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FUR-MITES OF THE GENUS *ATOPOMELUS* TROUSSART, 1918

(ACARI: ATOPOMELIDAE) LIFE-CYCLE

PHYLOGENY AND HOST PARASITE-ASSOCIATIONS

BY A.V. BOCHKOV* 1,2, P.B. KLIMOV1, & B.M. OCONNOR1

(Accepted January 2005)

**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 *Didelphoeclius* Fain were selected as close outgroups and *Listrophorus leuckarti* (Listrophicidae) 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 Palaeartic.

**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 Australian 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).

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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 Trouessart (1918) for a single species *Atopomelus locusta* Trouessart, 1918, described from *Hylomys (=Neotetracus) sinensis* (Trouessart, 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 crocidurae* Fain & Lukoschus, 1977 was described from two females collected from *Crocidura attenuata aequicaudata* Robinson & Kloss, 1918 (=*Crocidura aequicauda* [sic]) (Soricidae) from Sumatra (Fain & Lukoschus, 1977) and *A. talpae* Fain, Lukoschus & Cauwenberge, 1973, was described from both sexes collected from *Talpa romana* Thomas, 1902 (Talpidae) 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 20th 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 (\(\mu\)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 Talpidae) and Afroscorida (including Chrysochloridae and Tenrecidae) (Stanhope et al., 1998). Specimen depositories and reference numbers are cited using the following abbreviations:
Cladistics. Three species representing genera of Atopomelidae that are morphologically similar to Atopomelus were used as close outgroups: Didelphocucis 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 & Freckop, 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 Didelphocucis is in need of a separate taxonomic review, therefore, we simply selected a species showing many ancestral character states for this genus. Listrophorus leuckarti Pagenstecher, 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 (Sorenson, 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, paraproct suckers ps1 absent, pretarsal ambulacrum or sucker-like setae, subequal in length to femurogen. 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 femurogen. Female: idiosoma strongly elongated, hysteronotal shield absent, hysterosoma completely covered by triangular cuticular microtrichae.
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: sxx, si, se, c2, c3, cp, dl, 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, π), tarsus 10-11 (wu,
ra, la, ba, f3, d, e, f, oI and o3); II trochanter 1 (pR), femur 1 (vF), genu 3 (cG, mG, o), tibia 2 (gT, q), tarsus 8-9 (wa, ra, la, ba, f3, d, e, f, o); III trochanter 1 (sR), femur 0, genu 1 (o), tibiotarsus 8 (tibia — kT, q, tarsus — ra, sa, la, ba, f2, h3); IV trochanter 0, femur 0, genu 0, tibiotarsus 8 (tibia — kT, q, tarsus — 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 el unsclerotized. Setae hI 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.

### Table 2. — Data matrix. (0 plesiomorphy, 1 apomorphy, – inapplicable)

<table>
<thead>
<tr>
<th>Species</th>
<th>Character</th>
</tr>
</thead>
<tbody>
<tr>
<td>Listrophorus leuckarti</td>
<td>11111111112</td>
</tr>
<tr>
<td>Didelphoecius sarinamensis</td>
<td>12222222223</td>
</tr>
<tr>
<td>Lemuroptes potto</td>
<td>33333333334</td>
</tr>
<tr>
<td>Microptamogalichus congensis</td>
<td>1234567890</td>
</tr>
<tr>
<td>Atopomelus crocidurae</td>
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</tr>
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<td>Atopomelus hylomys</td>
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</tr>
<tr>
<td>Atopomelus locusta</td>
<td>1234567890</td>
</tr>
<tr>
<td>Atopomelus priapae</td>
<td>1234567890</td>
</tr>
<tr>
<td>Atopomelus talpae</td>
<td>1234567890</td>
</tr>
</tbody>
</table>

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 protubercures. Hysterosoma completely covered by large triangular microtrichae. Epignum 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, e3, ep, 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, oI), tibia 2 (gT, q), tarsus 9 (wa, ra, ba, la, d, e, f, oI); II trochanter 0, femur 1 (vF), genu 3 (cG, mG, o), tibia 2 (gT, q), tarsus 8 (wa, ra, la, ba, d, e, f, oI); III trochanter 0, femur 0, genu 1 (o), tibiotarsus 8 (tibia — kT, q, tarsus — wa, ra, d, e, f). Solenidion o III very short.

Protonymph (Fig. 11 F-L). Postscapular shield absent. Setae f2, h3, p3, 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 o 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 q added on tibia IV, and setae e, f added on tarsus IV. Setae f2 and h3 macrosetae. Two pairs of distinct 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): *Atopometes locusta*, male. — Dorsal view. B.— Ventral view. C.— Tibiotarsus III, lateral. D.— Tibiotarsus IV, lateral. Scale bars 100 μm (A, B) and 50 μm (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. Opisthontotal 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, dl, d2, and e1. Setae dl 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, dl 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 q 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; ω I-IV 60-70; ω 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 dl, 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. 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, ep 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: ω1 I-II 22-25, ω3 I 27-30; ω I-III 40-45, IV 17-20; ω I-II 15-22, III 17-22.


Specimen deposition. Lectotype and female paralectotypes (designated by Fain & Lukoschus, 1977, not examined) are deposited in MNHP. Voucher specimens 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)


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 h2. 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 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 shorter than ventral spur, situated in median part of segment. Femurogen 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 para- types 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;

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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 µm (A, B), 50 µm (C, D), and 25 µm (E, 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; posterior ventral spur of femurogenu IV 20, 20-22 long, posterior dorsal spur 8, 6-8 long. Length of idiosomal setae: I about 18-20. Length of solenidia: I 23, d2, e1, e2, h1, h2, ps3 — all 22-25, f2 and h3 about 80, 3a, 3b, g and h4 all about 10. Setae of d1-II distinctly shorter than respective solenidion o1; setae d III-IV about 2 times shorter than respective tubiotarsi, 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, dl, d2, el, e2, h1, h2, ps3 — all 22-25, f2 and h3 about 80, 3a, 3b, g and h4 all about 10. Setae of d1-II distinctly shorter than respective long. Length of solenidia: o1 I-II about 22, o3 123; q I-II about 22, III 35, IV 14; σ I-II 6, III 8.

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


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 ps long, 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, dl, d2, and el. Setae dl and d2 thin and short, subequal in length, much shorter than el. Length ratio between postscapular and hysteronotal shields subequal, 1.2:1. Unsclerotized cuticle of opisthosa 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 o1; seta d III 3 times shorter than tubiotarsus, excluding ambulacrum. Tro-
Fig. 6 (A-E). *Atopomeles priapus* sp. nov., male. A. — Gnathosoma, lateral. B. — Dorsal view. C. — Ventral view. D. — Tibiotarsus III, lateral. E. — Tibiotarsus IV, lateral. Scale bars 100 µm (C, B) and 50 µm (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 µm (A, B) and 50 µm (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. Femurogenu 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; 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 femurogenu IV 3, 3-5 long; posterior ventral spur of femurogenu IV about 2, 2-3 long. Length of idiosomal setae: d1, d2 about 2, 2-3 long; setae e1, e2, h1, h2, 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: o1 I about 13, II about 20, o3 I about 22; p1-I-II about 35, III 55, 55-58, IV 47, 45-50; p1-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 o1; 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: o1 I-II 14-16, o3 I 10-12; p1-I-III 20-25, IV 6-8; p1-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.


**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. Femurogenu IV with two ventral spurs.
Fig. 8 (A–F). *Atopomela 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 µm (A, B) and 50 µm (C–F).
Fig. 9 (A-E). *Atopomelas crocidurae*, female. A. — Dorsal view. B. — Ventral view. C. — Dorsal scales of idiosoma. D. — Tibiotarsus III, lateral. E. — Tibiotarsus IV, lateral. Scale bars 100 µm (A, B) and 50 µm (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 unscerotized patches situated near to bases of setae *d2*. Diameter of these patches subequal to bases of setae *d2*. Setae *d1* thickened, subequal in length, or *f2* to respective tibiotarsi, excluding ambulacra. 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).


**Material examined.** One female ex *Crocidura atte nuata* 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 clasping 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 clasping organ of coxa II, pa — posterior apodeme of coxa II.
Fig. 12 (A–F). Atopomelus crocidurae, teleonymph. 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 teolyymphs, 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 expung Sedahan, 15 August 1999, coll. A.J. Gorog (AJG 472); 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 teolyymphs from Crocidura malayana Robinson & Kloss, 1911, MALAYSIA: Selangor, Ulu Langat Kajang, 14 June 1954, coll. M. Nadchatram; 11 males, 10 females, and 1 teolyymph (BMOC 92-1400-100) ex Crocidura minorus 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 teolyymphs, 1 protonymph, and 1 larva (BMOC 92-1400-097) ex C. minorus (FMNH 146789), same data, 7 March 1992, coll. S.M. Goodman (SMG 5131); 11 males, 9 females, and 5 teolyymphs (BMOC 92-1400-092) ex C. minorus (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 teolyymphs, 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 teolyymphs (BMOC 01-0920-006) ex C. grayi (FMNH 168974), same data, 19 March 2001, coll. L.R. Heaney (LRH 6363); 2 females, 8 teolyymphs, 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 teolyymphs, 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 teolyymphs, 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: Hysteronal shield mushroom-like. Setae d1 3 times longer than d1; setae e2 long; setae ps2 present. Tarsus IV with two subequal apices. Femurogenu IV without spurs. Trochanter IV without dorsal spur; ventral spur bifurcate. Female: Postascapular 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. Hysteronal 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 postascapular 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 re-
pective trochanter, bifurcate, with apices subequal in length. Femurogenus 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; femurogenus 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 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 idiosomal setae: $o1$ I-II 25-28, $o3$ I 37-38; $q$ I-II 42-45, III 29-30, IV 15-16; $a$ I-II 20-22, III 10-12.

**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 idiosomal setae: $o1$ I-II 25-28, $o3$ I 37-38; $q$ I-II 42-45, III 29-30, IV 15-16; $a$ I-II 20-22, III 10-12.

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

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 TROUSSART, 1818
   — 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.

Key to females of the genus Atopomelus

1. 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 TROUSSART, 1918
3. Copulatory opening on a narrow, subterminal papilla. Distal part of spermatheca slightly inflato 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 \( \text{ra} \) and \( \text{wa II} \) (38), saber-like tibiotarsus IV of male (39), and setae \( \text{d IV} \) 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 \( \text{ps2} \) in male (23), and setae \( \text{s I-II} \) (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 postcapular 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. hylomys* and *A. priapus* is only supported by two characters, 10 (genital valves fused) and 42 (seta \( \text{d III-IV} \) 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. gymnura* (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. gymnura* 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 *Atopomelus* has been reported 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 Palaearctic 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 Palaearctic, 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 Palaearctic *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 Hylomy-
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 Hylyomys, 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. hylyomys. This may be merely an artifact of inadequate sampling.

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Appendix


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. 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, see, c2, c3, cp, d1, d2, e1, e2, h1, h2, 1a, 3b*. Leg setation: I trochanter 0, femur 1 (*vF*), genu 3 (*cG, mG, oF*), tibia 2 (*gT, q*), tarsus 9 (*wa, ra, la, d, e, f, eoF, eoI*), setae *ba* and *s* not observed; II trochanter 0, femur 1 (*vF*), genu 3 (*cG, mG, oF*), tibia 2 (*gT, q*), tarsus 7 (*wa, ra, la, d, e, eF, o1*), seta *ba* not observed; III trochanter 0, femur 0, genu 1 (*o*), tibiotarsus 8 (tibia — *kT, q*, 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 *q* added on tibia IV, and setae *e, f* added on tarsus IV. Setae *f2* and *h3* microsetae. 2 pairs of genital papillae present between coxae IV. Setae *3a* microsetae, situated between coxae IV in anterior part.


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 medially. Setation of legs I-IV: I trochanter 0, femur 1 (vF), genu 3 (cG, mG, σ1), tibia 2 (gT, q), tarsus ?; II trochanter 0, femur 1 (vF), genu 3 (cG, mG, σ), tibia 2 (gT, q), tarsus ?; III trochanter 0, femur 0, genu 1 (σ), tibiotarsus 8 (tibia — kT, q, tarsus — wa, ra, d, e, f); IV trochanter 0, femur 0, genu 0, tibiotarsus 8 (tibia — kT, q, 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 & Freckkop, 1955), CONGO: Orientale Prov., Tshabunda, Kisanga, 23 June 1960, coll. RAHM.

Genus *Didelphoecius* Fain, 1970