and not hypertrophied (0), fused and hypertrophied (1); CI 0.5
- 34\*. Femurogenu IV in male without spurs (0), with spurs (1); CI 1
- 35\*. Femurogenu IV in male with 1 spur (0), with 2 spurs (1); CI 1
36. Tarsus II not curved (0), curved ventral (1); CI 1
- 37\*. Tibia and tarsus III-IV separated (0), fused (1); CI 1
38. Setae *wa* and *ra* II filiform (0), strongly inflated in posterior half (1); CI 1
39. Tibiotarsus IV in male not modified (0), modified (1); CI 0.5
40. Setae *s* I-II present (0), absent (1); CI 0.5
41. Seta *d* III in male shorter than tibiotarsus (0), longer or subequal (1); CI 0.5
42. Seta *d* III-IV in female shorter than tibiotarsus (0), longer or subequal; CI 0.33
43. Setae *d* IV in male short (0), macroseta (1); CI 1
44. Seta *ra* IV in male filiform (0), modified (1); CI 0.5
45. Ambulacrum of leg II-III not flattened (0), flattened dorso-ventrally (1); CI 0.5
46. Ambulacrum of legs IV in male present (0), absent (1); CI 0.5

TABLE 1. — List of characters (0 – plesiomorphy, 1 – apomorphy, CI – consistent index, \* – autapomorphy)

*Description.* Adults. Gnathosoma, except for *A. talpae*, oblong, approximately 1.4 times longer than wide, bearing pair of well developed ventro-lateral valves. Idiosomal dorsum bearing propodosomal and undivided postscapular shields. Hair clasping organs of coxae I not developed, clasping organs of coxae II represented by pair of well developed valves. Setation of idiosoma: *scx*, *si*, *se*, *c2*, *c3*, *cp*, *d1*, *d2*, *e1*, *e2*, *f2*, *h1*, *h2*, *h3*, *ps3*, *1a*, *3a*, *3b*, *g*, *4a*; setae *ps2* present in male of *A. talpae*. Cupules not observed.

Legs inserted ventrally, coxal fields III and IV closely associated. Paired anterior apodemes of all coxae fused mesally. Ventral surfaces of femora and genua I-II covered by fine longitudinal striation. Femora I-II slightly expanded paraxially in anterior half. Tarsus II strongly modified, rotated and curved paraxially. All pretarsal ambulacra, except for ambulacra of legs I, strongly flattened dorso-ventrally. Setation of legs I-IV: I trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*, *σ1*), tibia 2 (*gT*, *φ*), tarsus 10-11 (*wa*,

*ra, la, ba, [s] d, e, f, ε, ω1 and ω3*); II trochanter 1 (*pR*), femur 1 (*vF*), genu 3 (*cG, mG, σ*), tibia 2 (*gT, φ*), tarsus 8-9 (*wa, ra, la, ba, [s], d, e, f, ω*); III trochanter 1 (*sR*), femur 0, genu 1 (*σ*), tibiotarsus 8 (tibia — *kT, φ*, tarsus — *wa, ra, s, d, e, f*); IV trochanter 0, femur 0, genu 0, tibiotarsus 8 (tibia — *kT, φ*, tarsus — *wa, ra, d, e, f*). Setae *wa* and *ra* II strongly inflated in basal half. Setae *wa* and *ra* on legs III and IV, except for leg IV in male, thorn-like. Setae *s* I-II present only in *A. talpae*.

Male. Idiosoma elongate, 2.5 times longer than wide. Postscapular and hysteronotal shields well

developed, covering most part of dorsal surface, only idiosomal surface behind level of setae *e1* unsclerotized. Setae *h1* thin and short. Postgenital shield absent. One pair of small adanal suckers present. Opisthosoma without membranous terminal expansion. Legs IV hypertrophied, at least 1.5 times longer than legs III. Trochanter IV with ventral spur, femur and genu IV fused and strongly sclerotized. Tibiotarsus saber-like, without ambulacrum, subequal to femurogenu, all its setae filiform, setae *d* macrosetae.

Species	Character				
	1	1111111112	2222222223	3333333334	444444
	1234567890	1234567890	1234567890	1234567890	123456
<i>Listrophorus leuckarti</i>	0000-0-0--	0000000000	00000000-0	000--00000	000000
<i>Didelphoecius surinamensis</i>	0000-0-10-	0000101100	00000000-1	000--01000	000100
<i>Lemuroptes potto</i>	0000-100--	0001010100	01001000-0	1011-01011	010101
<i>Micropotamogalichus congoensis</i>	1000-000--	0001001100	01001000-0	100--0100?	010100
<i>Atopomelus crocidurae</i>	1111020101	0000001111	1011010111	0111111111	111011
<i>Atopomelus hylomys</i>	1111021100	1111101111	1011011101	0111111111	101011
<i>Atopomelus locusta</i>	1111021111	1011101111	1111011101	0111011111	111011
<i>Atopomelus priapus</i>	1111021110	1011111111	1011011101	0111111111	001011
<i>Atopomelus talpae</i>	011112010-	0000001111	1101010111	0110-11110	111011

TABLE 2. — Data matrix. (0 plesiomorphy, 1 apomorphy, - inaplicable)

Female. Idiosoma strongly elongate, 3-4 times longer than wide. Hysteronotal shield absent. Unsclerotized propodonotal surface covered by transverse striations and broadly rounded scales, ventral surface of propodosoma covered by longitudinal striations and rounded protuberances. Hysterosoma completely covered by large triangular microtrichae. Epigynum fused with anterior apodemes of coxae III. Genital valves situated between coxae III. Opisthonal setae *f2* and *h3* macrosetae. Two pairs of reduced genital papillae present.

*Description of developmental stages based on A. crocidurae.* Larva (FIG. 11A-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, 3b*. Setae *h2* macrosetae, situated dorsally. Leg setation: I trochanter 0, femur 1 (*vF*), genu 3 (*cG, mG, σ1*), tibia 2 (*gT, φ*), tarsus 9 (*wa, ra, ba, la, 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 — *wa, ra, la, d, e, f*). Solenidion *σ* III very short.

Protonymph (FIG. 11 F-L). Postscapular shield absent. Setae *f2, h3, ps3*, and *g* added. Only setae *f2* macrosetae. One pair of indistinct genital papillae present between coxae IV. Epimera IV fused mesally. Leg setation with setae *d, ra*, and *wa* of tarsus IV added, and solenidion *σ* of genu III subequal in length to this segment.

Teleonymph (FIG. 12). Postscapular shield absent. Setae *3a* and *4a* 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. Setae *f2* and *h3* macrosetae. Two pairs of indistinct genital papillae between coxae IV. Setae *3a* microsetae, situated between coxae IV in anterior part; setae *f2* and *h3* macrosetae.

*Morphological notes.* 1. The hair clasping organs of coxae II consist of a pair of valves derived from the anterior and posterior coxal apodemes and the sur-

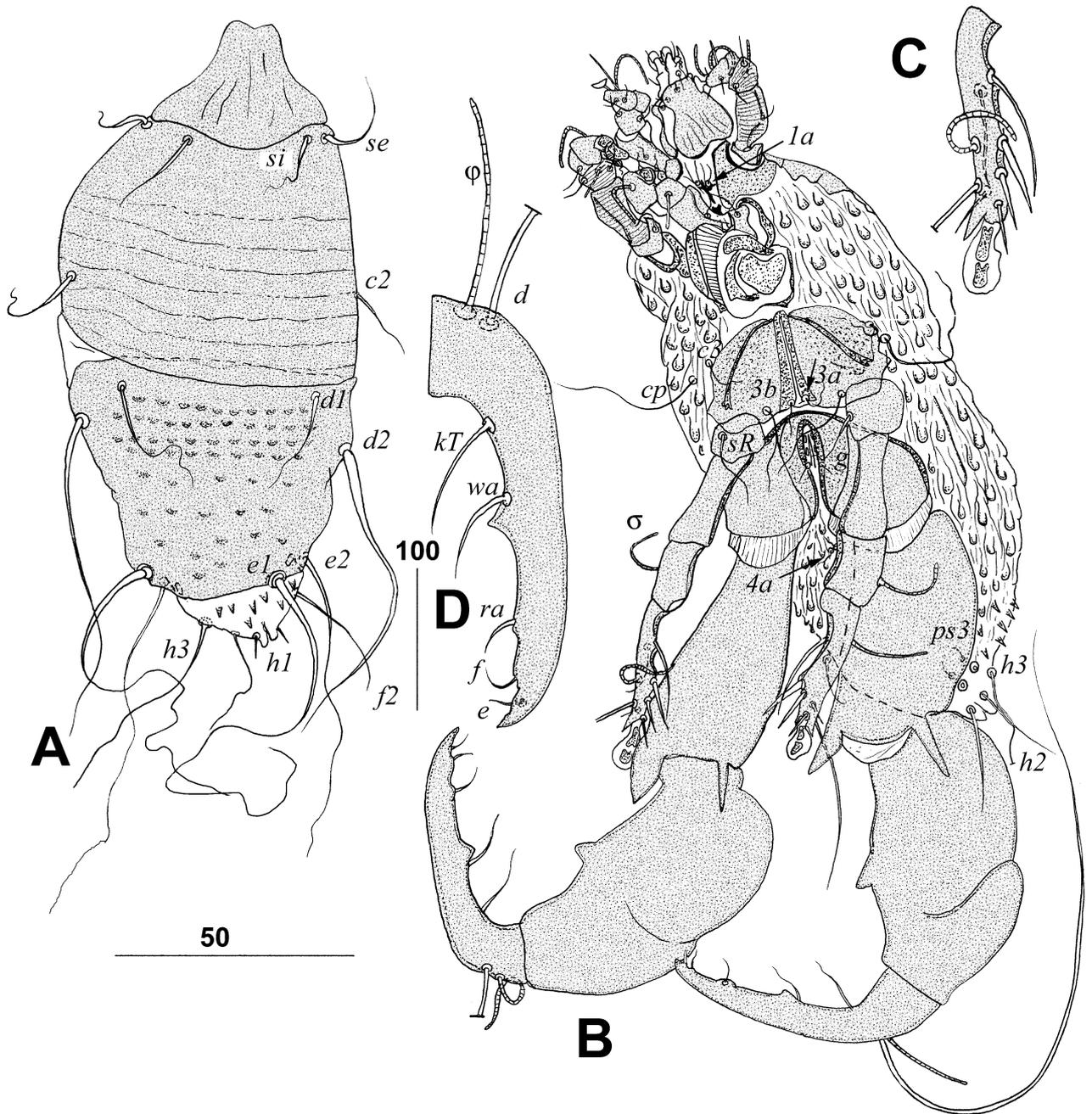


FIG. 1 (A-D) : *Atopomelus locusta*, male. A. — Dorsal view. B. — Ventral view. C — Tibiotarsus III, lateral. D. — Tibiotarsus IV, lateral. Scale bars 100  $\mu\text{m}$  (A, B) and 50  $\mu\text{m}$  (C, D).

face of the coxal fields (FIG. 10 B). The inner surface of the valves is distinctly striated for stronger attachment to the host hair.

2. Tarsus I and II are both strongly modified. All their setae, however, retain their ancestral positions. Tarsus I is less modified than tarsus II. This segment is shortened, bent terminally, and situated on the inner side of the dorsally expanded tibia (FIGS. 2 F, 14 A, B). Tarsus II is further modified. It is flattened basally, and setae *wa*, *ra*, *la* and *s* (if present) are situated on the same side. The apical part of tarsus II is curved paraxially forming a functional attachment organ (FIGS. 2 G, 14 C).

Species group “*locusta*”. The three species associated with Erinaceidae form a distinct lineage characterized by the following:

Male: Postscapular shield covered by transverse lines. Opisthonal surface behind hysteronotal shield covered by tubercles. Opisthogaster completely covered by scales or tubercles. Dorsal spur present on trochanter IV, ventral spur not bifurcate, except for heteromorphic male of *A. hylomys* sp. nov. Female: Hysteronotum covered by scales that wider than long. Genital papillae contiguous. Distal part of spermatheca inflated.

*Atopomelus locusta* TROUESSART, 1918

*Atopomelus locusta* TROUESSART, 1918: 157;

FAIN *et al.*, 1973: 29; FAIN & LUKOSCHUS, 1977: 29

(FIGS. 1-3)

*Diagnosis.* Male: Hysteronotal shield tuberculate. Ventral spur of trochanter IV with single apex; dorsal spur well developed, slightly longer than ventral spur. Female: Vulvar plates widely separated each from other. Median scales of hysterosoma in form of wide triangles. Genital papillae contiguous. Distal part of spermatheca inflated, globose. Setae *d* III-IV subequal in length to respective tibiotarsi, excluding ambulacra.

*Description* (specimens from *Hylomys sinensis*). Male (n=3, FIG. 1). Body elongate, length/width ratio 2.5 : 1. Postscapular shield with transverse lines. Hysteronotal shield trapeziform, covered by indistinct tubercles, bearing 3 pairs of setae, *d1*, *d2*, and *e1*. Setae *d1* short, *d2* subequal or 2-4 times longer than

*d1*. Pair of round unsclerotized patches near bases of setae *d2* present or absent. Setae *e1* and *e2* range from subequal in some specimens, to *e2* significantly shorter, 1:10. Length ratio between postscapular and hysteronotal shields subequal, 1.2:1. Unsclerotized surface of opisthosoma tuberculate. Setae *f2* 2.5-6 times shorter than *h3*. Aedeagus short, about 3 times shorter than femur III. Leg IV 1.8 times longer than leg III. Setae *d* I-II subequal in length to respective solenidia *ω1*; seta *d* III subequal in length to tibiotarsus, excluding ambulacrum. Trochanter IV with ventral and dorsal spurs, ventral spur with single apex, dorsal spur well developed, 1.3 times longer than ventral spur, situated in basal part of this segment. Femurogenu IV with one ventral spur. Tarsus IV with single pointed apex (FIG. 1D).

*Measurements.* Body 450-540 long, 165-230 wide; gnathosoma 70-75 long, 45-55 wide; prescapular shield 100-120 long; postscapular shield 175-200 long; hysteronotal shield 130-165 long; leg III 230-300 long; leg IV 485-550 long; femurogenu IV 175-185 long; tibiotarsus III 75-80 long; tibiotarsus IV 145-155 long; ventral spur of trochanter IV 27-30 long, dorsal spur 40-45 long; anterior ventral spur of femurogenu IV 9-10 long. Length of idiosomal setae: *si* 35-55, *se* 55-80, *c2* 55-60, *c3* 30-35, *cp* 110-145, *d1* 40-75, *d2* 55-320, *e1* 190-215, *e2* 20-187, *f2* 30-85, *h1* 8-10, *h2* 50-60, *h3* 180-210, *4a* and *ps* — all about 7, *3a* 19-22, *3b* 25-30, and *g* 12-15. Setae *d* I — II 27-30, III 85-90, IV 240-310. Length of solenidia: *ω1* I-II about 30, *ω3* I 30-33; *φ* I-IV 60-70; *σ* I-II about 15, III 60-70.

Female (n=10, FIGS. 2, 3). Body about 4 times longer than wide. Postscapular shield well developed, covered by scale-like pattern, with posterior median incision. Length ratio of this incision and postscapular shield 1 : 4-6, width ratio 1 : 5. Setae *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, and *ps3* short, subequal in length. Hysteronotum covered medially by triangular scales that are wider than their length. Genital papillae contiguous. Genital valves widely separated from each other, triangular, each bearing setae *3a* and *g*. Sclerotized areas of coxae IV fused in posterior part, and setae *4a* situated on common sclerotized plate (FIG. 2C). Distal part of spermatheca inflated, globose (FIG. 2D). Setae *d* I-II subequal in length to respective solenidia *ω1*; setae *d* III-IV subequal in length to respective tibiotarsi, excluding ambulacra.

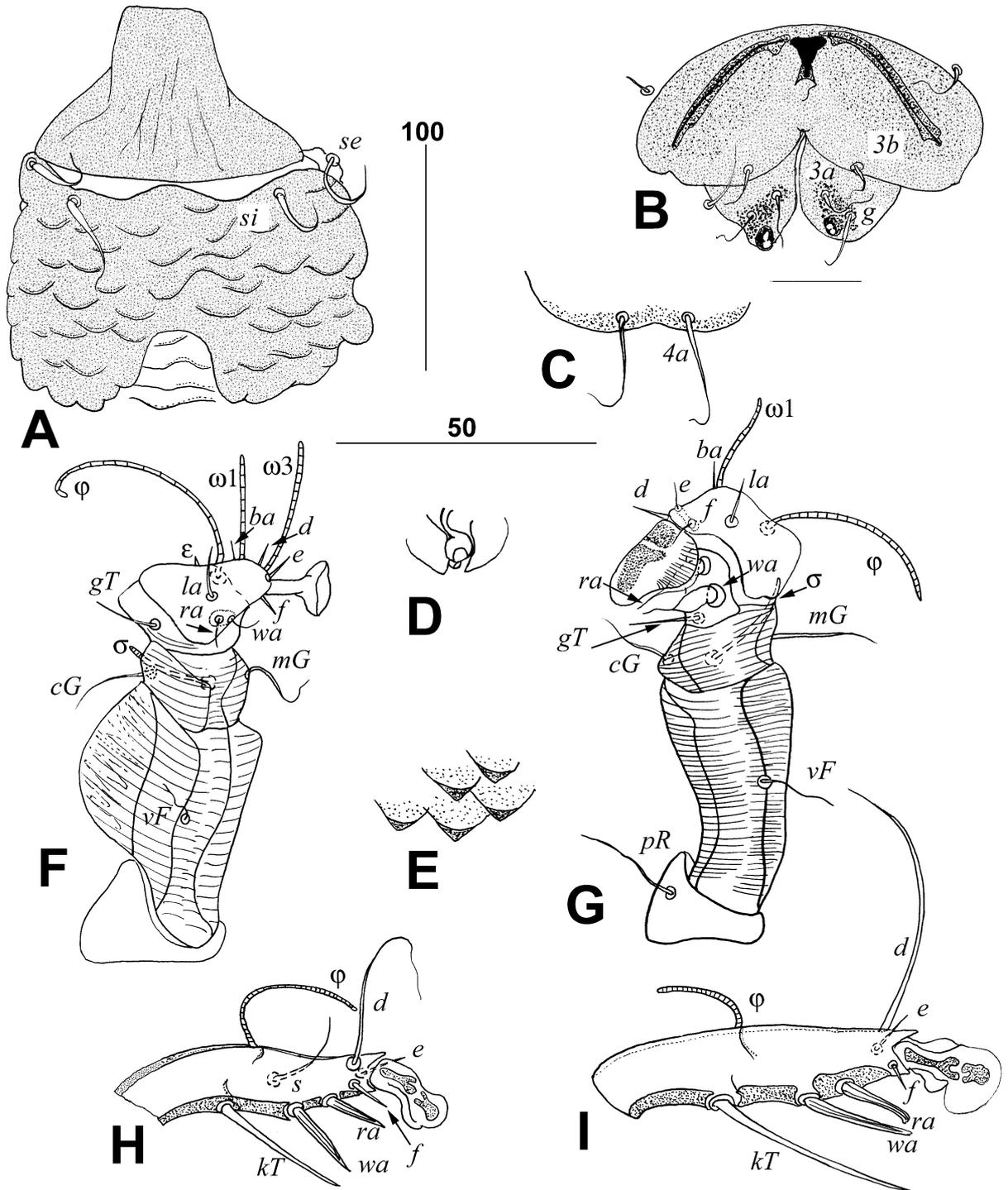


FIG. 2 (A-I). *Atopomelus locusta*, female. A. — Postscapular shield. B. — Vulva. C. — Posterior part of coxal fields IV. D. — Distal part of spermatheca. E. — Dorsal scales of idiosoma. F. — Leg I, ventral. G. — Leg II, ventral. H. — Tibiotarsus III, lateral, I. — Tibiotarsus IV, lateral. Scale bars 100  $\mu\text{m}$  (A) and 50  $\mu\text{m}$  (B-I).

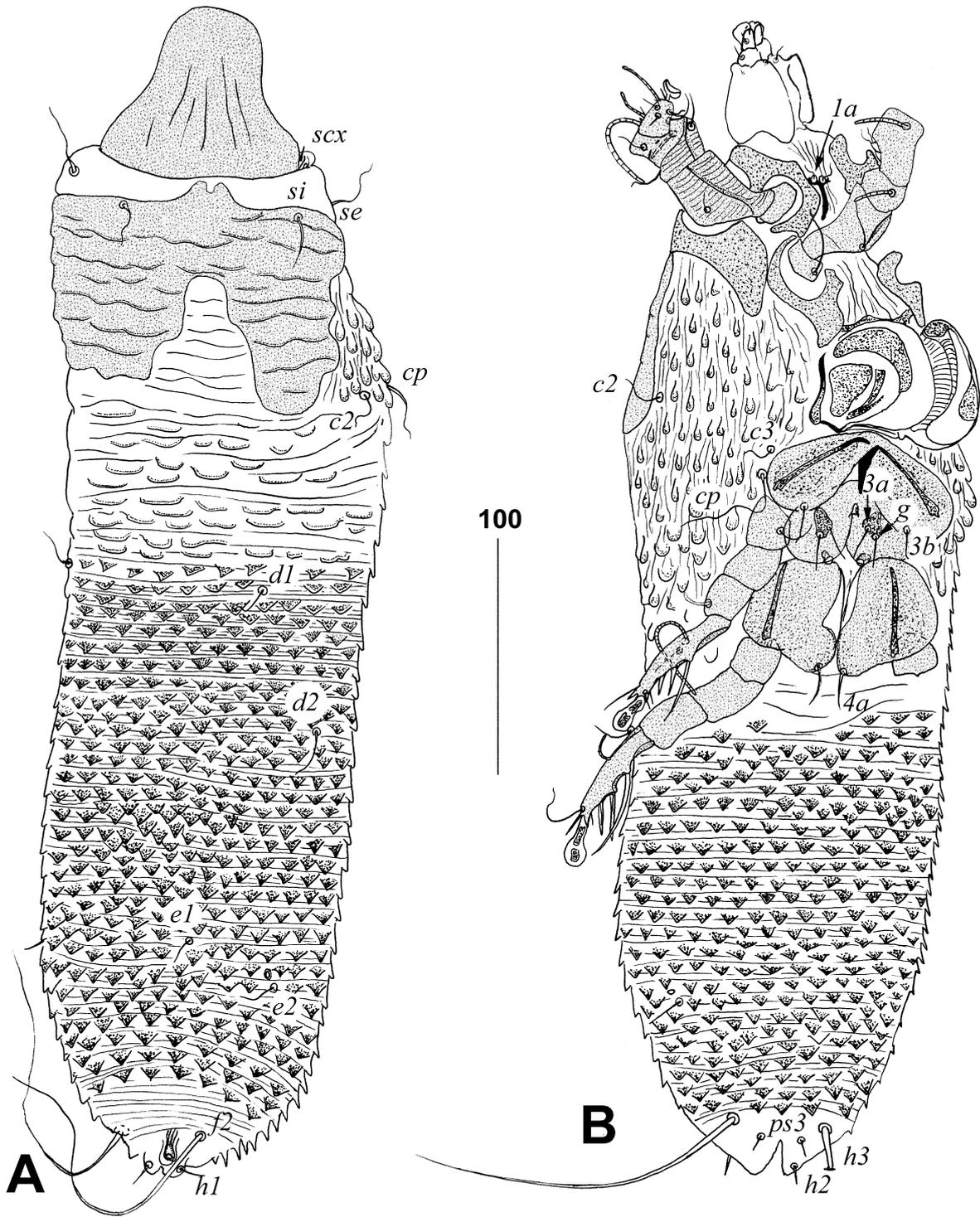


FIG. 3 (A-B). *Atopomelus locusta*, female. A. — Dorsal view. B. — Ventral view.

*Measurements.* Body 580-650 long, 165-175 wide; gnathosoma 75-85 long, 55-60 wide; prescapular shield 90-120 long; postscapular shield 85-90 long, 120-150 wide, median incision of this shield 25-30 long, 30-35 wide; leg III and IV 120-145 long; tibiotarsus III-IV 45-60 long. Length of idiosomal setae: *si* and *se* 35-45, *c2* 25-30, *c3* 15-17, *cp* 65-75, *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, *ps3* — all 22-33, *f2* and *h3* 170-180, *3a* 14-17, *3b* 19-20, *g* and *4a* 15-18. Setae *d* I-II 18-25, III-IV 45-55. Length of solenidia:  $\omega 1$  I-II 22-25,  $\omega 3$  I 27-30;  $\varphi$  I-III 40-45, IV 17-20;  $\sigma$  I-II 15-22, III 17-22.

*Material examined.* Three males, 1 female, 3 teleonymphs, and 1 protonymph (BMOC 76-0823-031) ex *Hylomys sinensis* (USNM 258128), CHINA: Sichuan Prov., Kwanshien, 29 November 1932, coll. unknown; 1 female, 3 females pharate in teleonymphal cuticle, and 1 teleonymph (BMOC 76-0823-030) ex *H. sinensis* (USNM 258129), same data; 1 female (BMOC 04-0331-086) ex *H. sinensis* (FMNH 37020), CHINA: Sichuan Prov., Dan Shi Go, 25 November 1931, coll. F.T. SMITH; 1 male and 2 females (BMOC 04-0331-088) ex *H. sinensis* (FMNH 37023), same data, 14 December 1931, coll. F.T. SMITH; 1 female (BMOC 04-0331-089) ex *H. sinensis* (FMNH 37023), CHINA: Shandong Prov., Mouping, 37° 23' N, 121° 35' E, 18 December 1931, coll. F.T. SMITH; 1 female (BMOC 04-0331-092) ex *H. sinensis* (FMNH 35777), CHINA: Yunnan Prov., Mu-cheng, 11 February 1917, coll. E. HELLER; 2 males and 11 females (BMOC 04-0331-084) ex *H. sinensis* (FMNH 38891), VIETNAM: Lao Cai Prov, Hoang Lien So'n Mts, Sa Pa, 22° 21' N, 103° 52' E, 29 November 1928, coll. DELACOUR; 19 males, 13 females, 8 teleonymphs, and 1 protonymph (BMOC 80-0124-001) ex *Hylomys suillus* MÜLLER, 1840 (FMNH 98438), MALAYSIA: Pahang, Janda-Baik, 2000 ft, 03° 21' N, 101° 53' E, 10 December 1963, coll. D.D. DAVIS; 2 males and 1 female (BMOC 04-0331-110) ex *H. suillus* (FMNH 98443), same data, 17 December 1963, coll. D.D. DAVIS (DDD 308); 2 males and 9 females (BMOC 04-0331-107) ex *H. suillus* (FMNH 32308), LAOS: Phong saly, Maylo, 10 May 1929, coll. KELLEY-ROOSEVELT expedition.

*Specimen deposition.* Lectotype and female paralectotypes (designated by FAIN & LUKOSCHUS, 1977, not examined) are deposited in MNHP. Voucher spe-

cimens from this study deposited in FMNH, UMMZ, USNM, and ZISP.

*Remarks.* Male characters are strongly variable in size and relative proportions. For example, the body length in 10 males from *H. suillus* is 425-525; length ratio of setae *f2* and *h3* is 1 : 1.3 — 6, *d1* and *d2* — 1:1.2-8. In one specimen (BMOC 76-0823-31, 1), tarsi IV are bifurcate.

*Atopomelus hylomys* sp.nov.

(FIGS. 4, 5)

*Diagnosis.* Male: Hysteronotal shield devoid of ornamentation. Dorsal spur of trochanter IV situated in median part of segment. Female: Postscapular shield with short median incision. Median scales of hysterosoma in form of broad triangles. Genital papillae contiguous. Distal part of spermatheca only slightly inflated, enclosed in small nipple-like protrusion. Setae *d* III-IV 2-2.5 times shorter than respective tibiotarsi.

*Description.* Male (holotype, FIG. 4). Body elongate, length/width ratio 2.6 : 1. Postscapular shield covered by transverse lines. Hysteronotal shield trapeziform, devoid of ornamentation, bearing 3 pairs of setae, *d1*, *d2*, and *e1*. Pair of round non sclerotized patches near to bases of setae *d2* present or absent. Setae *d2* subequal to 2 times longer than *d1*. Setae *e1* 5 times longer than *e2*. Length ratio of postscapular and hysteronotal shields subequal, 1.3:1. Unsclerotized integument of opisthosoma tuberculate. Setae *h3* 2 times longer than *f2*. Setae *h2* 2.6 times shorter than *h3*. Aedeagus short, about 3 times shorter than femur III. Legs IV 1.6 times longer than legs III. Setae *d* I -II 3 times shorter than respective solenidia  $\omega 1$ ; seta *d* III subequal in length to tibiotarsus, excluding ambulatorium. Trochanter IV with ventral and dorsal spurs, ventral spur with single apex, dorsal spur well developed, 1.3 times shorter than ventral spur, situated in median part of segment. Femurogenu IV with 2 ventral spurs. Tarsus IV with single or bifurcate apex (FIG. 4D), seta *ra* IV situated on small angular projection.

*Measurements.* Body 365, 350-380 long in 6 paratypes and 140, 130-140 wide; gnathosoma 65, 65-67 long, 45, 40-45 wide; prescapular shield 75, 70-75 long; postscapular shield 115, 115-140 long; hysteronotal shield 90, 90-110 long; leg III 200, 200-210 long;

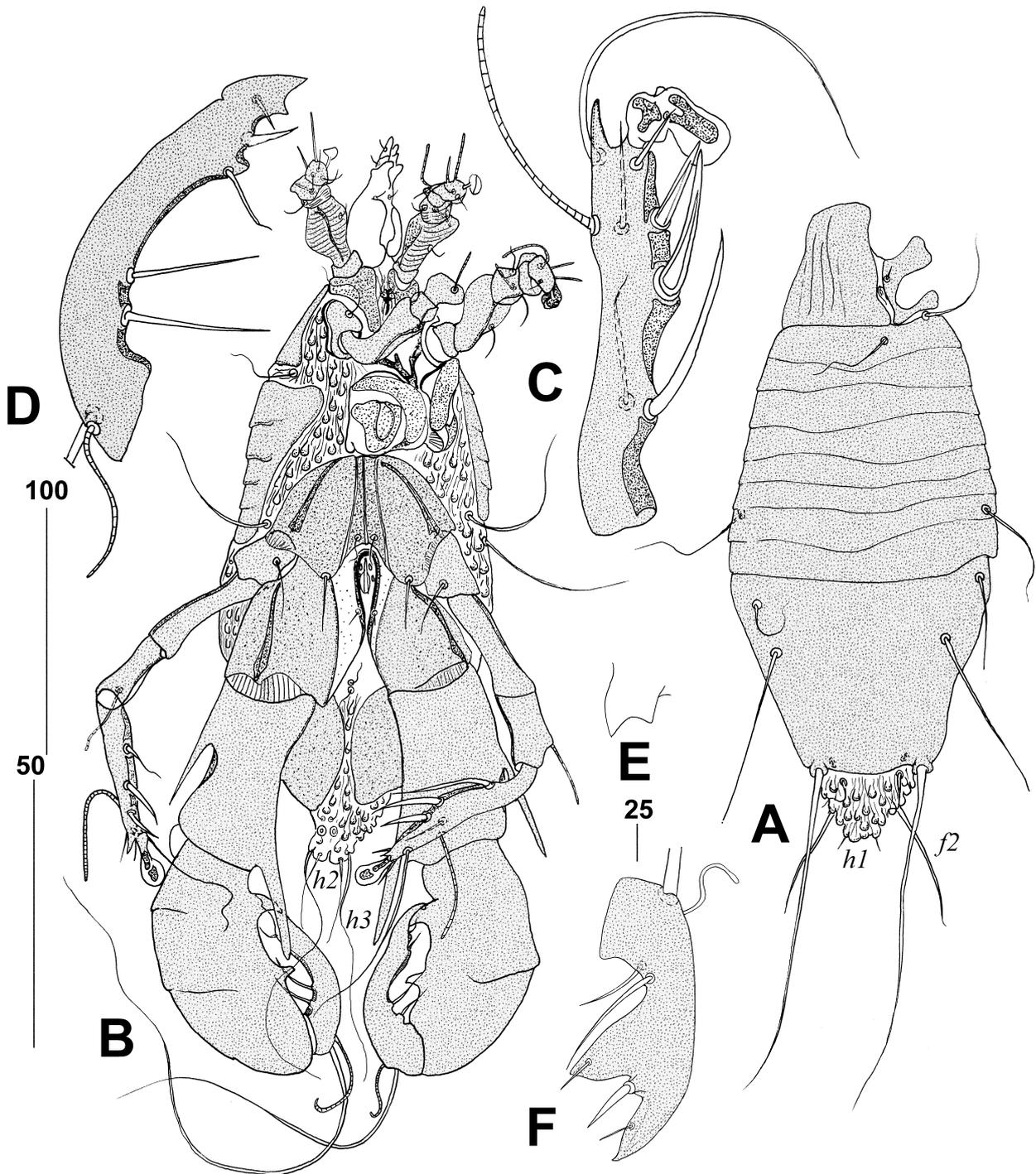


FIG. 4 (A-F). *Atopomelus hylomys* sp. nov., male. A. — Dorsal view. B. — Ventral view. C. — Tibiotarsus III, lateral. D. — Tibiotarsus IV, lateral. E. — Ventral spur of trochanter IV of heteromorphic form. F. Tibiotarsus IV of heteromorphic form, lateral. Scale bars 100  $\mu$ m (A, B), 50  $\mu$ m (C, D), and 25  $\mu$ m (E, F).

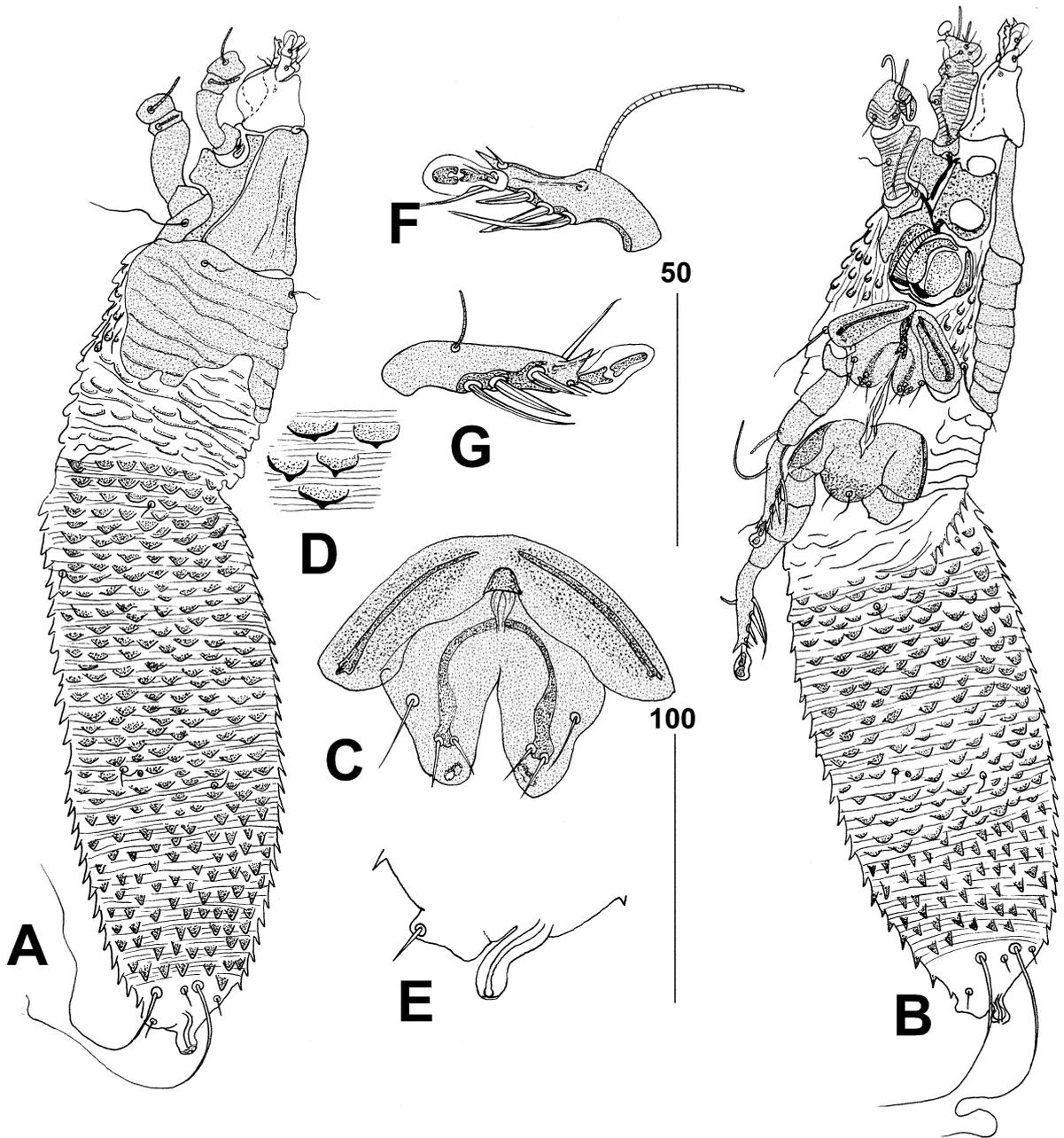


FIG. 5 (A-G). *Atopomelus hylomys* sp. nov., female. A. — Dorsal view. B. — Ventral view. C. — Vulva. D. — Dorsal scales of idiosoma. E. — Opisthosomal papilla. F. — Tibiotarsus III, lateral. G. — Tibiotarsus IV, lateral. Scale bars 100  $\mu$ m (A, B) and 50  $\mu$ m (C-F).

leg IV 330, 325-370 long; femurogenu IV 115, 115-130 long; tibiotarsus III 70, 70-80 long; tibiotarsus IV 90, 85-90 long; ventral spur of trochanter IV 45, 45-55 long, dorsal spur 35, 35-40 long; anterior ventral spur of femurogenu IV 20, 20-22 long, posterior dorsal spur 8, 6-8 long. Length of idiosomal setae: *si* 40, 22-40, *se* 50, 40-50, *c2* 65, 55-65, *c3* 15, 15-20, *cp* 75, 65-90, *d1* 35, 33-45, *d2* 70, 50-70, *e1* 145, 145-155, *e2* 29, 28-30, *f2* 60, 60-75, *h1* 8, 6-8, *h2* 50, 50-55, *h3* 130, 130-150, *4a* 17, 15-17, *ps* 5, 4-5, *3a* 13, 11-13, *3b* 25, 23-25, and *g* 9, 9-10. Setae *d* I — II about 5, III 65, 65-100, IV 155, 55-205. Length of solenidia:  $\omega$  I I-II 15, 13-15,  $\omega$  3 I 18, 18-20;  $\varphi$  I-II 38, 37-40, III-IV 50, 48-53;  $\sigma$  I about 7, II about 12, III 25, 25-33.

Heteromorphic male (FIGS. 4E,F). Body 405-410 long in 2 paratypes. Ventral spur of femurogenu IV bifurcate, 8-10 long, 2.5 times shorter than dorsal spur. Seta *ra* IV situated on well developed triangular projection, length of this projection 17-19.

Female (3 paratypes, FIGS. 5). Body about 2.6 times longer than wide. Postscapular shield well developed, covered by sinuous lines, with short posterior median incision, length ratio of this incision to shield 1 : 3, width ratio 1 : 8. Setae *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, and *ps3* short, subequal in length. Hysteronotum covered by triangular scales medially that are wider than long. Genital papillae contiguous. Genital valves fused in anterior part forming arch-like sclerite, bearing setae *3a* and *g*. Sclerotized areas of coxae IV fused posteriorly, and setae *4a* situated on common sclerotized plate. External terminus of spermathecal duct slightly inflated, situated in short, cylindrical protrusion (FIG. 5E). Setae *d* I-II distinctly shorter than respective solenidia  $\omega$  I; setae *d* III-IV about 2 times shorter than respective tibiotarsi, excluding ambulacra.

*Measurements.* Body 460-525 long, 175-180 wide; gnathosoma 60-65 long, 35-40 wide; prescapular shield 65-75 long; postscapular shield 65-77 long, 85-90 wide; median incision of shield 22-24 long, 10-14 wide; nipple-like protrusion of opisthosoma 10-12 long; leg III and IV about 90-110 long; tibiotarsus III-IV about 40-45 long. Length of idiosomal setae: *si* and *se* about 25, *c2* 30-33, *c3* 15-17, *cp* 75, *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, *ps3* — all 22-25, *f2* and *h3* about 80, *3a*, *3b*, *g* and *4a* all about 10. Setae *d* I-II about 7, III-IV about 18-20. Length of solenidia:  $\omega$  I I-II about 22,  $\omega$  3 I 23;  $\varphi$  I-II about 22, III 35, IV 14;  $\sigma$  I-II 6, III 8.

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

*Material examined.* Male holotype (BMOC 99-0510-008, 1), 2 male and 1 female paratypes (BMOC 99-0510-008, 2-4) ex *Hylomys suillus* (MVZ 186403), VIETNAM: Vinh Phuc Prov, Vinh Yen Dist., Tam Dao, 700-1000 m, 14 June 1997, coll. J.L. PATTON (JMP 16918); 4 male and 2 female paratypes (BMOC 04-0331-104, 1-6) ex *H. suillus* (FMNH 98438), MALAYSIA: Pahang, Janda-Baik, 2000 ft, 03° 21' N, 101° 53' E, 10 December 1963, coll. D.D. DAVIS; 3 male and 1 female paratypes (BMOC 04-0331-105, 1-4) ex *H. suillus* (FMNH 168563), CAMBODIA: Kampot Prov., Bokor, Nam-Tino River, near Burma border, 1080 m, 25 July 2000, coll. R.H. PINE.

*Type deposition.* Holotype deposited in EMEC, paratypes in FMNH, UMMZ and ZISP.

*Remarks.* Differential characters of this species are given in the key below.

*Atopomelus priapus* sp.nov.

(FIGS. 6, 7)

*Diagnosis.* Male: Hysteronotal shield tuberculate. Ventral spur of trochanter IV with single apex; dorsal spur weakly developed, 2.5 times shorter than ventral spur. Aedeagus about 3 times longer than femur III. Female: Median scales of hysterosoma broadly triangular. Genital papillae contiguous. Distal part of spermatheca broadened. Setae *d* III-IV 2-2.5 times shorter than respective tibiotarsi.

*Description.* Male (holotype, FIG. 6). Body elongate, length/width ratio 3 : 1. Postscapular shield with 8 transverse lines. Hysteronotal shield trapeziform, covered by indistinct tubercles, bearing 3 pairs of setae, *d1*, *d2*, and *e1*. Setae *d1* and *d2* thin and short, subequal in length, much shorter than *e1*. Length ratio between postscapular and hysteronotal shields subequal, 1.2:1. Unsclerotized cuticle of opisthosoma tuberculate. Setae *e2* microsetae, setae *f2* 6-7 times longer than *h2*. Setae *h2* and *h3* subequal. Aedeagus long, about 2.5 times longer than femur III. Legs IV 1.5 times longer than legs III. Seta *d* I-II 3-4 times shorter than solenidion  $\omega$  I; seta *d* III 3 times shorter than tibiotarsus, excluding ambulacrum. Tro-

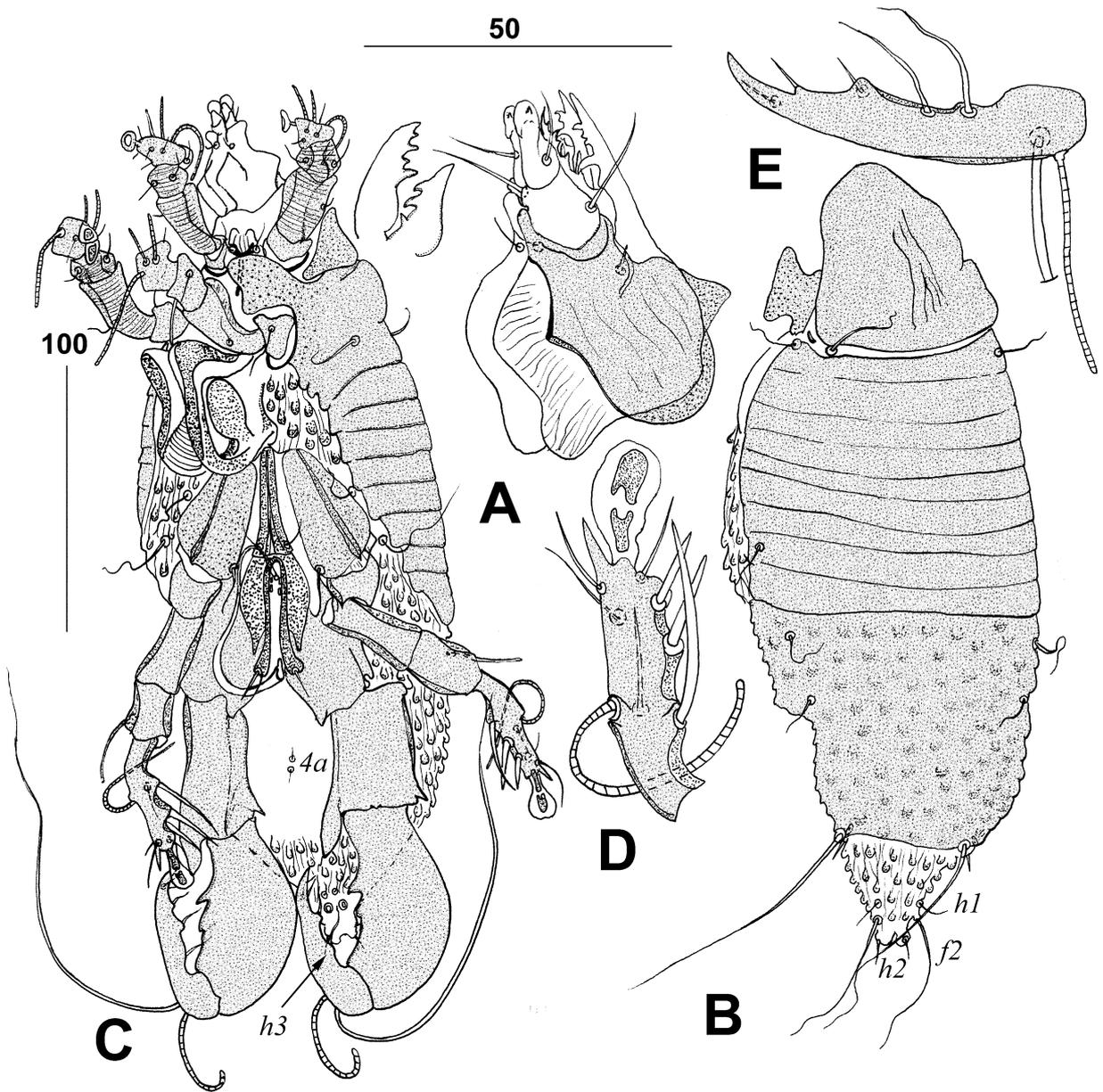


FIG. 6 (A-E). *Atopomelus priapus* sp. nov., male A. — Gnathosoma, lateral. B. — Dorsal view. C. — Ventral view. D. — Tibiotarsus III, lateral. E. — Tibiotarsus IV, lateral. Scale bars 100  $\mu$ m (C, B) and 50  $\mu$ m (A, D, E).

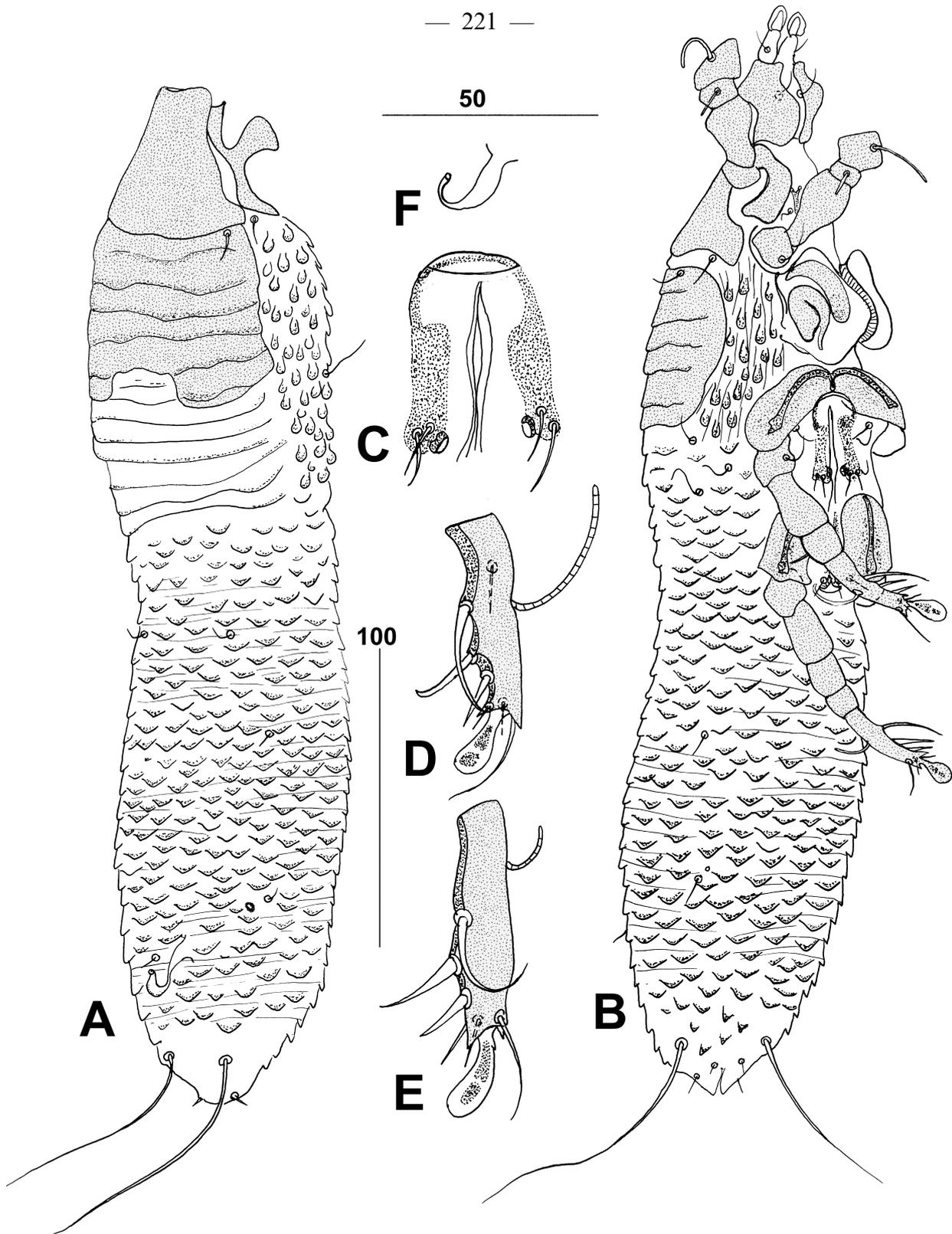


FIG. 7 (A-F). *Atopomelus priapus* sp. nov., female. A. — Dorsal view. B. — Ventral view. C. — Vulvar plates. D. — Tibiotarsus III, lateral. E. — Tibiotarsus IV, lateral. F — Distal part of spermatheca. Scale bars 100  $\mu\text{m}$  (A, B) and 50  $\mu\text{m}$  (C-F).

chanter IV with ventral and dorsal spurs, ventral spur with single apex, dorsal spur weakly developed, 2.5 times shorter than this segment. Femurogeni IV with two ventral spurs. Tarsus IV with single pointed apex (FIG. 6E).

*Measurements.* Body 350, 340-360 long, 117, 115-120 wide; gnathosoma 55, 55-60 long, 33, 33-35 wide; prescapular shield 75, 70-77 long; postscapular shield 110, 100-110 long; hysteronotal shield 90, 90-95 long; leg III 130, 120-135 long; leg IV 200, 175-210 long; femurogeni IV 75, 70-85 long; tibiotarsus III 45, 43-48 long; tibiotarsus IV 65, 60-65 long; ventral spur of trochanter IV about 15, 15-20 long, dorsal spur 4, 4-6 long; anterior ventral spur of femurogeni IV 3, 3-5 long; posterior ventral spur of femurogeni IV about 2, 2-3 long. Length of idiosomal setae: *si* 20, 18-20, *se* 22, 22-24, *c2* and *c3* about 25, *cp* 33, 30-35, *d1* and *d2* about 22, *e1* 125, 120-130, *e2* 5, 5-6, *f2* 50, 45-55, *h1*, *h2*, *h3*, *4a*, and *ps* — all about 5, *3a*, *3b*, and *g* about 15. Setae *d I* — II about 5, III about 17, IV about 175. Length of solenidia:  $\omega 1$  I about 13, II about 20,  $\omega 3$  I about 22;  $\varphi$  I-II about 35, III 55, 55-58, IV 47, 45-50;  $\sigma$  I-II about 9, III about 18.

Female (10 paratypes, FIG. 7). Body 3.3-3.5 times longer than wide. Postscapular shield well developed, covered by sinuous lines, with very short median incision, length ratio of this incision and shield 1 : 4, width ratio 1 : 3-3.5. Setae *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, and *ps3* short, subequal in length. Hysteronotum covered medially by triangular scales that are wider than long. Genital papillae contiguous. Genital valves fused anteriorly forming arched sclerite, bearing setae *3a* and *g*. Distal part of spermatheca broadened (FIG. 6F). Setae *d I*-II about 3 times shorter than respective  $\omega 1$ ; setae *d III*-IV subequal in length to respective segments, excluding ambulacra.

*Measurements.* Body 470-520 long, 140-150 wide; gnathosoma 55-60 long, 48-50 wide; prescapular shield 65-75 long; postscapular shield 75-80 long, 100-110 wide, median incision of shield 20-25 long, 25-30 wide; leg III and IV 95-100 long; tibiotarsus III-IV 35-38 long. Length of idiosomal setae: *si* and *se* 15-20, *c2* 10-12, *c3* 8-10, *cp* 19-23, *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, *ps3* — all 7-10, *f2* and *h3* 130-140, *3a* 10-12, *3b* 12-14, *g* and *4a* 5-8. Setae *d I*-II about 5, III-IV 12-15. Length of solenidia:  $\omega 1$  I-II 14-16,  $\omega 3$  I 10-12;  $\varphi$  I-III 20-25, IV 6-8;  $\sigma$  I -II 5-8, III 9-10.

*Etymology.* This species is named after Priapus, the ancient Greek god of fertility, in reference to the large aedeagus. This species name is a noun in apposition.

*Material examined.* Male holotype (BMOC 76-0823-30, 1), 1 female, 3 pharate females in teleonymph cuticle, and 1 teleonymph paratypes (BMOC 76-0823-30, 2-6) ex *Hylomys sinensis* (USNM 258129), CHINA: Sichuan Prov., Kwanshien, 29 November 1932, coll. unknown; 1 male and 7 female paratypes (BMOC 04-0331-085, 1-8) ex *H. sinensis* (FMNH 37017), CHINA: Sichuan Prov., Dan Shi Go, 10 November 1931, coll. F.T. SMITH; 2 male and 6 female paratypes (BMOC 04-0331-086, 1-8) ex *H. sinensis* (FMNH 37020), same data, 25 November 1931, coll. F.T. SMITH; 3 male paratypes (BMOC 04-0331-087, 1-3) ex *H. sinensis* (FMNH 37021), same data, 3 December 1931, coll. F.T. SMITH; 1 male paratype (BMOC 04-0331-088) ex *H. sinensis* (FMNH 37023), same data, 14 December 1931, coll. F.T. SMITH; 1 female paratype (BMOC 04-0331-090, 1-3) ex *H. sinensis* (FMNH 36995), CHINA: Sichuan Prov., Tao Cho Fu, 11 February 1932, coll. F.T. SMITH; 2 male paratypes (BMOC 04-0331-091, 1-2) ex *H. sinensis* (FMNH 36667), same data, 14 March 1932, coll. F.T. SMITH; 5 male and 1 female paratypes (BMOC 04-0331-093, 1-3) ex *H. sinensis* (FMNH 35780), CHINA: Yunnan Prov., Mu-cheng, 11 February 1917, coll. E. HELLER; 1 male and 9 female paratypes (BMOC 04-0331-083, 1-10) ex *H. sinensis* (FMNH 38888), VIETNAM: Lao Cai Prov., Hoang Lien So'n Mts, Sa Pa, 22° 21' 00" N, 103° 52' 00" E, 28 November 1928, coll. DELACOUR.

*Type deposition.* Holotype deposited in USNM, paratypes in FMNH, UMMZ, and ZISP.

*Remarks.* Differential characters of this species are given in the key below.

The following two species possess more plesiomorphic characters and are not grouped.

*Atopomelus crocidurae* FAIN & LUKOSCHUS, 1977  
*Atopomelus crocidurae* FAIN & LUKOSCHUS, 1977: 29  
 (FIGS. 8-12)

*Diagnosis.* Male: Dorsal shields without ornamentation. Setae *d1* and *d2* subequal in length. Setae *e2* microsetae. Femurogeni IV with two ventral spurs.

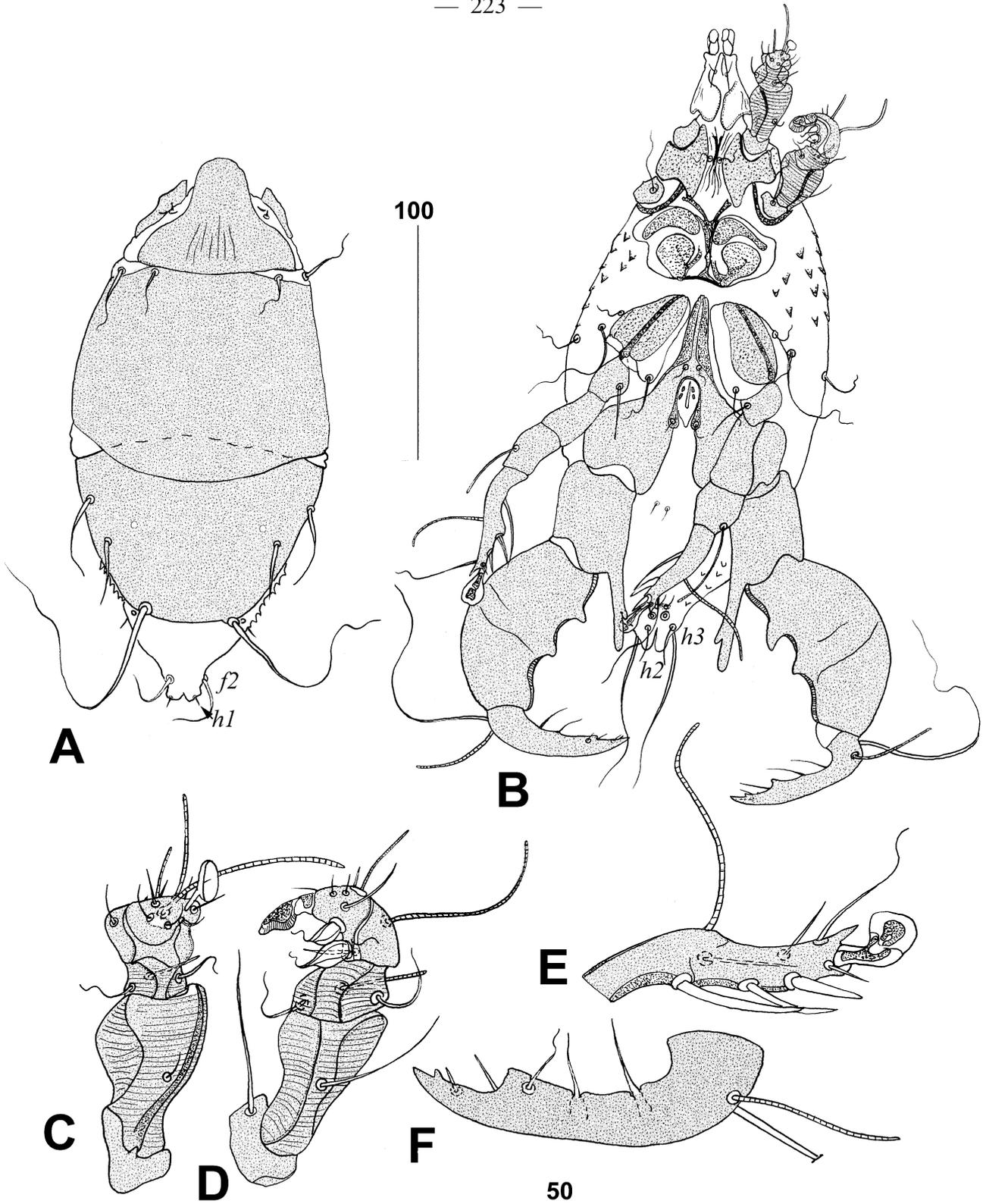


FIG. 8 (A-F). *Atopomelus crocidurae*, male. A. — Dorsal view. B. — Ventral view. C. — Leg I, ventral. D. — Leg II, ventral. E. — Tibiotarsus III, lateral. F. — Tibiotarsus IV, lateral. Scale bars 100  $\mu\text{m}$  (A, B) and 50  $\mu\text{m}$  (C-F).

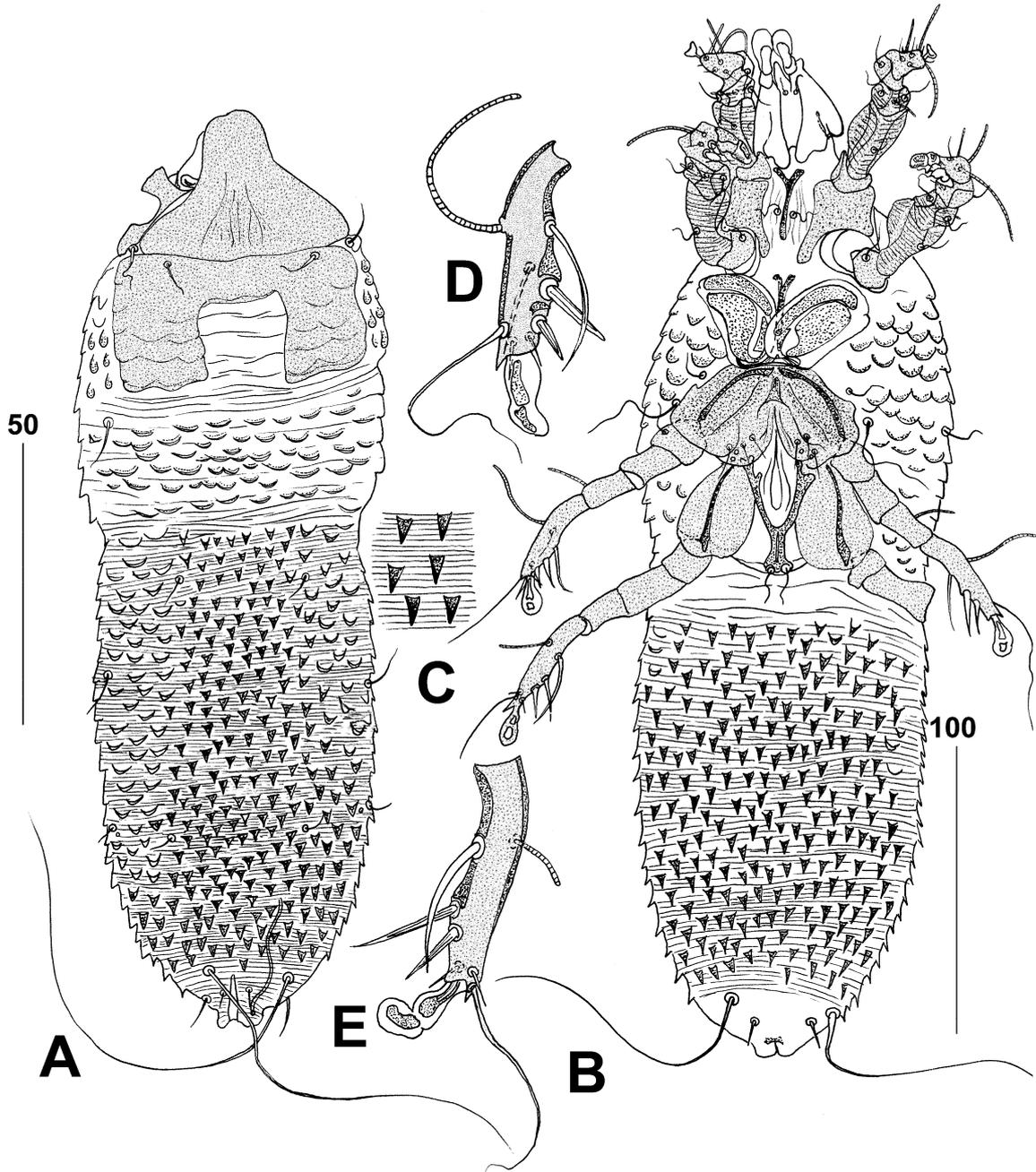


FIG. 9 (A-E). *Atopomelus crocidurae*, female. A. — Dorsal view. B. — Ventral view. C. — Dorsal scales of idiosoma. D. — Tibiotarsus III, lateral. E. — Tibiotarsus IV, lateral. Scale bars 100  $\mu\text{m}$  (A, B) and 50  $\mu\text{m}$  (C-E).

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.

*Description* (based on specimens from *Crocidura mindorus*, the Philippines). Male (n=10, FIGS. 8, 10A, B). Body elongate, length/width ratio 2.5 : 1. Dorsal shields devoid of ornamentation. Hysteronotal shield 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 devoid of 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. Legs IV 2 times longer than legs III. Setae *d* I-II much shorter than respective solenidia  $\omega 1$ ; 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. 8F).

*Measurements*. Body 330-360 long, 130-140 wide; gnathosoma 55-60 long, 40-45 wide; prescapular shield 73-77 long; postscapular shield 120-130 long; hysteronotal shield 100-110 long; 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. 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* 23-25, *3b* 28-32, *g* 10-12, *4a* 6-7, *ps3* 5-6. Setae *d* I-II 4-5, III 57-65, IV 180-190. Length of solenidia:  $\omega 1$  I-II 14-15,  $\omega 3$  I 20-22;  $\varphi$  I-II 40-43, III 48-53, IV 38-40;  $\sigma$  I-II 11-12, III 30-32.

Female (n=10, FIGS. 9, 10C). Body 3 times longer than wide. Postscapular shield well developed, cove-

red 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. Setae *d* I-II much shorter than respective solenidia  $\omega 1$ ; seta *d* III-IV slightly longer or subequal to respective tibiotarsi, excluding ambulacra.

*Measurements*. Body 420-435 long, 125-135 wide; gnathosoma 55-60 long, 35-40 wide; prescapular shield 68-75 long; postscapular shield 45-50 long, 87-90 width; leg III 95-100 long; leg IV 100-115 long; tibiotarsus III-IV 38-40 long. 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* 12-14, *3b* 20-22, *g* and *4a* 18-20. Setae *d* I-II 4-5, III-IV 45-50. Length of solenidia:  $\omega 1$  I-II 15-20,  $\omega 3$  I 19-20;  $\varphi$  I-III 38-43, IV 10-12;  $\sigma$  I-II 12-13, III 10-11.

*Material examined*. One female ex *Crocidura attenuata aequicaudata* (NHMW), INDONESIA: Sumatra Is., Padan, October 1896, coll. A.J. SCHILD (collected from the same host specimen as the holotype); 2 females and one teleonymph (BMOC 99-0301-004) ex *Crocidura monticola* PETERS, 1870 (UMMZ 174666), INDONESIA: Kalimantan Barat, Regency of Ketapang, Gunung Palung National Park, Cabang Panti Research Station, 20-35 m, 3 August 1998, coll. A.J. GOROG (AJG 008); 2 males, 3 females, 3 teleonymphs, and 1 larva (BMOC 99-0301-032) ex *C. monticola* (UMMZ), same data, 17 September 1998, coll. A.J. GOROG (AJG 064); 1 male, 1 female and 1 teleonymph (BMOC 99-0301-012) ex *C. monticola* (UMMZ 174669), same data, 13 August 1998, coll. A.J. GOROG (AJG 026); 1 male (BMOC 99-0301-006) ex *C. monticola* (UMMZ 174667), same data, 8 August 1998, coll. A.J. GOROG (AJG 012); 1 teleonymph (BMOC 99-0301-079) ex *C. monticola* (UMMZ 174687), same data, 1000-1100 m, 3 November 1998, coll. A.J. GOROG (AJG 148A); 1 male, 2 females, and 2 teleonymphs (BMOC 99-0301-198), from *C. monticola* (UMMZ 174686), INDONESIA: Kalimantan Barat, Regency of Sintang, Bukit Baka-Bukit Raya Nat. Park, Juoi Entry, Bukit

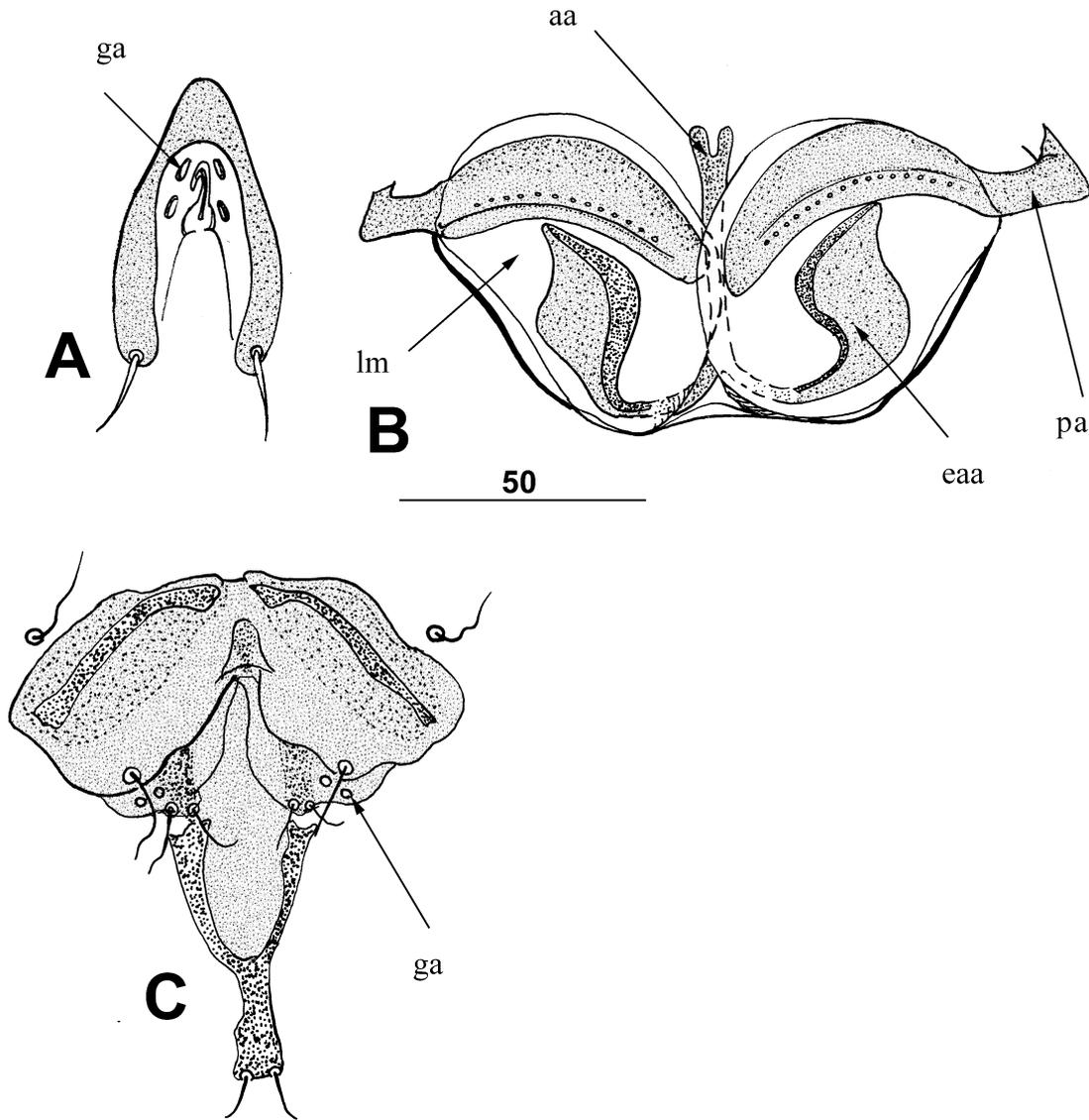


FIG. 10 (A-CD). *Atopomelus crocidurae*. A. — Aedeagus. B. — Male clasp organ of coxae II. C. — Vulva. aa — anterior apodeme of coxa II, eaa — enlarged part of anterior apodeme of coxa II, ga — genital acetabula, la — lateral membrane of clasp organ of coxa II, pa — posterior apodeme of coxa II.

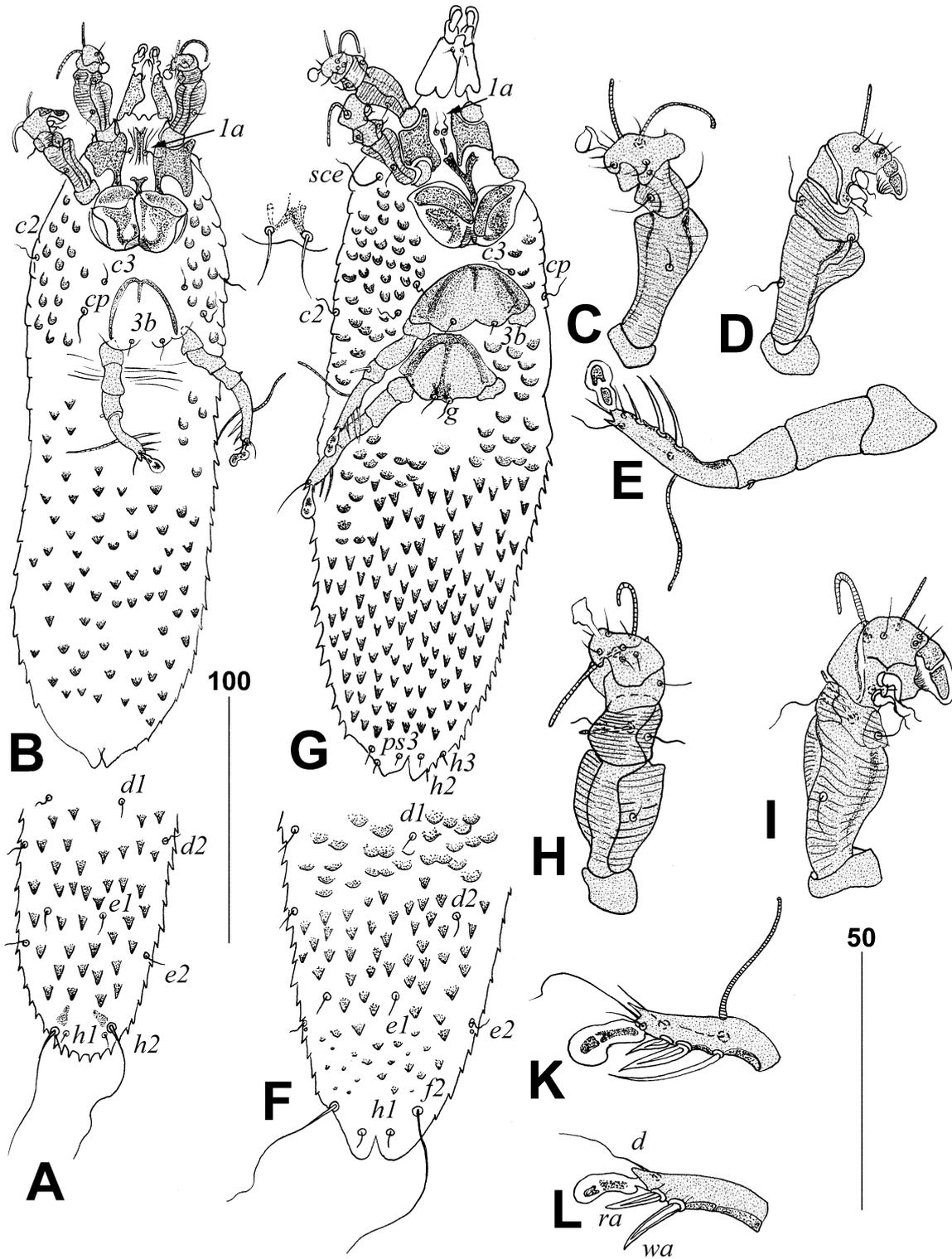


FIG. 11 (A-L). *Atopomehus crocidurae*. Larva (A — E). A. — Hysteronotum. B. — Ventral view. C. — Leg I, ventral. D. — Leg II, ventral. E. — Tarsus III, lateral. Protonymph (F-L). F. — Hysteronotum. G. — Ventral view. H. — Leg I, ventral. I. — Leg II, ventral. K. — Tibiotarsus III, lateral. L. — Tibiotarsus IV, lateral. Scale bars 100  $\mu\text{m}$  (A, B, F, G) and 50  $\mu\text{m}$  (C-E, H-I).

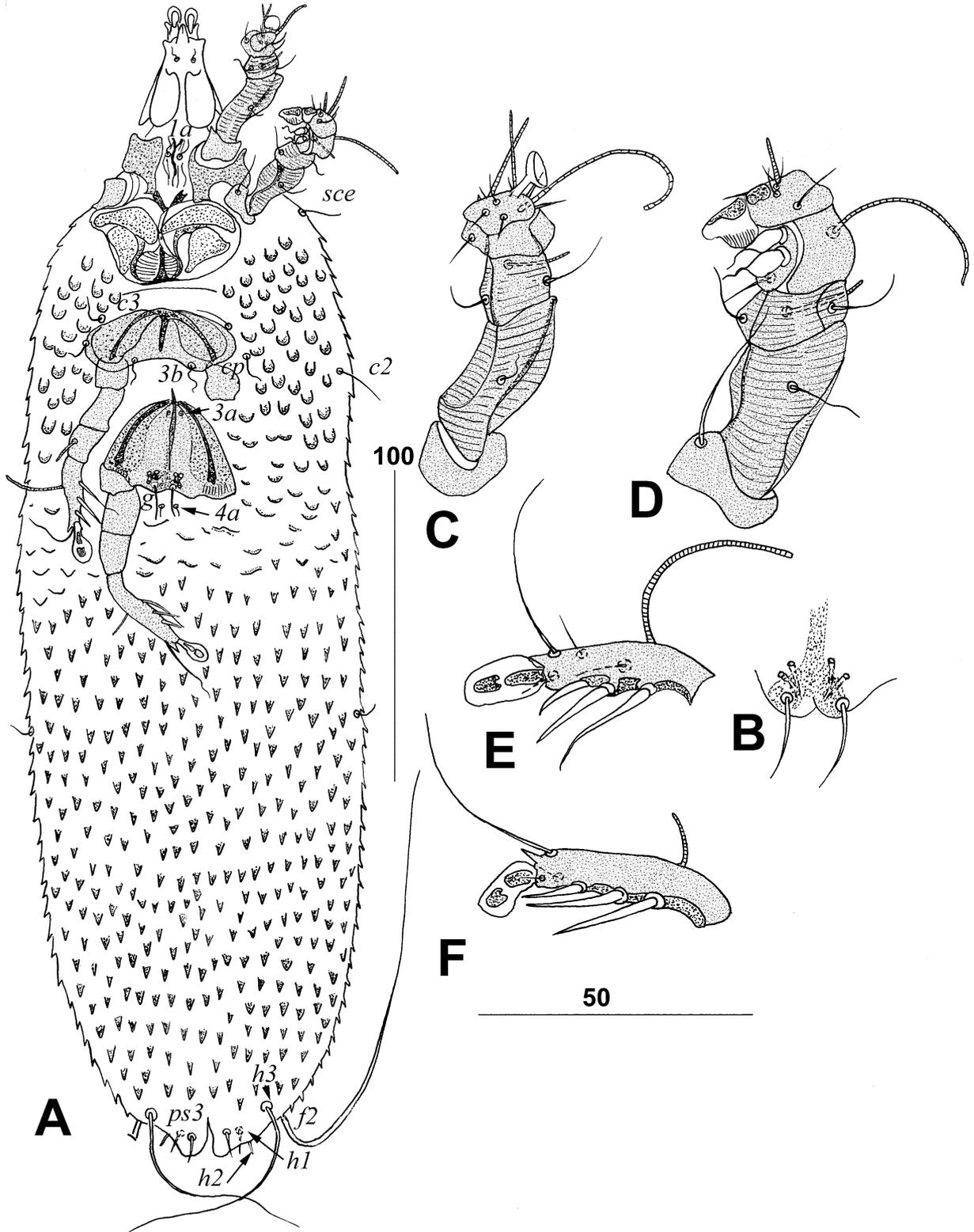


FIG. 12 (A-F). *Atopomelus crocidurae*, telonymph. A. — Ventral view. B. — Genital acetabulae. C. — Leg I, ventral. D. — Leg II, ventral. E. — Leg III, lateral. F. — Leg IV, lateral. Scale bars 100 μm (A) and 50 μm (B-G).

Lubang Tedung, 300-350 m, 22 December 1998, coll. A.J. GOROG (AJG 472); 4 males, 1 female, 4 teleonymphs, and 1 protonymphs (BMOC 99-0301-210) ex *Crocidura fuliginosa foetida* PETERS, 1870 (UMMZ 175108), INDONESIA: Kalimantan Barat, Regency of Ketapang, Gunung Palung National Park, Kampung Sedahan, 15 August 1999, coll. A.J. GOROG (AJG 496); 1 female (BMOC 99-0301-041) ex *C. fuliginosa foetida* (UMMZ 175105), same data, 525 m, 1 October 1998, coll. A.J. GOROG (AJG 080); 1 male, 2 females, and 2 teleonymphs from *Crocidura malayana* ROBINSON & KLOSS, 1911, MALAYSIA: Selangor, Ulu Langat Kajang, 14 June 1954, coll. M. NADCHATRAM; 11 males, 10 females, and 1 teleonymph (BMOC 92-1400-100) ex *Crocidura mindorus* MILLER, 1910 (FMNH 146790), PHILIPPINES: Sibuyan Is., Romblon Prov., 6.75 km S, 4.5 km E Magdiwang, 1325 m, 9 March 1992, coll. S.M. GOODMAN (SMG 5153); 12 males, 7 females, 6 teleonymphs, 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 teleonymphs (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 *Crocidura grayi* DOBSON, 1890 (FMNH 168976), Luzon Is., Kalinga Prov., Balbalan Munic., Balbalasang Brgy., Am-licao, 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 teleonymphs, 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 teleonymphs (BMOC 01-0920-006) ex *C. grayi* (FMNH 168974), same data, 19 March 2001, coll. L.R. HEANEY (LRH 6363); 2 females, 8 teleonymphs, 5 protonymphs, and 2 larvae (HK 87-0620-001) ex *Crocidura beatus* MILLER, 1910 (USNM 458960), Bohol Is., 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, 9 teleonymphs, 3 protonymphs, and 3 larvae (BMOC 95-1214-002), from *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 teleonymphs, 5 protonymphs, and 6 larvae (BMOC 95-1214-003) ex *C. beatus* (FMNH 167855), same data, coll. B.R. TABARANZA (BRT 148).

*Specimen deposition.* Holotype deposited in NHMV (not examined), female paratype (examined) in IRSNB; voucher specimens from above hosts in FMNH, MBBJ, UMMZ, UPPC, ZISP.

*Atopomelus talpae* FAIN,  
LUKOSCHUS & CAUWENBERGE, 1973  
*Atopomelus talpae* FAIN *et al.*, 1973: 59  
(FIGS. 13-14)

*Diagnosis.* In both sexes: Tarsus I with setae *s* I-II present, seta *e* II inflated. Male: Hysteronotal shield mushroom-like. Setae *d2* 3 times longer than *d1*; setae *e2* long; setae *ps2* present. Tarsus IV with two subequal apices. Femurogen IV without spurs. Trochanter IV without dorsal spur; ventral spur bifurcate. Female: Postscapular shield triangular with sclerotized median band. Median scales of hysterosoma narrowly triangular. Genital papillae separate. Genital valves unsclerotized. Setae *4a* situated on soft cuticle between fields of coxae IV.

*Description.* Male (paratype, FIG. 13 E-I). Body elongate, length/width ratio 2.6 : 1. Gnathosomal length and width subequal, 1.2 : 1. Dorsal shields devoid of ornamentation. Hysteronotal shield narrowed medially, with anterior lateral lobes, bearing 2 pairs of setae, *d1* and *d2*, setae *e1* situated off this shield. Setae *d3* 3 times longer than *d1*. Setae *e1* and *e2* long. Length ratio of postscapular and hysteronotal shields subequal, 1.2:1. Unsclerotized integument of opisthosoma devoid of ornamentation, and only few scales present in its lateral parts. Setae *f2* about 3 times longer than *h2* and subequal to *h3*. Aedeagus short, 2 times shorter than femur III. Setae *g* widely separated from each other. Setae *ps2* present. Legs IV 2 times longer than legs III. Setae *d* I-II longer than respective solenidia *ω1*; setae *d* III 1.5 times longer than tibiotarsus, excluding ambulacrum. Setae *s* I-II present. Seta *e* II inflated. Trochanter IV without dorsal spur, ventral spur 2.5 times shorter than res-

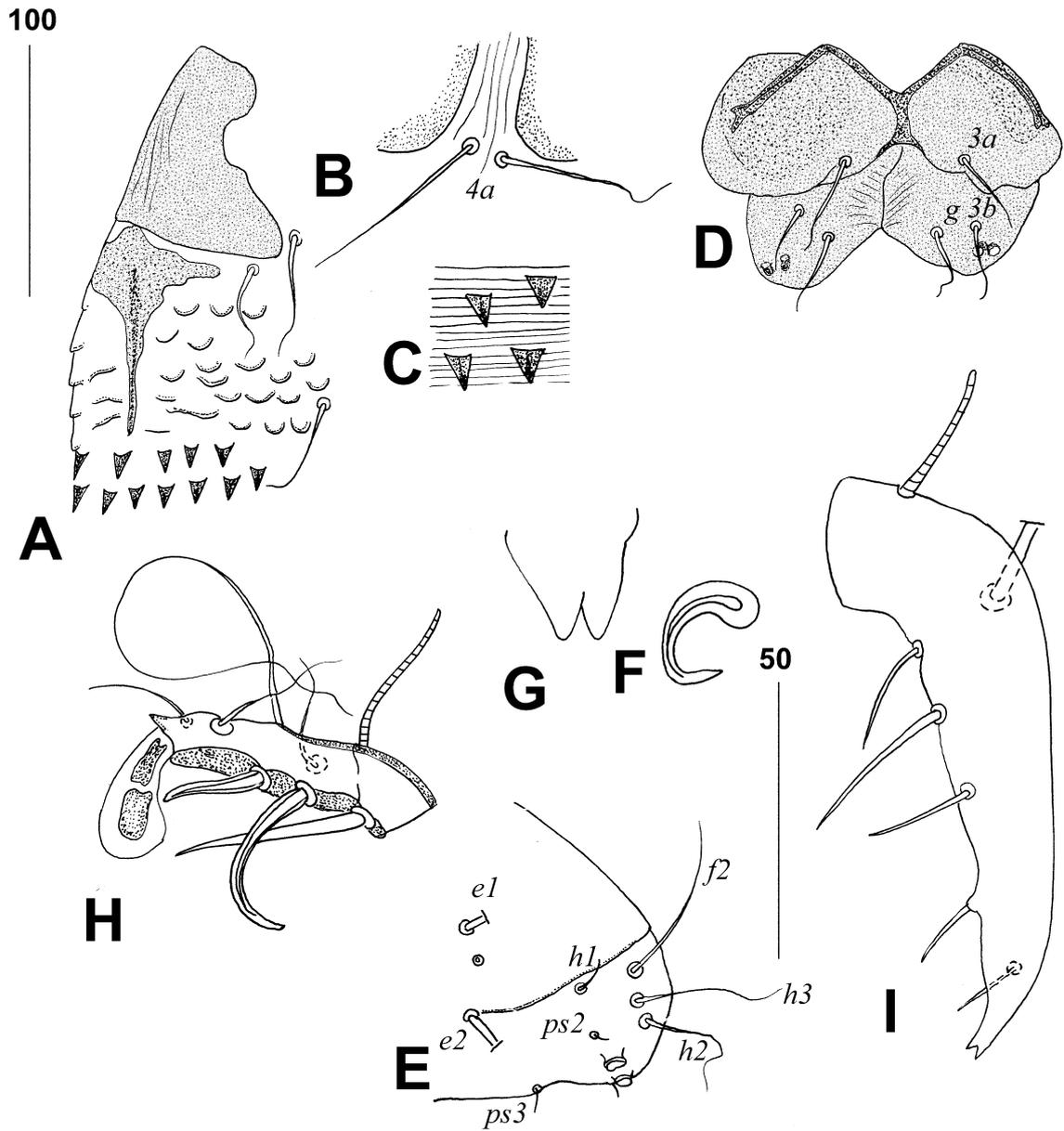


FIG. 13 (A-I). *Atopomelus talpae*. A. — Propodonotum of female. B. — Posterior part of coxal fields IV, female. C — Dorsal scales of idiosoma, female. D. — Vulva. E. — Male opisthosoma, lateral. F. — aedeagus. G. — Ventral spur of trochanter IV, male. H. — Tibiotarsus III of male, lateral. I. — Tibiotarsus IV of male, lateral. Scale bars 100  $\mu\text{m}$  (A, E) and 50  $\mu\text{m}$  (B-D, F-I).

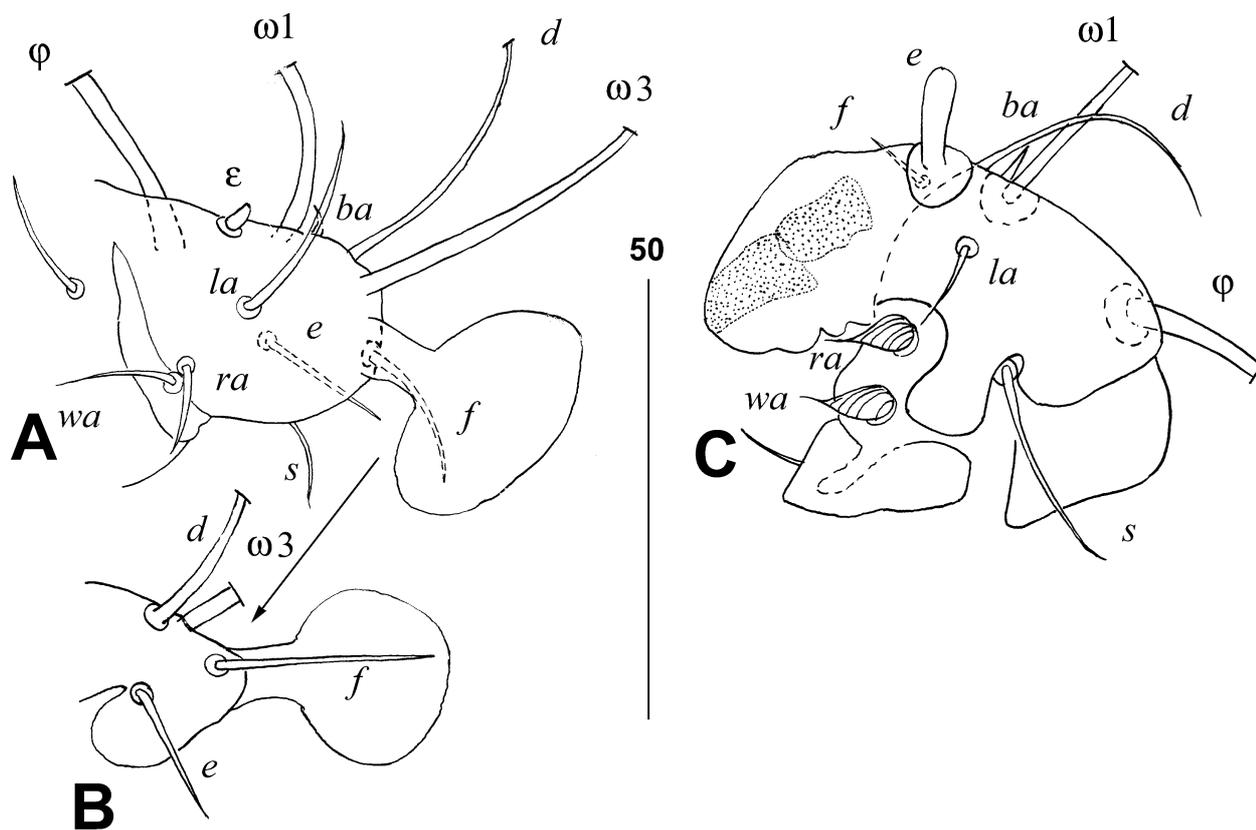


FIG. 14 (A-C). *Atopomelus talpae*, female. A — Tarsus I, ventral. B — Apical part of tarsus I, dorsal. C — Tarsus II, ventral.

pective trochanter, bifurcate, with apices subequal in length. Femurogenu IV without ventral spurs. Tarsus IV with two subequal apices (FIG. 13 I).

**Measurements.** Body 550 long, 210 wide; gnathosoma 65 long, 55 wide; prescapular shield 70 long; postscapular shield 175 long; hysteronotal shield 145 long; leg III 175 long; leg IV 320 long; femurogenu IV 160 long; tibiotarsus III 75 long; tibiotarsus IV 110 long; ventral spur of trochanter IV 20 long; aedeagus 25 long. Length of idiosomal setae: *si* 65, *se* 55, *c2* 55, *c3* 60, *cp* 77, *d1* 42, *d2* 125, *e1* 165, *e2* 170, *f2* 100, *h1* 15, *h2* 30, *h3* 105, *3a* 60, *3b* 45, *g* 25, *4a* 9, *ps3* 10. Setae *d* I 35, II 25, III 37, IV 250. Length of solenidia:  $\omega 1$  I-II about 25,  $\omega 3$  I 32;  $\varphi$  I-II about 55, III 37, IV 25;  $\sigma$  I-II about 13, III 15.

Female (2 paratypes, FIG. 13 A-D, 14). Body 3.5 times longer than wide. Postscapular shield distinctly triangular, with distinct longitudinal apodeme medially. Setae *d1*, *d2*, *e1*, and *e2* at least 3 times longer than *h1*, *h2*, and *ps3*. Hysteronotum covered

medially by triangular scales that are longer than wide. Genital papillae separate. Genital valves unsclerotized. Setae *4a* situated on soft cuticle between sclerotized areas of coxae IV. Distal part of spermatheca narrow. Setae *d* I-II longer than respective solenidia  $\omega 1$ ; setae *d* III distinctly longer than tibiotarsus, excluding ambulacrum. Setae *s* I-II present. Seta *e* II inflated.

**Measurements.** Body 770-790 long, 210-220 wide; gnathosoma 70-77 long, 55-60 wide; prescapular shield 75-80 long; postscapular shield 80-85 long; legs III-IV 135-140 long; tibiotarsus III 45-50 long; tibiotarsus IV 50-55 long. Length of idiosomal setae: *si* 40-55, *se* 48-60, *c2* and *c3* 40-45, *cp* 57-65, *d1* 35-45, *d2* 45-55, *e1* 60-65, *e2* 55-60, *h1*, *h2*, *ps3* — all about 10, *f2* and *h3* about 220, *3a*, *3b* 20-22, and *g* — all about 20, *4a* 40-42. Setae *d* I 45-55, II 37-40, III 85-110, IV 110-120. Length of solenidia:  $\omega 1$  I-II 25-28,  $\omega 3$  I 37-38;  $\varphi$  I-II 42-45, III 29-30, IV 15-16;  $\sigma$  I-II 20-22, III 10-12.

*Specimens examined.* Holotype deposited in ISZAF (not examined). One male and 2 female paratypes (UMMZ, ZISP) ex *Talpa romana*, ITALY: L'Aquila Prov., Abruzzi, Pescasseroli, Abruzzi National Park, 20 October 1972, coll. F.S. LUKOSCHUS.

KEY TO MALES OF THE GENUS *Atopomelus*

- 1. Postscapular shield with transverse lines. Opisthonotal surface behind hysteronotal shield tuberculate. Opisthogaster completely covered by scales or tubercles. Trochanter IV with dorsal spur species group "*locusta*". 2
  - Postscapular shield without ornamentation. Opisthonotal surface behind hysteronotal shield unornamented. Opisthogaster with few scales restricted to lateral parts. Trochanter IV without dorsal spur. . . . . 4
- 2. Aedeagus about 2 times shorter than femur III. Seta *d* III subequal in length to tibiotarsus. Dorsal spur of trochanter IV subequal in length to ventral spur or longer. . . . . 3
  - Aedeagus about 2.5 times longer than femur III. Seta *d* III about 3 times shorter than tibiotarsus III. Dorsal spur of trochanter IV about 3 times shorter than ventral spur. . . . . *A. priapus* sp.nov.
- 3. Hysteronotal shield tuberculate. Dorsal spur of trochanter IV situated basally. Femurogenu IV with one ventral spur. . . . . *A. locusta* TROUSSERT, 1918
  - Hysteronotal shield devoid of ornamentation. Dorsal spur of trochanter IV situated in median part of segment. Femurogenu IV with two ventral spurs. . . . . *A. hylomys* sp.nov.
- 4. Hysteronotal shield strongly narrowed posteriorly. Setae *e1* and *e2* relatively long, subequal in length. Setae *ps2* present. Setae *s* I-II present; seta *e* II inflated. Femurogenu IV without spurs. Ventral spur of trochanter IV with 2 subequal apices. Tarsus IV with 2 subequal apices. . . . . *A. talpae* FAIN, LUKOSCHUS & CAUWENBERGE, 1973
  - Hysteronotal shield broadly trapeziform. Setae *e2* microsetae, much shorter than *e1*. Setae *ps2* absent. Seta *s* absent on all tarsi; seta *e* II filiform. Femurogenu IV with two ventral spurs. Ventral spur of trochanter IV with 2 apices unequal in length. Tarsus IV with 2 unequal apices. . . . . *A. crocidurae* FAIN & LUKOSCHUS, 1977

KEY TO FEMALES OF THE GENUS *ATOPOMELUS*

- 1. Hysteronotum covered medially by triangular scales that are wider than long. Genital papillae contiguous. Distal part of spermatheca inflated ... species group "*locusta*". . . . . 2

- Hysteronotum covered medially with triangular scales that are longer than wide. Genital papillae separated. Distal part of spermatheca narrow . . . . . 4
- 2. Body 460-530 long. Seta *d* III-IV 2-3 times shorter than respective tibiotarsi. Genital valves fused to each other anteriorly, forming arched sclerite. Distal part of spermatheca broadened, but not globose. . . . . 3
  - Body 580-650 long. Seta *d* III-IV subequal in length to tibiotarsus. Genital valves widely separated from each other. Distal part of spermatheca globose . . . . . *A. locusta* TROUSSERT, 1918
- 3. Copulatory opening on a narrow, subterminal papilla. Distal part of spermatheca slightly inflated within copulatory papilla . . . . . *A. hylomys* sp.nov.
  - Copulatory papilla absent. Distal part of spermatheca longer and distinctly broadened . . . . . *A. priapus* sp.nov.
- 4. Postscapular shield triangular, with strongly sclerotized median apodeme. Genital valves unsclerotized. Setae *4a* situated on soft cuticle between sclerotized areas of coxae IV, almost 2 times longer than setae *g*. Seta *s* I-II present. Seta *e* II inflated . . . . . *A. talpae* FAIN, LUKOSCHUS & CAUWENBERGE, 1973
  - Postscapular shield rectangular, with deep and wide posterior median incision, covered by scale-like pattern. Genital valves sclerotized, separated, triangular in shape. Setae *4a* situated on fused sclerotized areas of coxae IV, subequal in length to setae *g*. Seta *s* absent on all tarsi. Seta *e* II filiform . . . . . *A. crocidurae* Fain & Lukoschus, 1977.

PHYLOGENETIC ANALYSIS

The analysis yielded a single most parsimonious tree (length = 63, CI excluding uninformative characters 0.72, RI 0.83, RC 0.62) (FIG. 15). In this cladogram, the genus *Didelphoecius* is the sister group to *Atopomelus* while the two other close outgroup species form a separate clade. Analysis of character states across the entire family will be necessary to properly place *Atopomelus* phylogenetically, but certain retained plesiomorphies such as the presence of seta *pR* II suggest that the genus is a relatively early derivative lineage within the family.

The monophyly of *Atopomelus* is strongly supported in this analysis. The clade joining species of *Atopomelus* has the strongest Bremer support (16) and is diagnosed by 20 character state changes. Many of these changes such as the loss of clasping organs of coxae I (character 2), structure of the clasping organs of coxae II (3), ventrally curved tarsus II (36), stron-

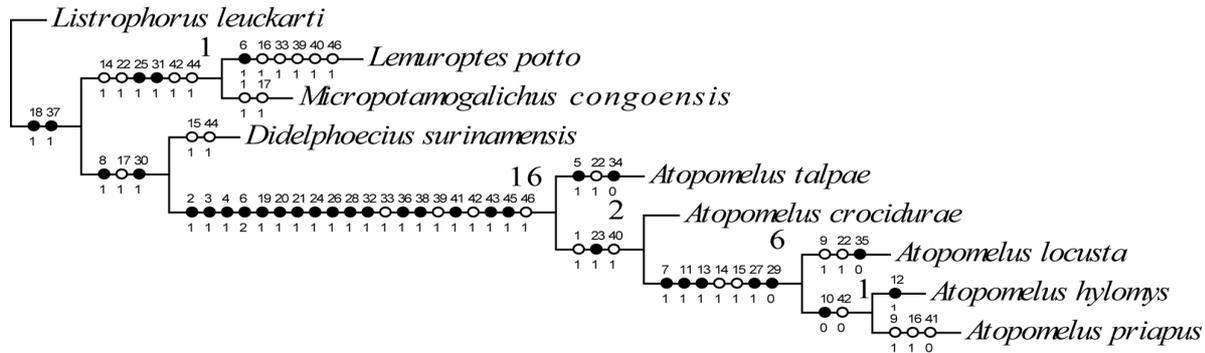


FIG. 15. The single most parsimonious tree (length = 66, CI excluding uninformative characters 0.7, RI 0.8, RC 0.59) found with the branch-and-bound search option obtained for the unordered and non-weighted data set. Character numbers are indicated on the tree above branches (DELTRAN optimization), their state changes indicated below branches, non-homoplasious state changes are in black, homoplasious state changes are in white, the numbers above branches indicate Bremer support indices.

gly inflated setae *ra* and *wa* II (38), saber-like tibiotarsus IV of male (39), and setae *d* IV represented by macrosetae in male (41) are unique within the family.

The species *A. talpae* occupies the basal position in the genus. This species retains several plesiomorphic character states such as the short gnathosoma (character 1), presence of setae *ps2* in male (23), and setae *s* I-II (40).

The species group “*locusta*” is monophyletic. It has a high Bremer support index (6) and is diagnosed by seven character state changes, the ornamented postscapular shield in the male (character 7), genital papillae in female contiguous (11), distal part of spermatheca inflated (13), idiosomal scales of female wider than longer (14), presence of protuberances behind the hysteronotal shield in male (15), presence of a dorsal spur on trochanter IV in male (28), and the ventral spur on trochanter IV with a single apex in normal male (29 — reversal). Although relationships among the three species of this group are completely resolved, the node joining the species *A. hylomyis* and *A. priapus* is only supported by two characters, 10 (genital valves fused) and 42 (seta *d* III-IV shorter than the segment). This node has a low Bremer support index (1). Therefore, it is possible that the sister relationship between these two species may change if additional species are discovered.

#### HOST PARASITE-ASSOCIATIONS

*Atopomelus* species are mainly associated with oriental insectivores, gymnures of the genus *Hylomys*

(Erinaceidae: Hylomyinae) and shrews of the genus *Crocidura* (Soricidae: Crocidurinae), with *A. talpae* being the only species found outside this region.

The gymnure genus *Hylomys* includes four species, and atopomelid mites of the group “*hylomys*” are known from two of them. *Atopomelus locusta* and *A. priapus* parasitize *H. sinensis*, and *A. hylomys* infects *H. suillus* in Vietnam. The two other species, *Hylomys hainanensis* (SHAW & WONG, 1959) and *H. megalotis* JENKINS & ROBINSON, 2002 are known from few specimens and have not yet been examined for ectoparasites. Since the erinaceid subfamily Hylomyinae includes two other genera, *Podogymnura* with two species endemic to the Philippines, and *Echinosorex* with one species, *E. gymmura* (RAFFLES, 1822), which is widely distributed in the Oriental region, we examined available specimens of these hosts for the presence of *Atopomelus* species. We examined sixty-four specimens of *Podogymnura truei* MEARNS, 1905, from Mindanao island, however no atopomelids were found. We believe this sampling demonstrates that these mites are completely absent on this host. The second species of *Podogymnura*, *P. aureospinula* HEANEY & MORGAN, 1982, which occurs only on Dinagat Island, has not been examined yet. We have examined fourteen specimens of *E. gymmurus* without recovering *Atopomelus* specimens, however, additional material should be examined before a final conclusion is reached.

Fur mites in general, and *Atopomelus* in particular are probably completely absent on hedgehogs of the subfamily Erinaceinae. We have examined numerous specimens of several species without encountering

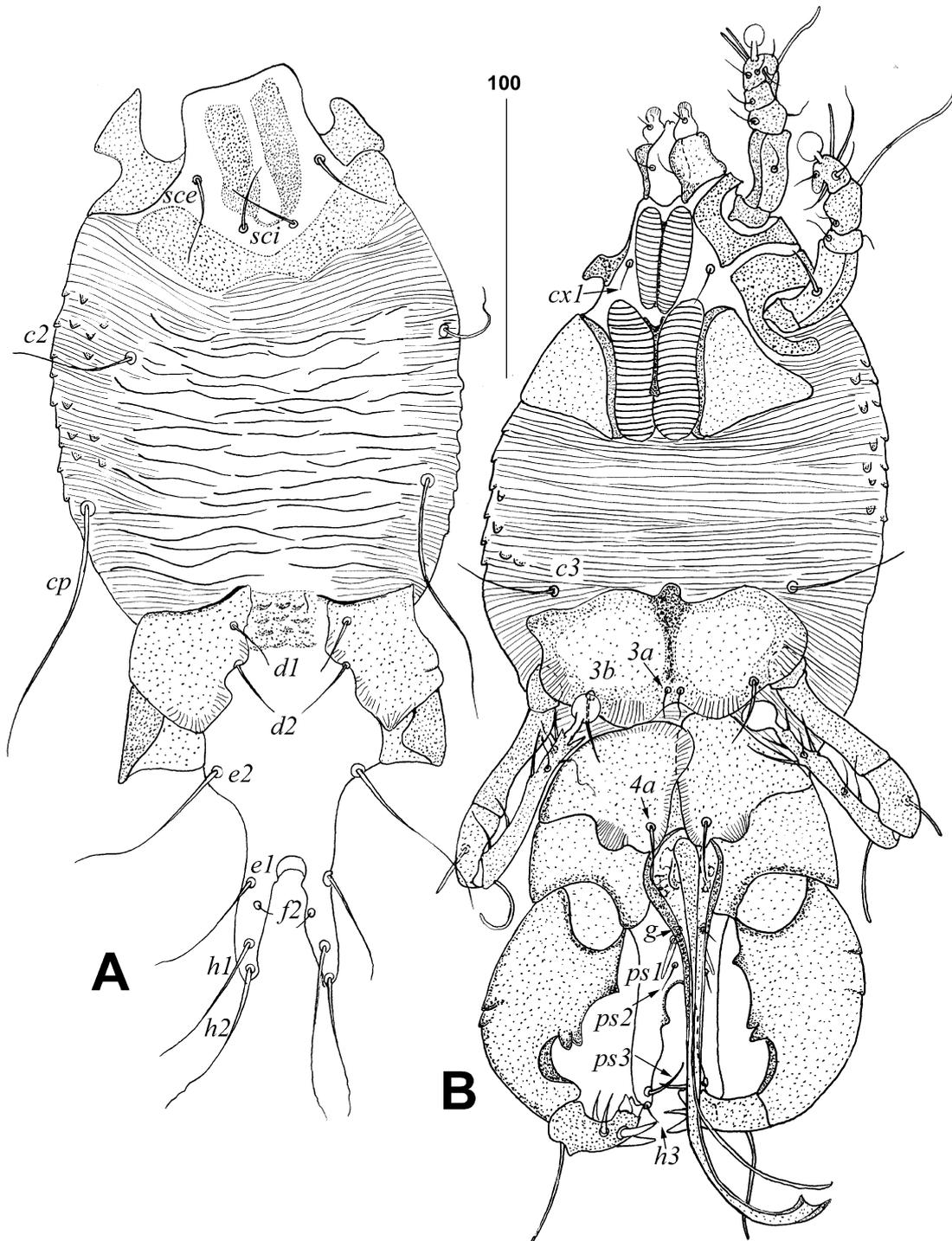


FIG. 16. *Lemuroptes potto* stat. nov., male. A. — Dorsal view. B. — Ventral view.

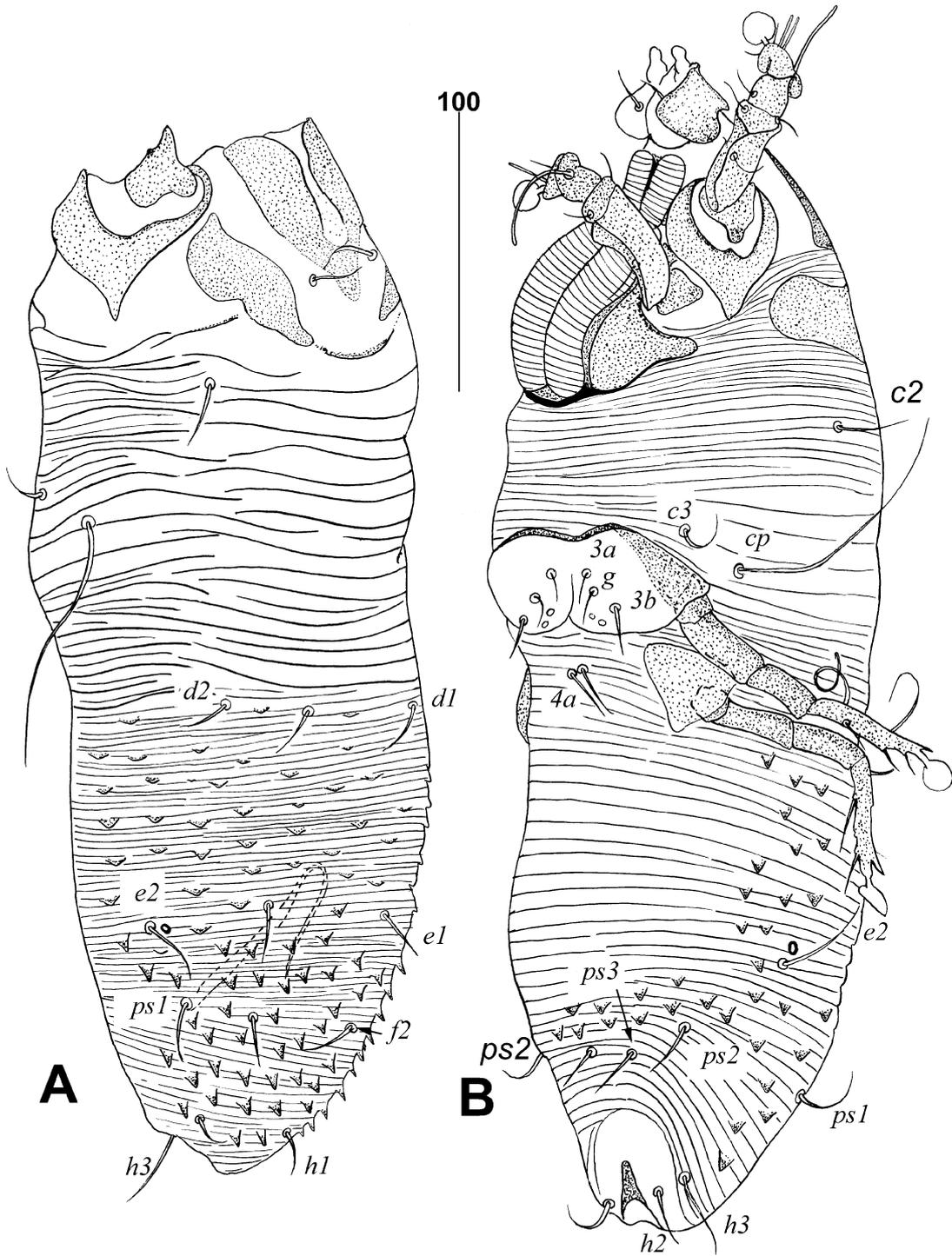


FIG. 17. *Lemuroptes potto* stat. nov., female. A. — Dorsal view. B. — Ventral view.

these mites. On these hosts, the biotope of atopomelids, the thin body hairs, has largely undergone strong modification into spines. Non-spiny hairs are, however, still present and could serve as habitat for fur mites as they do on the morphologically convergent Madagascar spiny-tenrecs (Afrosoricida: Tenrecidae: Tenrecinae) that harbor atopomelid mites of genera other than *Atopomelus*.

A single species of *Atopomelus*, *A. crocidurae* has been collected on seven shrew species of the genus *Crocidura*. This species was relatively common on the Oriental shrews we examined (9 of 30 individuals representing 3 host species from Borneo; 21 of 31 individuals representing 4 host species from the Philippines). However, atopomelids of this genus are completely absent on African shrews, including many species of *Crocidura*, based on our examination of several hundred host specimens representing many species from different regions of East and Central Africa. A modern phylogenetic hypothesis for Southeast Asian shrews was proposed by Ruedi & Vogel (1995). *Atopomelus crocidurae* is associated with hosts belonging to different clades of their cladogram (Ruedi & Vogel, 1995, p. 212, FIG. 5), suggesting either an old association with the Asian lineage or more recent colonization of different host species.

*Atopomelus talpae* was described from *Talpa romana* (Talpidae) in Italy (Fain *et al.*, 1973). This record was not the result of museum contamination because the mites were collected directly from a freshly collected host animal. No other species of Atopomelidae are known from native mammals in Europe, nor are any reported from other species of Talpidae.

The distribution of *Atopomelus* species on these host taxa is an intriguing problem. Comparing our phylogeny with published host phylogenies is difficult because different data sets have led to different phylogenetic conclusions with respect to the host taxa. Traditional morphological analyses yielded two different phylogenies of the three host families as follows (Erinaceidae (Talpidae + Soricidae)) (Butler, 1988) vs. (Soricidae (Erinaceidae + Talpidae)) (McKenna & Bell, 1997), while more recent molecular studies support (Talpidae (Erinaceidae + Soricidae)) (Douady *et al.*, 2002) or place Erinaceidae outside a more inclusive group of eutherian orders

(Mouchaty *et al.*, 2000). Grenyer & Purvis (2003) conducted a supertree analysis combining phylogenetic information from 47 published sources to arrive at a conclusion congruent with the hypothesis of Butler (1988) above. Using this last hypothesis as an estimate of the host phylogeny, there are three alternative scenarios for the origin of host parasite associations in these mites. Because of the restricted host ranges of the *Atopomelus* species, the parasite phylogeny cannot be congruent with that of their hosts, necessitating some hypotheses of colonization and/or extinction.

According to the first scenario, these mites were originally associated with the common ancestor of Eulipotyphla and coevolved with these hosts. However, replacing the hosts for the parasites in the parasite phylogeny yields a pattern completely incongruent with the family level host phylogeny of Grenyer & Purvis (2003). This hypothesis is, however, congruent at the family level with the host phylogeny of Douady *et al.*, (2002) but would still require very extensive extinction of the parasite lineage on most extant host groups.

The second scenario is that the ancestor of *Atopomelus* was originally associated with Palaeartic crocidurine shrews and secondarily colonized a talpid in Europe and gymnures in Asia. The phylogeny of the Crocidurinae is highly unsettled, but recent work suggests that the genus *Crocidura* probably originated in Africa, followed by migration to the western Palaeartic, finally reaching the Indomalayan region relatively recently (Ruedi & Vogel, 1995). Thus, the absence of *Atopomelus* on African *Crocidura* species suggests that the association with Oriental shrews was the result of a later colonization. This scenario also requires the extinction of *Atopomelus* on the surviving Palaeartic *Crocidura* species and a very slow rate of speciation yielding a single *Atopomelus* species on a number of different Asian shrew hosts, while more rapid speciation yielded the three known species on gymnures.

The third, and we believe most likely scenario is that *Atopomelus* was originally associated with gymnures. The relatively plesiomorphic morphology of this genus suggests a great age for the lineage. Although currently restricted to the Oriental region, the fossil record of the gymnure subfamily Hylomyi-

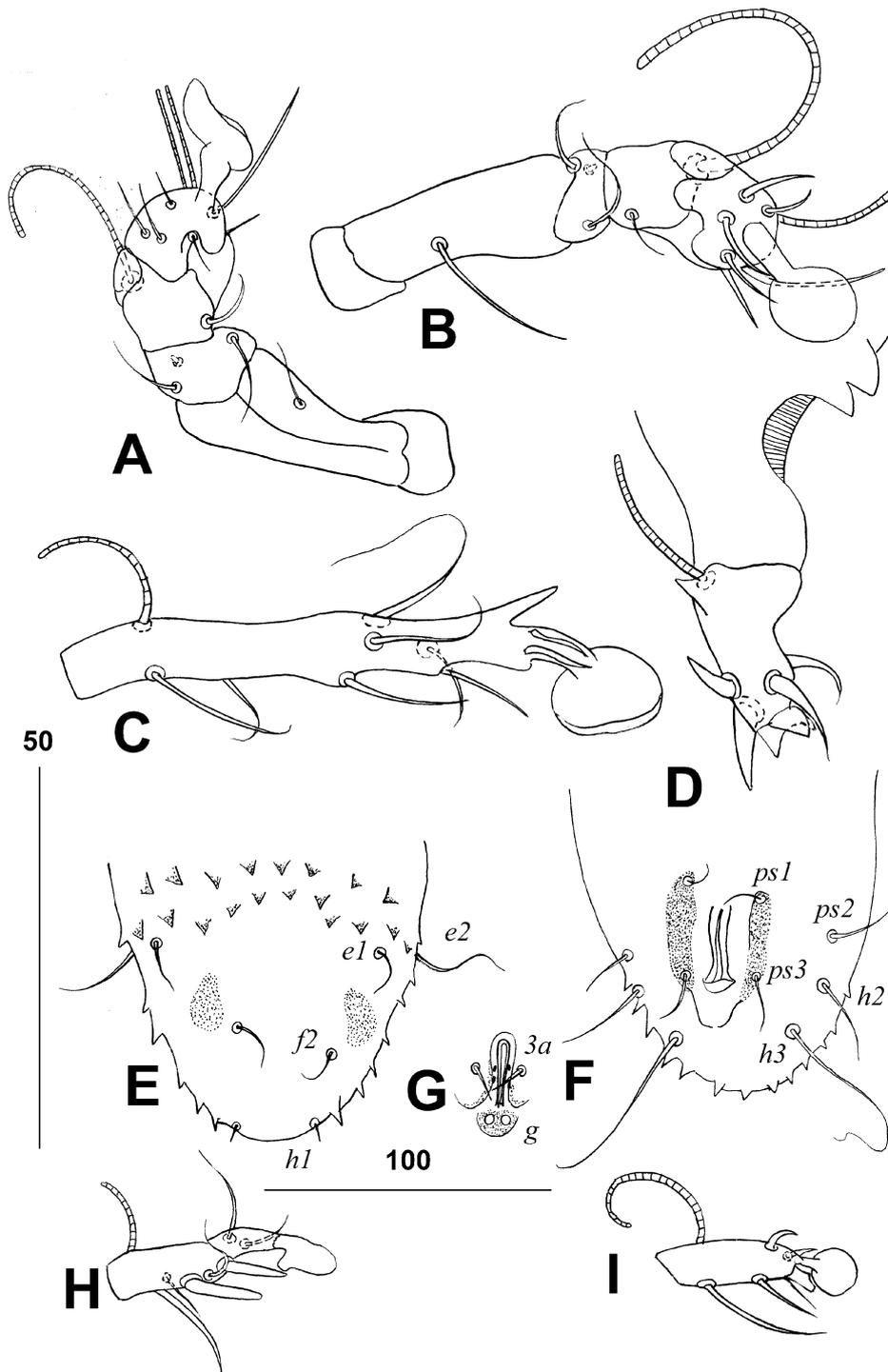


FIG. 18. (A-I). *Lemuroptes potto* stat. nov., male (A-D). A. — Leg I, ventral. B. — Leg II, dorsal. C. — Tibiotarsus III, lateral. D. — Tibiotarsus IV, lateral. *Micropotamogolishus congoensis*, male (E-I). E. — Opisthonotum, dorsal. F. — Opisthogaster. G. — Aedeagus. H. — Tibiotarsus III, lateral. I. — Tibiotarsus IV, lateral.

nae extends from the Oligocene to the Pliocene of Europe (BUTLER, 1988; MCKENNA & BELL, 1997), where these hosts were sympatric with both Talpidae and Crocidurinae. An early colonization of the lineage onto a talpid would be represented by the basal, relictual species, *A. talpae*. A later colonization onto an early Asian *Crocidura* is represented by *A. crocidurae*, which has spread throughout the region. Finally, the species of the “*locusta*” group may have co-speciated with the genus *Hylomys*, but only after an *in situ* speciation yielding two *Atopomelus* lineages on the common ancestor of *H. suillus* and *H. sinensis*. This process is necessary to explain the occurrence of *A. locusta* on both host species, while each species in the sister-lineage is restricted to one of the two hosts. Curiously, although *A. locusta* and *A. priapus* were found together on the same individual *H. sinensis* in several instances, *A. locusta* was not found on any *H. suillus* that harbored *A. hylomys*. This may be merely an artifact of inadequate sampling.

#### ACKNOWLEDGEMENTS

We thank Drs. LAWRENCE HEANEY (FMNH), ANTONIA GOROG (UMMZ), and JAMES PATTON (MVZ) who provided access to the majority of host specimens examined in this study. We thank Prof. ALEX FAIN (IRSNB) and Dr. HENRI ANDRE (MRAC) for access to type specimens of mites. We express our appreciation to Dr. MIKHAIL ZAITZEV (ZISP) for his information about the host phylogeny and palaeontology. This research was supported by a grant from the U.S. National Science Foundation DEB-0118766 (PEET) to BMOC.

#### REFERENCES

- BOCHKOV (A.V.) & FAIN (A.), 2003 — Revision of the subgenus *Marquesania* (Acari: Atopomelidae: *Listrophoroides*). — *Invert. Syst.*, **17**: 575-604.
- BUTLER (P.M.) 1988. — Phylogeny of Insectivores. pp. 119-141. In: BENTON (M.J.) (ed.). *The Phylogeny and classification of Tetrapods. Vol. 2: Mammals. The Systematics Association. 35B.* Oxford.
- DOUADY (CH.J.), CHATELIER (P.I.), MADSEN (O.), JONG DE (W.W.), CATZEFELIS (F.), SPRINGER (M.S.), & STANHOPE (M.J.), 2002 — Molecular phylogenetic evidence confirming the Eulipotyphla concept and in support of hedgehogs as the sister group to shrews. — *Mol. Phyl. Evol.*, **25**: 200-209.
- FAIN (A.), 1972. — Les Listrophoridés en Afrique au Sud du Sahara (Acarina: Sarcoptiformes). — *Ann. Mus. r. Afr. Cent.*, Ser 8° (Sci.Zool.), **197**: 1-200.
- FAIN (A.), 1994. — Adaptation, specificity and host-parasite coevolution in mites (Acari). — *Int. J. Parasitol.*, **24**: 1273-1283.
- FAIN (A.) & LUKOSCHUS (F.), 1977. — Une nouvelle espèce du genre *Atopomelus* TROUËSSART, 1917 (Acarina, Astigmatas, Listrophoroidea). — *Bull. Ann. Soc. r. belge d'Entomol.*, **113**: 29-31.
- FAIN (A.), LUKOSCHUS (F.), & CAUWENBERGE (A.), 1973. — Un nouvel acarien de la famille Atopomelidae *Atopomelus talpae* sp. n. parasite de la taupe romaine *Talpa romana* (Listrophoroidea: Sarcoptiformes). — *Redia*, **54**: 59-62.
- GRANDJEAN (F.), 1939. — La chaetotaxie des pattes chez les Acaridae. — *Bull. Soc. Zool. France*, **64**: 50-60.
- GRENAYER (R.) & PURVIS (A.), 2003. — A composite species-level phylogeny of the ‘Insectivora’ (Mammalia: Order Lipotyphla HAECKEL, 1866). — *J. Zool. (Lond.)*, **260**: 245-257.
- GRIFFITHS (D.A.), ATYEO (W.T.), NORTON (R.A.) & LYNCH (C.A.), 1990 — The idiosomal chaetotaxy of astigmatid mites. — *J. Zool. (Lond.)*, **220**: 1-32.
- MCKENNA (M.C.) & BELL (S.K.), 1997. *Classification of mammals above the species level.* Columbia University Press, New York.
- MOUCHATY (S.K.), GULLBERG (A.), JANKE (A.) & ARNASON (U.), 2000. The phylogenetic position of the Talpidae within Eutheria based on analysis of complete mitochondrial sequences. — *Mol. Biol. Evol.*, **17**: 60-67.
- NIXON (K.C.), 1999. — ‘WINCLADA. Version 0.9.9b. Program and documentation in cladistic.com.’ Ithaca. New York.
- OCONNOR (B.M.), 1982. — Astigmata. pp. 146-169. In: *Synopsis and Classification of Living Organisms.* PARKER (S.B.) (ed.). McGraw-Hill. New-York.
- PAGE (R.D.M.), 2001. — ‘NDE: NEXUS Data Editor 0.5.0.’ — University of Glasgow: Glasgow.
- RADFORD (C.D.), 1950. Systematic check list of mite genera and type species. International Union of Biological Sciences, Series C (Entomology section), **1**: 1-232.
- RUEDI (M.) & VOGEL (P.), 1995. — Chromosomal evolution and zoogeographic origin of southeast Asian shrews (genus *Crocidura*). — *Experientia*, **51**: 174-178.

- SORENSEN (M.D.), 1999. — 'TreeRot, version 2'. — Department of Biology. Boston University: Boston. Massachusetts.
- STANHOPE (M.J.), WADDELL (V.G.), MADSEN (O.), DE JONG (W.W.), HEDGES (S.B.), CLEVEN (G.C.), KAO (D.), & SPRINGER (M.S.), 1998. — Molecular evidence for multiple origins of Insectivora and for a new order of African insectivore mammals. — Proc. Nat. Acad. Sci., **95**: 9667-9672.
- SWOFFORD (D.L.), 2001. — 'PAUP\*. Phylogenetic Analysis Using Parsimony (\* and other Methods). — Version 4'. Sinauer Associates. Sunderland. Massachusetts.
- TROUESSART (E.L.), 1917. — Troisieme note sur les Sarcopitides Pilicoles et description de genres nouveaux. — Bull. Soc. Zool. France, **42**: 151-158
- WILSON (E.) & REEDER (M.), 1992. — Mammal species of the world. A taxonomic and geographic reference. 1207 pp. (2nd ed.). Washington. London.
- WURST (E.), 1993. — Investigations on the anatomy and the behaviour of the fur mite *Listrophorus leuckarti* (Acari: Listrophoridae). — Stuttgart. Beitr. Naturk., Serie A (Biol.), **53**: 1-68.

## Appendix

Emended diagnoses of the genera *Lemuroptes* LAWRENCE, 1958 and *Micropotamogalichus* FAIN, 1970 and list of comparative materials.

### Genus *Lemuroptes* LAWRENCE, 1958

*Type species: Lemuroptes primarius* LAWRENCE, 1958, by monotypy.

*Description.* Adults. Length and wide of gnathosoma subequal, bearing a pair of well developed ventro-lateral valves. Prescapular shield with deep anteromedian incision. Coxae I and II with well developed striated membranes. Setation of idiosoma: *scx*, *si*, *se*, *c2*, *c3*, *cp*, *d1*, *d2*, *e1*, *e2*, *f2*, *h1*, *h2*, *h3*, *ps1-3*, *1a*, *3a*, *3b*, *g*, *4a*. Cupules not observed. Coxal fields of legs III closely situated to each other, coxal fields of legs IV distinctly separated. Anterior apodemes of coxae I-III each fused mesally. Setation of legs I-IV: I trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*,  $\sigma$ 1), tibia 2 (*gT*,  $\varphi$ ), tarsus 9 (*wa*, *ra*, *la*, *d*, *e*, *f*,  $\epsilon$ ,  $\omega$ 1,  $\omega$ 3), seta *ba* not observed; II trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*,  $\sigma$ ), tibia 2 (*gT*,  $\varphi$ ), tarsus 7 (*wa*, *ra*, *la*, *d*, *e*, *f*,  $\omega$ 1), seta *ba* not observed; III trochanter 0, femur 0, genu 1 ( $\sigma$ ), tibiotarsus 8 (tibia — *kT*,  $\varphi$ , tarsus — *wa*, *ra*, *s*, *d*, *e*, *f*); IV trochanter 0, femur 0, genu 0, tibiotarsus 8 (tibia — *kT*,  $\varphi$ , tarsus — *wa*, *ra*, *d*, *e*, *f*). Male (FIGS. 14, 16A-D). Idiosoma elongated, 2 times longer than wide. Postscapular shield very short, hysteronotal shield short, separated medially, bearing only setae *d1* and *d2*. Postgenital shield absent. Adanal suckers absent. Opisthosomal lobes well developed, bearing setae *e1*, *f2*, *h1-3*, and *ps3*. Opisthosoma without membranous posterior extension. Legs IV hypertrophied, distinctly longer than legs III. Femur and genu IV fused and strongly reinforced. Tarsus III with distinct apical dorsal spur. Tibiotarsus IV short, about 2 times shorter than tibiotarsus III, without ambulacrum, all its setae thick, setae *ra* and *f* expanded, membranous, terminally positioned. Female (FIG. 15). Idiosoma strongly elongated, about 3 times longer than wide. Postscapular shield very short, separated medially. Hysteronotal shield absent. Soft cuticle of idiosoma covered by transverse striations,

protuberances and scales. Epygium completely fused with anterior apodemes of coxae III. Genital valves situated between coxae III. 2 pairs of genital papillae present. Tarsi III and IV with distinct apical dorsal spur. Larva. Gnathosoma as in adults. Idiosoma as in female but postscapular shield absent. Idiosomal setation: *scx*, *sci*, *sce*, *c2*, *c3*, *cp*, *d1*, *d2*, *e1*, *e2*, *h1*, *h2*, *1a*, *3b*. Leg setation: I trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*,  $\sigma$ 1), tibia 2 (*gT*,  $\varphi$ ), tarsus 9 (*wa*, *ra*, *la*, *d*, *e*, *f*,  $\epsilon$ ,  $\omega$ 1), setae *ba* and *s* not observed; II trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*,  $\sigma$ ), tibia 2 (*gT*,  $\varphi$ ), tarsus 7 (*wa*, *ra*, *la*, *d*, *e*, *f*,  $\omega$ 1), seta *ba* not observed; III trochanter 0, femur 0, genu 1 ( $\sigma$ ), tibiotarsus 8 (tibia — *kT*,  $\varphi$ , tarsus — *wa*, *ra*, *s*, *d*, *e*, *f*). Protonymph. Postscapular shield absent. Setae *f2*, *h3*, *ps1-3*, *3b*, and *g* added. One pair of genital papillae present between coxae IV. Leg setation as in larva, except setae *d*, *ra*, and *wa* of tarsus IV added. Teleonymph. Postscapular shield absent. Setae *3a* and *4a* added on idiosoma, setae *kT* and  $\varphi$  added on tibia IV, and setae *e*, *f* added on tarsus IV. Setae *f2* and *h3* macrosetae. 2 pairs of genital papillae present between coxae IV. Setae *3a* microsetae, situated between coxae IV in anterior part.

*Included species. Lemuroptes primarius* LAWRENCE, 1958, *L. bursatus* FAIN, 1972, *L. zumpti* FAIN, 1972, and *L. attenuatus* FAIN, 1972, *L. potto* FAIN, 1977 stat. nov. (FIGS. 16, 17, 18 A-D) (*L. primarius potto*).

*Material examined. Lemuroptes attenuatus:* Holotype female (MRAC 140063) ex *Galagoides demidoff* (FISCHER, 1806) (= *Galago demidovi*) (MRAC 16513), CONGO: Kingshasa, Makala. *Lemuroptes bursatus:* Holotype female (MRAC 140064) ex *Otolemur* (= *Galago*) *crassicaudatus* (GEOFFROY, 1812), SOUTH AFRICA: Mbuzi, 7 March 1965, coll F. ZUMPT; male paratype (MRAC 140065) *O. crassicaudatus* (MRAC 31204), CONGO: Shaba, Lubumbashi, coll. POELMAN. *Lemuroptes potto:* Male holotype (MRAC 140061) and paratype female (MRAC 140062) ex *Perodicticus potto* (MÜLLER, 1766), CONGO: Virunga National Park, Mutwanga, 1956; 4 males, 26 females, 1 larva, 8 protonymphs and 12 teleonymphs (BMOC 92-0605-132) ex *P. potto* (FMNH 148986), BURUNDI: Cibitoke Prov., Kibira National Park, Ndora Zone, Giserama Coline., 24 August 1991, J.C. KERBIS (JCK 2971). *Lemuroptes zumpti:* Holotype female (MRAC

140066) ex *Otolemur* (=Galago) *crassicaudatus* (MRAC 31204), CONGO: Shaba, Lubumbashi, coll. POELMAN; male paratype (MRAC 140067) from *O. crassicaudatus*, SOUTH AFRICA: Mbuzi, 7 March 1965, coll F. ZUMPT.

Genus *Micropotamogalichus* FAIN, 1970 *Type species*: *Micropotamogalichus congoensis* FAIN, 1970

*Description*. Adults. Gnathosoma distinctly longer than wide, bearing a pair of well developed ventrolateral valves. Prescapular shield widely separated medially; postscapular shield strongly reduced, represented by pair of lateral sclerotized patches. Coxae I and II with well developed striated membranes. Setation of idiosoma: *scx*, *si*, *se*, *c2*, *c3*, *cp*, *d1*, *d2*, *e1*, *e2*, *f2*, *h1*, *h2*, *h3*, *ps1-3*, *1a*, *3a*, *3b*, *g*, *4a*. Cupules not observed. Coxal fields of legs III closely situated to each other, coxal fields of legs IV distinctly separated. Anterior apodemes of coxae I-III each fused mesally fused. Setation of legs I-IV: I trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*,  $\sigma 1$ ), tibia 2 (*gT*,  $\varphi$ ), tarsus ?; II trochanter 0, femur 1 (*vF*), genu 3 (*cG*, *mG*,  $\sigma$ ), tibia 2 (*gT*,  $\varphi$ ), tarsus ?; III trochanter 0, femur 0, genu 1 ( $\sigma$ ), tibiotarsus 8 (tibia — *kT*,  $\varphi$ , tarsus — *wa*, *ra*, *s*, *d*, *e*, *f*); IV trochanter 0, femur 0, genu 0, tibiotarsus 8 (tibia — *kT*,  $\varphi$ , tarsus — *wa*, *ra*, *d*, *e*, *f*). Male. Idiosoma elongated, more 2 times longer than wide. Hysteronotal shield short, broadly divided medially, devoid of setae. Postgenital shield absent. Adanal suckers

absent. Anal fold well sclerotized. Opisthosomal lobes and membrane absent. Legs IV not modified. Tibiotarsus IV similar to tibiotarsus III, with ambulacrum, setae *ra* modified, occupying terminal position. Female. Idiosoma strongly elongated, about 3 times longer than wide. Postscapular shield very short, divided medially. Hysteronotal shield absent. Unsclerotized cuticle of idiosoma covered by transverse striations and scales. Epyginum completely fused with anterior apodemes of coxae III. Genital valves situated between coxae III. 2 pairs of genital papillae present.

*Included species*. *Micropotamogalichus congoensis* FAIN, 1970 (FIG. 16E-I).

*Material examined* Holotype male (MRAC 140069) and female paratype (MRAC 140068) ex *Micropotamogale ruwenzorii* (de WITTE & FRECHKOP, 1955), CONGO: Orientale Prov., Tshabunda, Kisanga, 23 June 1960, coll. RAHM.

Genus *Didelphoecius* FAIN, 1970

*Material examined*. *Didelphoecius surinamensis* FAIN, 1976: One male and 1 female ex *Caluromys philander* (L., 1758), SURINAM: Lelydorp, 24 February 1970, coll. F.S. LUKOSCHUS (FSL 185) (UMMZ).