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TWO NEW SPECIES OF *MARMOSOPUS*
(ACARI: ASTIGMATA) FROM RODENTS OF THE
GENUS *SCOTINOMYS* (CRICETIDAE)
IN CENTRAL AMERICA

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Fain and Lukoschus (1977) proposed the genus *Marmosopus* for three species of mites which were collected as deutonymphs in the hair follicles of small Neotropical marsupials (Didelphidae and Caenolestidae). Additional species of this genus have been recovered from other small Neotropical marsupials (Lukoschus et al., 1982). Thus, it was with some surprise that deutonymphs of *Marmosopus* were discovered in the hair follicles of a rodent, *Scotinomys teguina* (Alston, 1876), preserved in fluid at the University of Michigan, by one of us (BMOC). It was even more surprising when specimens of a *Marmosopus* species were collected from field captured *Scotinomys xerampelinus* (Bangs, 1902) by R. H. Pine and R. J. Izor and made available to one of us (FSL) as part of a study on Panamanian mammals and their associated parasites, cosponsored by the Smithsonian Institution and the Field Museum of Natural History. The discovery of these mites on rodent hosts suggests a number of hypotheses concerning the transfer of

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parasitic mites among various hosts which will be discussed following the descriptions of the new species. In the following descriptions, measurements are given for the holotypes followed by the mean and range among 10 paratypes. All measurements are in micrometers (μm). Chaetotactic designations for body setae are those used by Fain and Lukoschus (1977); designations for leg setae are based on the system developed by Grandjean (1939).

Marmosopus mesoamericanus n. sp.

DESCRIPTION.—Deutonymph. Body of “unengorged” individuals dorso-ventrally flattened; body of “engorged” individuals globose, somewhat egg-shaped; length 191 (190, 178–207), width 143 (141, 128–154). Color of alcohol-preserved specimens slightly yellowish to white.

Gnathosoma. Gnathosomal remnant well sclerotized, bifid anteriorly, and fused to idiosoma posteriorly as in other members of subfamily. Gnathosomal solenidion curved, length 19 (19, 18–20); anterior gnathosomal seta weakly barbed, length 10 (no variation); posterior gnathosomal seta somewhat expanded basally, length 6 (6, 6–8); remnants of alveoli of subcapitular setae visible as spots of thin cuticle.

Dorsal prosoma (Fig. 1). Prosomal sclerite well developed. Internal vertical setae (*vi*) strongly barbed, situated on a prominent ventral tubercle, length 17 (19, 17–22); external vertical setae (*ve*) more anterolaterally positioned, barbed, length 7 (9, 7–10). Sejugal furrow well developed dorsally, extending ventrally. Internal scapular setae (*sci*) short, barbed, length 14 (15, 14–18); external scapular setae (*sce*) much longer, barbed, length 75 (75, 69–79); supracoxal setae (*scx*) situated in cavity of anterior leg.

Dorsal hysterosoma. Hysterosoma with well developed sclerite bearing dorsal and lateral setae; separate pygidial sclerite present, bearing lateral extensions curving ventrally. Hysterosomal setae d_1 , d_2 , l_1 , and h thickened, strongly barbed; other hysterosomal setae thin, smooth, or only weakly barbed; setal lengths as follow: d_1 48 (52, 48–56), d_2 44 (46, 41–53), d_3 6 (6, 5–7),

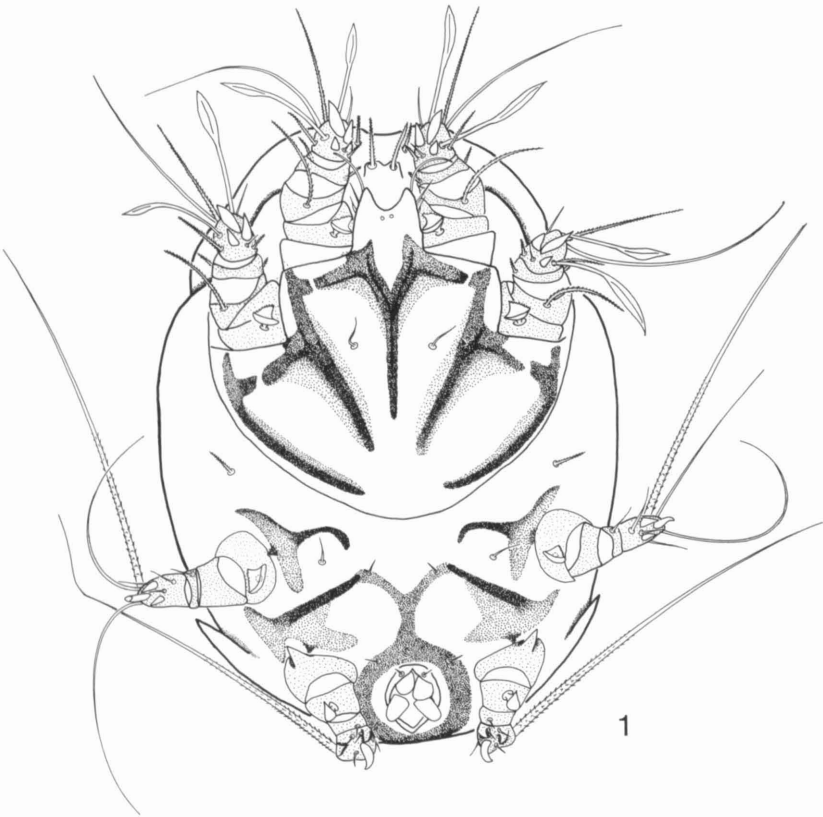
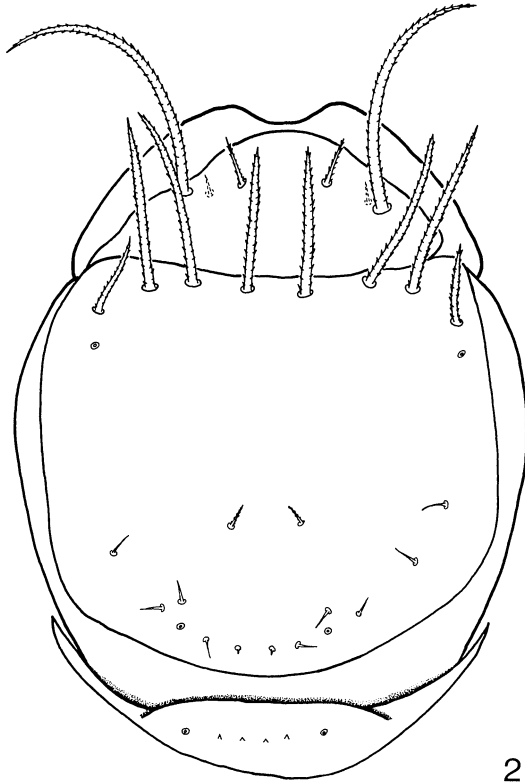


Figure 1. *Marmosopus mesoamericanus*, deutonymph. Dorsum.

d_4 6 (no variation), d_5 2 (no variation), l_1 53 (55, 51-60), l_2 7 (7, 7-8), l_3 7 (7, 6-7), l_4 6 (no variation), l_5 6 (no variation), h 18 (21, 17-24). Three pairs of hysterosomal cupules visible: *ia* positioned slightly posterior to seta *h*; *ip* posterior to seta d_4 ; *ih* on pygidial sclerite, positioned laterad of a transverse row of four small triangular denticles; no traces of cupules *im* or of the opisthosomal gland openings were observed in any specimen.

Venter (Fig. 2). Ventral sejugal furrow well developed, continuous posterior to coxal fields II. Anterior apodemes of coxal fields I fused to form an elongate sternum; anterior



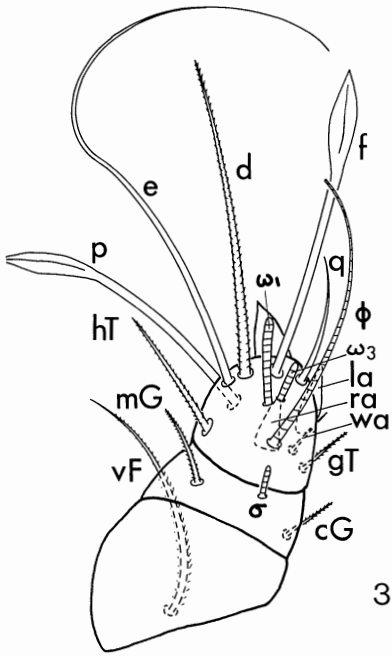
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Figure 2. *Marmosopus mesoamericanus*, deutonymph. Venter.

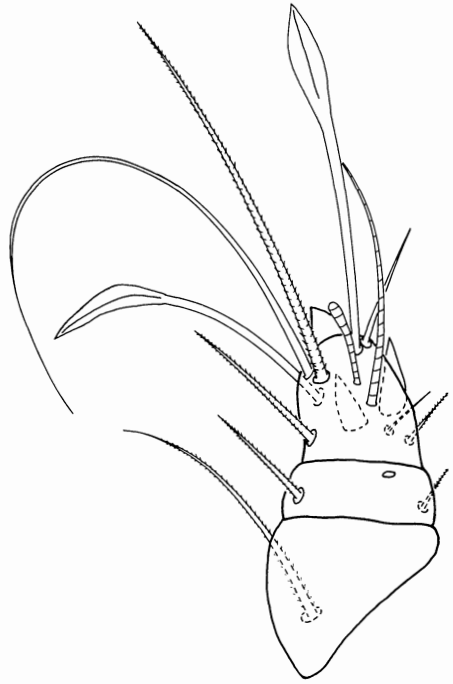
apodemes of coxal fields II strongly developed, not fused medially with posterior apodemes of coxal fields II which underly ventral sejugal furrow; anterior apodemes of coxal fields III short, curved posteriorly in medial region, not fused to apodemes of coxal fields IV or circumgenital apodeme; anterior apodemes of coxal fields IV fused medially then to circumgenital apodeme. Setae of coxal fields I, III, and IV short, filiform; anterior and posterior genital setae present, short, filiform. Subhumeral setae (*sh*) barbed, length 10 (10-12).

Legs (Figs. 3-6). Legs short and stout as in other species of the genus. Legs with 4, 4, 4, 3 freely articulated segments; tibia and tarsus of all legs fused with a distinct line of fusion visible

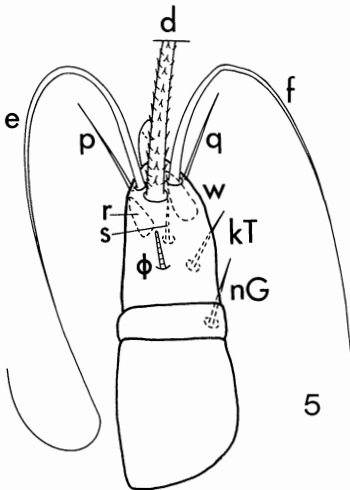
only on tibio-tarsus IV; femur and genu IV insensible fused. Empodial claws of pretarsi I-II short, stout, length 11 (no variation); claws of pretarsi III-IV strongly hooked, lengths 11, 7 (no variation). Leg setation as indicated in figures 3-6. Tarsal portion of tibio-tarsus I with the following setae: *la* a strong spine, length 9; *ra* a strong spine, length 9; *wa* short and filiform, length 6; *p* elongate and foliate, length 33; *q* filiform, length 14; *d* elongate, stiff, and strongly barbed, length 35 (37, 35-41); *e* elongate and filiform, length 65 (62, 57-66); *f* elongate and foliate, length 35; solenidion ω_1 slightly expanded apically, length 10; solenidion ω_3 , length 4 (4, 4-5). Tibial portion of tibio-tarsus I with seta *hT* strongly barbed, length 14; seta *gT* barbed, length 7; solenidion ϕ almost filiform, length 27 (26, 25-27). Genu I with seta *mG* barbed, length 10; seta *cG* barbed, length 6; solenidion σ short, length 1. Femur I with seta *vF* strongly barbed, length 25 (26, 25-28). Trochanter I with seta *pR* rhomboid and toothed along one edge only. Chaetotaxy of leg II generally similar to that of leg I; lengths of setae and solenidia as follow: *la* 9; *ra* 9; *wa* 7; *p* 33; *q* 12 *d* 44 (42, 40-44); *e* 66 (61, 57-66); *f* 35; solenidion ω distinctly clubbed, length 11 (11, 10-12); *hT* 20; *gT* 7; solenidion ϕ , 28 (29, 28-30); *mG* 13; *cG* 5; solenidion σ absent, represented by a vestigial alveolus; *vF* 28 (27, 25-32); *pR* rhomboid and toothed along one edge. Chaetotaxy of leg III as follows: seta *r* a strong spine, length 5; seta *w* also a strong spine, length 8; *s* filiform, length 5; *p* filiform, length 10; *q* filiform, length 10; *d* elongate, stout, and weakly barbed in its basal half, length 101 (101, 92-110); *e* filiform, length 84 (73, 70-84); *f* filiform, length 57 (52, 46-57); seta *kT* of the tibial portion of tibio-tarsus III filiform, length 7; solenidion ϕ length 5; seta *nG* of genu III filiform, length 7; seta *sR* of trochanter III similar in form to other trochanteral setae. Homology of setae of tarsal portion of tibio-tarsus IV uncertain. This segment bears seven total setae: *d* similar in form to *d* on tibio-tarsus III, length 128 (131, 121-143); four short, filiform setae and two spine-like setae. Tibial portion of tibio-tarsus IV with seta *kT* short and filiform; solenidion very short, but still distinguishable. Femoro-genu IV with femoral seta *wF* enlarged, bulbous, tapering somewhat anteriorly.



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Figures 3-6. *Marmosopus mesoamericanus*, deutonymph. 3, Leg I. 4, Leg II. 5, Leg III. 6, Leg IV.

DIAGNOSIS.—*Marmosopus mesoamericanus* may be distinguished from all other species of the genus by the following combination of character states: posterior dorsal setae very short and generally unbarbed; humeral setae much shorter than other anterior hysterosomal setae; setae d_1 and d_2 at least 40 μm in length; legs I-II with seta q short and simple; solenidion ϕ of genu II vestigial; trochanteral setae with teeth on one edge only; and empodial claw IV not bifid.

MATERIAL EXAMINED.—Holotype and 124 paratypes from the hair follicles of the tail of a female *Scotinomys teguina irazu* (Allen, 1904), COSTA RICA, Puntarenas Province, Monte Verde, James Farm, 1400 meters elevation, collected 4 February 1966 by W. S. James. Host specimen is in the University of Michigan Museum of Zoology (UMMZ) mammal collection #115362. A male *S. teguina* (UMMZ #115361) collected at the same time and place did not harbor *M. mesoamericanus*. Additional specimens of *M. mesoamericanus* (nonparatypes) were collected from other *S. teguina irazu* from the following localities (all host specimens in the UMMZ): COSTA RICA, Cartago Province, Cerro de la Muerte, 4 km. NE Copey, 2590 meters, 11–12 February 1975, M. D. Carleton (four of five females infested, #'s 123136, 123128, 123129, 123140, two of four males, #'s 123143, 123144); COSTA RICA, Alajuela Province, Volcan Poas, 1920 meters, 18–19 February 1975, P. Myers (three of 12 females, #'s 123099, 123100, 123145; three of seven males #'s 123106, 123107, 123109). Infestation ranged from two mites collected from specimen #123107 to 465 collected from specimen #123139. Specimens of *S. teguina irazu* in the UMMZ from other localities in Panama and Costa Rica were uninfested with *M. mesoamericanus*. These localities are as follow: COSTA RICA, Cartago Province, Volcan Irazú, various localities around San Juan Chicoa between 2850 and 2920 meters elevation, collected in early February 1975 by M. D. Carleton (14 females, nine males); Volcan Irazú, Highway Route 8, 1 August 1962 (three individuals); Moravia, 1116 meters, 22–29 June 1962, E. T. Hooper et al. (five females, six males); Puntarenas Province, Monteverde, Arthur Rockwell Cafetal, 1400 meters, 22 February 1966, M. S. Foster and W. Sturman (two males); San José

Province, 9 miles N. San Isidro del General, 4800 feet, 21 July 1962, D. J. Klingener (one female); PANAMA, Chiriquí Province, Rio Chiriquí, Viejo, 1860 meters, 9–10 May 1969, E. Barriga (two females, two males). The total infestation rate for *M. mesoamericanus* among fluid preserved *S. teguina irazu* in the UMMZ was 11 of 71 (15%).

TYPE DEPOSITION.—Holotype and paratypes in the Museum of Zoology, University of Michigan, Ann Arbor; additional paratypes in the (U.S.) National Museum of Natural History, Washington; Field Museum of Natural History, Chicago; Canadian National Collection, Ottawa; The Acarology Laboratory, Ohio State University, Columbus; Bernice P. Bishop Museum, Honolulu; Rijksmuseum van Natuurlijke Historie, Leiden; British Museum (Natural History), London; Zoologisches Institut und Zoologisches Museum, Hamburg; Institut de Medecine Tropicale, Antwerp; and in the authors' collections.

Marmosopus panamensis n. sp.

DESCRIPTION.—Deutonymph. Body somewhat larger than that of the preceding species, slightly dorso-ventrally flattened and ovoid in outline, length 230 (223, 208–245), width 184 (176, 152–196). Color of alcohol-preserved specimens yellow.

Gnathosoma. Gnathosoma as in preceding species, broadly bifid between anterior legs. Gnathosomal solenidion curved, length 17 (16, 15–18); anterior gnathosomal seta, length 11 (10, 9–11); posterior gnathosomal seta somewhat expanded basally, length 6 (7, 6–8); remnants of subcapitular setae not observed.

Dorsal prosoma (Figs. 8, 13). Prosomal sclerite well developed, internal vertical setae (*vi*) thickened and barbed, length 18 (19, 18–20); external vertical setae (*ve*) filiform, length 9 (8, 7–9). Sejugal furrow well developed dorsally, weakly developed ventrally. External scapular setae (*sce*) thick, heavily barbed, length 60 (61, 56–67); internal scapular setae (*sci*) sparsely barbed, length 15 (14, 12–15).

Dorsal hysterosoma. Dorsal hysterosomal sclerite bearing dorsal, lateral, and humeral setae; humeral setae (*h*) situated

only slightly posterior to the transverse row formed by setae d_2 , d_1 , and l_1 . These setae strongly barbed, other hysterosomal setae short and filiform; hysterosomal setal lengths: d_1 35 (36, 34–38); d_2 35 (35, 34–35); d_3 5 (6, 5–7); d_4 6 (6, 5–7); d_5 1 (1, 1–2); l_1 40 (42, 40–46); l_2 7 (7, 7); l_3 6 (6, 6–7); l_4 6 (6, 5–6); l_5 7 (7, 6–8); h 22 (21, 19–22). Three pairs of hysterosomal cupules visible as in the preceding species; an additional pore-like opening was visible in scanning electron microscope photographs (Fig. 13) slightly antero-mediad of the humeral seta. The homology of this structure, which was not visible in normal slide preparations viewed with light microscopy, is uncertain, but it may represent a vestige of the opisthosomal gland opening in a more anterior position than is found in other members of the family. Pygidial region with central sclerotized region bearing four triangular denticles and lateral regions expanded to form anchoring structures.

Venter (Fig. 7). Ventral sejugal furrow weakly developed, not visible posterior to coxal fields II. Coxal apodemes as in preceding species except for anterior apodemes of coxal fields IV. In larger specimens, these are strongly curved posteriorly and end freely, not fused with circumgenital apodeme. In smaller individuals, these apodemes are contiguous medially and fused to the circumgenital apodeme. Coxal and genital setae as in preceding species. Subhumeral setae (sh) barbed, length 13.

Legs (Figs. 9–12, 14). Leg segmentation and chaetotaxy similar to preceding species. Empodial claws similar to preceding species, but claw III slightly smaller, lengths 12, 12, 8, 7. Form of leg setae as in preceding species, lengths as follow: tibio-tarsus I, la 7 (7, 6–10), ra 4 (5, 3–6), wa 6 (6, 5–7), p 38 (35, 33–38), q 15 (16, 14–20), d 49 (44, 38–49), e 63 (63, 55–68), f 41 (39, 37–42); solenidion ω_1 9 (8, 7–9); solenidion ω_3 6 (5, 4–6); tibial setae hT 18 (15, 12–18), gT 6 (7, 6–8); solenidion ϕ 23 (23, 19–30); genu I, seta mG 18 (12, 8–18), cG 7 (7, 6–7); solenidion σ 4 (5, 4–6); femur I, vF 26 (25, 21–18); tibio-tarsus II, la 7 (7, 7–8), ra 4 (5, 3–6), wa 6 (5, 5–6), p 36 (35, 32–39), q 16 (16, 15–16), d 30 (40, 30, 46), e 62 (64, 59–70), f 38 (37, 34–38); solenidion ω_1 10 (9, 7–11); tibial seta hT 18 (16, 14–19), gT 7 (7, 6–8); solenidion ϕ 20 (24, 18–30); genu II, mG 20 (15, 13–20), cG 9 (8, 6–9); solenidion σ vestigial; femur II, vF 27 (26, 24–28); tibio-tarsus III, r 3, w 6 (6, 5–9), s 4 (5, 4–7), p

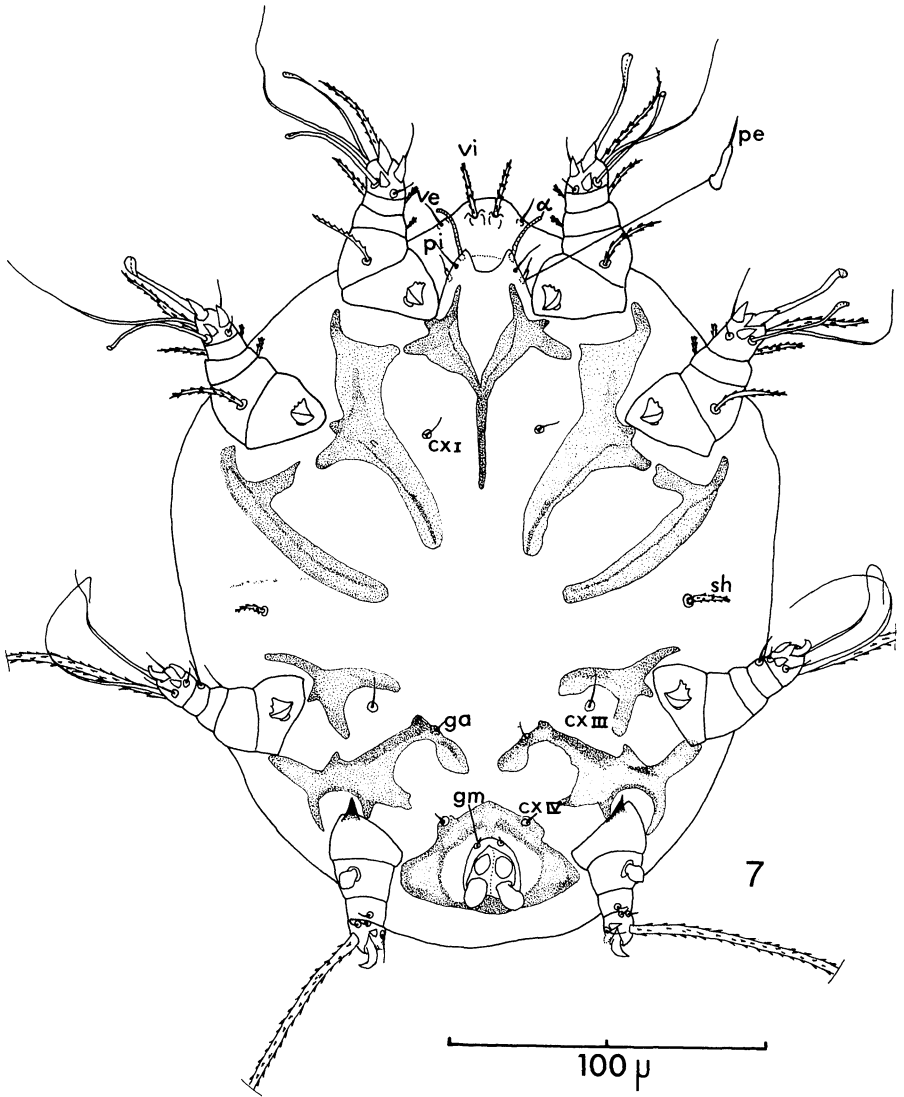


Figure 7. *Marmosopus panamensis*, deutonymph. Venter.

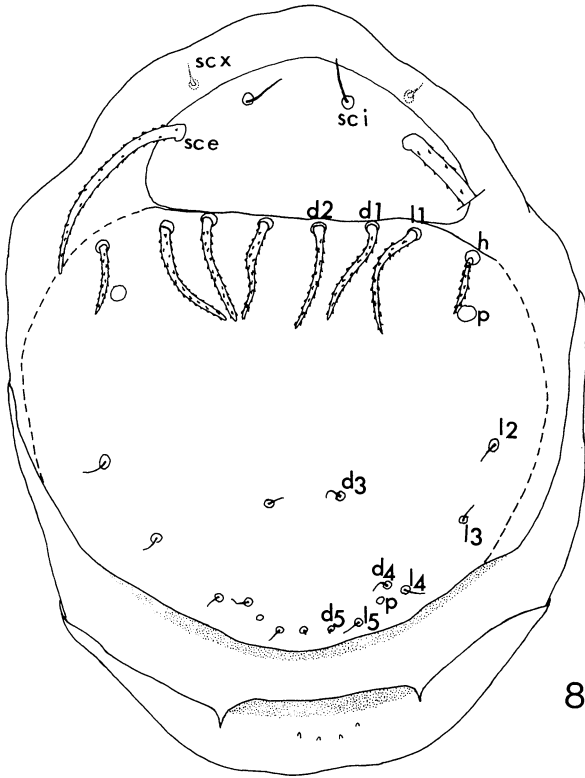
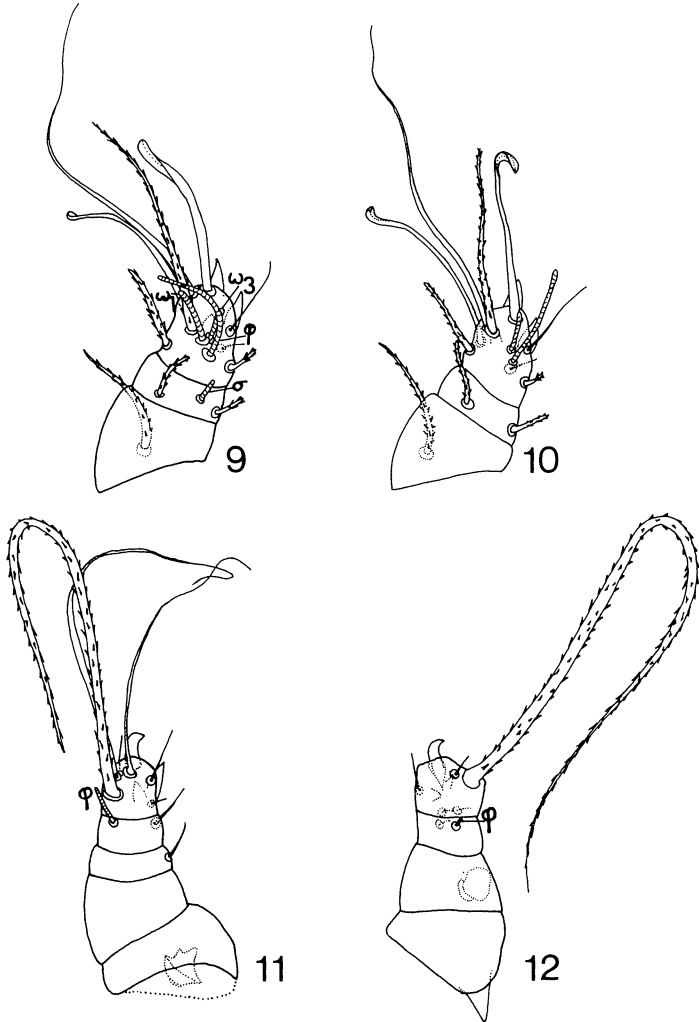


Figure 8. *Marmosopus panamensis*, deutonymph. Dorsum.

9 (8, 7-9), *q* 13 (11, 10-13), *d* 103 (101, 93-107), *e* 85 (83, 75-90), *f* 60 (59, 52-70); tibial seta *kT* 8 (9, 8-10); genu III, *nG* 9 (8, 7-9); tibio-tarsus IV chaetotaxy as in preceding species, length of seta *d* 140 (136, 122-147). Setae of trochanters I-III rhomboid, toothed along one edge as in preceding species (Fig. 15).

DIAGNOSIS.—*Marmosopus panamensis* may be distinguished from all other species of the genus by the following combination of character states: posterior dorsal setae very short and generally unbarbed; humeral setae shorter than other anterior opisthosomal setae; setae *d*₁ and *d*₂ less than 35 μm in length; legs I-II with seta *q* short and simple; trochanteral setae with teeth on one edge only; and empodial claw IV not bifid.



Figures 9–12. *Marmosopus panamensis*, deutonymph. 9, Leg I. 10, Leg II. 11, Leg III. 12, Leg IV.

MATERIAL EXAMINED.—Holotype and 176 paratypes from the hair follicles of the tail of a male *Scotinomys xerampelinus* (Bangs, 1902): PANAMA, Chiriquí Province, 3.5 km E. Escopeta, 81 50' W, 8 34' N, 1800–1856 meters elevation, col-

lected 5 July 1980 by R. H. Pine (RHP 8500). Host specimen is preserved as a skin and skull in the (U.S.) National Museum of Natural History (USNM) mammal collection #541313. Additional specimens were collected from two male *S. xerampelinus* at the same locality and date and preserved in the USNM as follows: RHP 8497 (USNM #541310) and RHP 8499 (USNM #541312). One additional male *S. xerampelinus* from the same locality, collected in cloud forest on Cerro Bollo, 28 June 1980 by R. J. Izor (RJI 116, USNM #541306), also harbored *M. panamensis*.

TYPE DEPOSITION.—Holotype and paratypes in the Field Museum of Natural History, Chicago; additional paratypes in the (U.S.) National Museum of Natural History, Washington; Canadian National Collection, Ottawa; The Acarology Laboratory, Columbus; Bernice P. Bishop Museum, Honolulu; Museum of Zoology, Ann Arbor; Rijksmuseum van Natuurlijke Historie, Leiden; British Museum (Natural History), London; Zoologisches Institut und Zoologisches Museum, Hamburg; Institut de Medecine Tropicale, Antwerp; and in the authors' collections.

SYSTEMATIC POSITION.—The species *Marmosopus mesoamericanus* and *M. panamensis* appear to be sister-species on the basis of two unique derived character states shared in common by the two species. In both species, solenidion of genu II is very reduced (completely vestigial in *M. mesoamericanus*) and the ratio of the lengths of the setae *e* and *f* on tarsus III is 1.4. In other *Marmosopus* species and in related genera, the solenidion is well developed and this setal length ratio is usually greater. These species share with *Marmosopus setzeri* Lukoschus, Gerrits, and Fain, 1982, and *M. dryas* Lukoschus, Gerrits, and Fain, 1982, the derived character state of the reduction of seta *q* on tarsi I–II from a large foliate form found in the other species in the genus and the nearest outgroups to a short, simple form. This group of four species shares with *Marmosopus inca* Fain and Lukoschus, 1976, and *M. crabilli* Lukoschus, Gerrits, and Fain, 1982, the possession of a large, sclerotized spur on trochanter IV,

a structure not found in the remaining species of *Marmosopus* (*M. peruvianus* and *M. mendezi*) or in the outgroups. *Marmosopus inca* may be distinguished from this group by the bifid form of the empodial claw of pretarsus IV.

DISCUSSION.—The genus *Marmosopus* was originally proposed in the subfamily Echimyopinae of the family Glycyphagidae (Fain and Lukoschus, 1977). In a phylogenetic analysis of higher order relationships in the Astigmata, OConnor (1981, 1982a, 1982b) regarded this group (given family rank and emended to Echimyopodidae) as the sister-group of a group comprising the families Aeroglyphidae, Rosensteiniidae, and a restricted Glycyphagidae. On the basis of phylogenetic relationships and known host distributions, OConnor (1982a) hypothesized that the Echimyopodidae were originally associated with the mammalian infraclass Metatheria (marsupials), while its sister-group was originally associated with the Eutheria or placental mammals. This dichotomy in the evolution of the mites parallels the dichotomy in mammalian evolution between the Metatheria and Eutheria (the latter following Marshall, 1979) and supports a hypothesis of coevolution (cospeciation) of the two groups (Brooks, 1979).

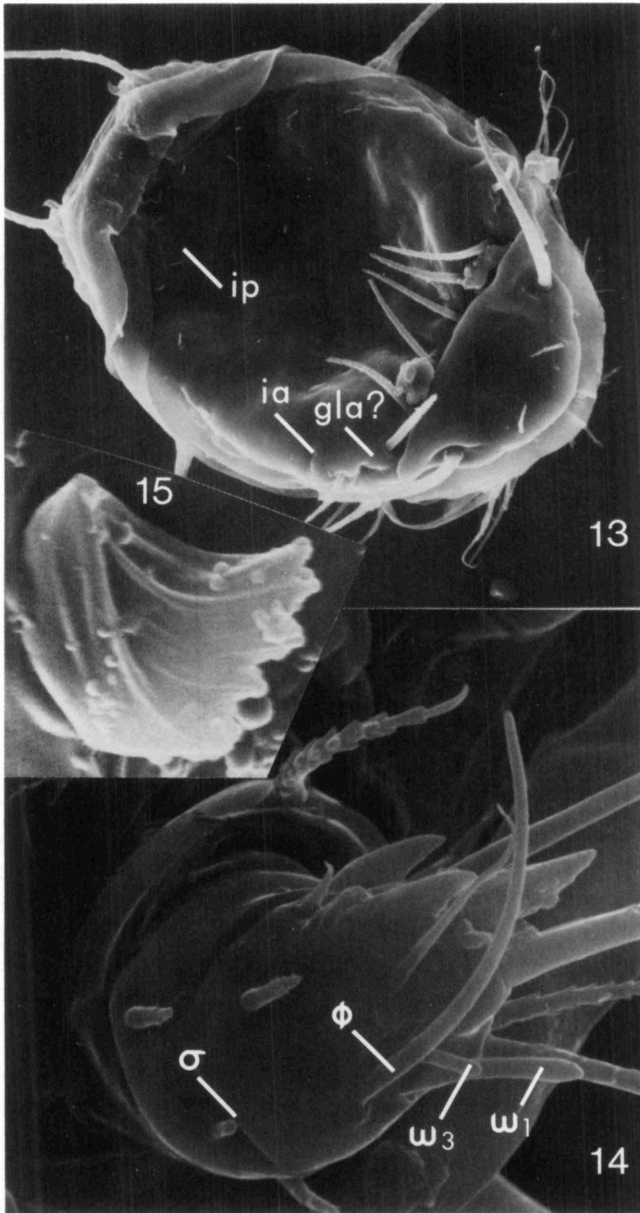
Within the Echimyopodidae, however, a strict cospeciation between mammalian hosts and associated mites is not always evident. In both subfamilies, the Australian Marsupiopodinae and the New World Echimyopodinae, secondary colonization of rodent hosts has occurred. In the New World, there is an apparent phylogenetic dichotomy between the genus *Marmosopus*, until now known only from marsupials, and its sister-group, comprising the sister-genera *Echimyopus* and *Oryzomyopus*, known only from rodents. The discovery of *Marmosopus* species associated with rodents in this study, and the discovery of *Echimyopus* species associated with marsupials (OConnor, unpublished), suggests a complicated pattern of host colonization and coaccommodation superimposed on a basic coevolutionary (cospeciating) system.

Some hypotheses concerning the evolution of this group of mites and its hosts may be tested using available data concerning host and mite relationships and the ecological compatibility of

the various host groups. It should be noted at the outset that the Echimyopodidae are parasitic only as deutonymphs, with the other stages presumed to be nest inhabitants. Although both deutonymphs and adults are known for only two species in the family, *Marsupiopopus zyzomys* (Lukoschus et al., 1979) and *Echimyopus orphanus* (Fain and Philips, 1981), the combination of parasitic deutonymph and free living nidicolous stages is frequently observed in the related families (OConnor, 1982a). Thus, the potential for colonizing new host groups is not restricted to mites involved in direct host to host transfers, but is probably greater for those individuals still in the nest of the original host. Reuse of nesting materials removed from burrows of other species, use of old nests by other species, or even direct nest usurpation by unrelated host species provide the best mode of contact between echimyopodid mites and potentially new host groups.

The first hypothesis concerning the evolutionary relationships of *Marmosopus mesoamericanus* and *M. panamensis* to their rodent hosts is that both are accidental parasites whose normal hosts are marsupials. This hypothesis is suggested by the original hypothesis mentioned above, that the Echimyopodidae have cospeciated with the Marsupialia. However, two observations provide evidence contrary to this hypothesis. First, *M. mesoamericanus* has been collected from its hosts, *S. teguina*, on numerous occasions and in fairly widely spaced localities, indicating that it occurs in viable populations in association with this rodent species. Similarly, *M. panamensis*, while presently known from a single locality, was collected from a number of host individuals. These data indicate that these mite species are true associates of their rodent hosts but do not indicate whether they are also associated with marsupial hosts.

A second hypothesis suggests that these *Marmosopus* species, while presently associated with *Scotinomys* species, may also still be associated with their ancestral marsupial hosts. This hypothesis may be tested by examination of marsupial hosts which are sympatric with *Scotinomys* species in Central America. Range maps published by Hall (1981) indicate 10 species of marsupials whose geographic ranges overlap the ranges of *Scotinomys* species (the range of *S. xerampelinus* lies



Figures 13–15. *Marmosopus panamensis*, deutonymph. 13, Scanning electron microscope photograph of dorsum; *ia* and *ip* cupules; *gla* ?opisthosomal gland opening remnant. 14, Leg I with solenidia as indicated. 15, Seta of trochanter I.

largely within the range of *S. teguina*). Of these species, six are large species (nomenclature following Kirsch and Calaby [1977]: *Didelphis marsupialis*, *D. virginiana*, *Philander opossum*, *Chironectes minimus*, *Metachirus nudicaudatus*, and *Caluromys derbianus*) that are not known to be hosts of *Marmosopus*. The other four species (*Marmosa alstoni*, *M. mexicana*, *M. robinsoni*, and *M. invicta*) are small species and are more likely potential hosts, particularly as species of *Marmosopus* are known associates of other *Marmosa* species. More crucial than just geographic range is the altitudinal range of these species. The species of *Scotinomys* are restricted to subtropical evergreen forest ranging from 1000–2940 meters for *S. teguina* and 2150–3300 meters for *S. xerampelinus*. The species are contiguously allopatric in some areas, but in any given locality their ranges do not overlap (Hooper and Carleton, 1976). Handley (1966) noted the altitudinal ranges of Panamanian mammals, and of the species mentioned above whose geographic ranges overlap that of *Scotinomys*, only *Didelphis marsupialis*, *Chironectes minimus*, *Marmosa invicta*, and *M. robinsoni* occurred at the same elevations as *Scotinomys* species. Hall (1981) also records *Marmosa alstoni*, which does not occur in Panama, at over 1000 meters. Finally, in considering potential ancestral hosts for the *Marmosopus* associated with *Scotinomys*, microhabitat preferences must be considered. *Scotinomys* species are almost completely terrestrial, and although their nesting behavior has not been observed in the wild, it may be presumed that they nest in subterranean burrows. Most of the sympatric marsupials, however, are largely arboreal (except the aquatic *Chironectes minimus*) and most described nests of small neotropical marsupials have been found in arboreal situations. A possible exception to this pattern is *Marmosa invicta*, which, according to Pine (1981), has been collected from a variety of terrestrial situations.

To test the hypothesis that *Marmosopus mesoamericanus* and *M. panamensis* are also associated with marsupials sympatric with *Scotinomys* species, we have examined fluid preserved representatives of all the above potentially sympatric marsupials housed in the UMMZ and other institutions, except *Marmosa alstoni* and *M. invicta* for which no specimens were

available. Of the examined marsupials, only *Marmosa robinsoni* (Lukoschus et al., 1982) and *M. mexicana* (OConnor, unpublished) harbored species of *Marmosopus*, and neither of these species appears more closely related to *M. mesoamericanus* and *M. panamensis* than *Marmosopus dryas* (Lukoschus et al., 1982). Until such time as specimens of *Marmosa invicta* and *M. alstoni* can be examined, the possibility remains that either of the *Scotinomys*-associated *Marmosopus* species may be ancestrally associated with one of these marsupial species.

A third hypothesis for the association between these *Marmosopus* species and their rodent hosts is suggested by the phylogenetic relationships among the known species of *Marmosopus*. The species *M. mesoamericanus* and *M. panamensis* are each other's closest relatives on the basis of the shared derived character states mentioned above. However, it is not now possible to determine if these are actually sister-species or whether one could be the ancestor of the other. A similar situation exists concerning the phylogenetic relationships of the species of *Scotinomys* (Hooper, 1972), with the two species *S. teguina* and *S. xerampelinus* each other's closest relatives, but the possibility existing that one is ancestral to the other. A hypothesis concerning the association of the *Marmosopus* species with the *Scotinomys* species, which is consistent with these relationships, is that the common ancestor of the two *Marmosopus* species became associated with the common ancestor of the *Scotinomys* species at some time in the past and that cospeciation has occurred (Brooks, 1979).

Another phylogenetic relationship supporting this hypothesis is the sister-group relationship between the species *M. mesoamericanus* and *M. panamensis* on one hand and *Marmosopus dryas* on the other. *Marmosa dryas*, the host of *Marmosopus dryas*, is restricted to cloud forest habitat at medium to high elevations in Venezuela (G. K. Creighton, pers. comm.), a habitat preference similar to that of *Scotinomys* species. This similarity of habitat could have, at some previous time, provided the opportunity for colonization of the rodent host by the ancestor of the *Scotinomys*-associated *Marmosopus*. That this colonization could have occurred in Central America during the Pleistocene is supported by data concerning the

relationships of the genus *Scotinomys* (Hooper, 1972; Carleton, 1980) and by palaeoclimatic studies.

According to the most recent studies of phylogenetic relationships among New World cricetid rodents (Carleton, 1980), the genus *Scotinomys* is a member of the North American cricetine group (Neotomine-Peromyscine) and not closely related to the South American cricetines. The Neotomine-Peromyscine cricetid rodents are not known to have dispersed far into South America at any time in the past, indicating that the colonization of *Scotinomys* or its ancestors by species of *Marmosopus* must have occurred in the present range of *Scotinomys* and not in South America.

The possible sympatry of *Scotinomys* and of the ancestors of the presently sympatric *Marmosa* species and of the ancestors of the *Marmosa* species inhabiting northern South America (e.g., *M. dryas*) in a more extensive band of montane forest may be postulated based on palaeoclimatic information reviewed for South America by Simpson and Haffer (1978). This information indicates that during glacial periods of the Pleistocene, the climate was cooler and drier, with lowland tropical forest restricted in area and the vegetation types with which *Scotinomys* species are now associated more extensive. As the Panamanian land bridge was fully functional as a corridor for mammalian dispersal at this time (Marshall et al., 1979), the actual sympatry of *Scotinomys* (or its ancestors) with present montane forest inhabiting *Marmosa* species or their ancestors in present-day Central America is probable. During interglacial periods such as the present, lowland forest is much more extensive, with the montane vegetation restricted to disjunct areas at higher elevations. The fragmentation of such formerly extensive habitat zones on mountain ranges provides a hypothesis for the present disjunct distributions of such altitudinally restricted species as *Scotinomys xerampelinus* (Hooper and Carleton, 1976).

An evolutionary scenario may be proposed based on the above hypotheses in which the ancestor of the present *Scotinomys* species was sympatric with a species of *Marmosa* inhabiting montane forest in Central America following the establishment of the Panamanian land bridge. The marsupial

may have been a relative of the present *Marmosa invicta* (subgenus *Marmosa*) or more closely related to *Marmosa dryas* (subgenus *Thylamys*). This marsupial harbored the species of *Marmosopus* ancestral to *M. panamensis* and *M. mesoamericanus* (and possibly *Marmosopus dryas*). The speciation event resulting in the ancestor of *M. panamensis* and *M. mesoamericanus* occurred either following the colonization of the rodent host or perhaps before this colonization. Further speciation resulting in the two *Scotinomys* associated species occurred as the two host populations differentiated and became isolated.

This scenario is testable insofar as the hypotheses on which it is based are testable. Those hypotheses may be tested by further examination of marsupial hosts in Central and northern South America for the presence of *Marmosopus* species. If either *Marmosopus mesoamericanus* or *M. panamensis* are found associated with present marsupials, the time of the colonization of the rodent hosts may be considered to be more recent than if either are not found on presently sympatric marsupials. Similarly, if the presently sympatric marsupials do not harbor *Marmosopus* species more closely related to the rodent associates than does *Marmosa dryas*, the time of colonization must be considered to be much earlier.

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