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Revision of the subgenus *Marquesania* (Acari : Atopomelidae : *Listrophoroides*)

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Abstract. The subgenus *Marquesania* Womersley (Acari: Atopomelidae: *Listrophoroides*) is revised. The species of this subgenus are permanent parasites living in the fur of rats (Rodentia: Murinae) in the Oriental region, Australia and New Guinea. Most of the type material has been examined. Two new species, *Listrophoroides melomys*, sp. nov. from *Melomys moncktoni* (Thomas) and *L. mordax*, sp. nov. from *Rattus mordax* (Thomas) are described from New Guinea. A new diagnosis of the subgenus *Marquesania*, detailed descriptions, and a key for all species is provided. The phylogenetic reconstruction of the subgenus *Marquesania* was effected by the method of parsimonius cladistics. The monophyly of the subgenus is strongly supported by this analysis, and most species from the Oriental region fall at the base of the cladogram. The distribution of *Marquesania* species on their hosts is discussed. It is suggested that these mites originated in the Oriental region and then migrated to Australia and New Guinea. The distribution of *Marquesania* species in the Australian and New Guinean regions is noticeably complicated, reflecting the complex settling history of their hosts.

Introduction

Mites of the family Atopomelidae (Acari: Astigmata) are permanent parasites of small mammals. They have developed elaborate organs for the attachment to the hairs of their hosts. Mites attach to hair by means of their anterior legs (e.g. Figs 3, 4). During the process of clasping, the anterior legs of the mite embrace the hair of the host and press it against striated coxal membranes. The atopomelids are more commensals than true parasites, because they feed on the secretions of hair glands and, probably, do not damage their hosts. Most of the atopomelid subgenera or genera are restricted to certain families or subfamilies of their hosts (Fain 1994); therefore, these mites are a good model for an analysis of the phenomenon of parallel evolution between parasites and their hosts. However, published studies on atopomelid mites are strictly limited to descriptive systematics and faunistic investigations. Phylogenetic studies of these mites using cladistic approach have never been performed.

The Atopomelidae include 46 genera and about 360 species. The genus *Listrophoroides* Hirst is the largest genus of the family, including 16 subgenera and more than 150 species (Fain 1981). These species are associated with rodents, shrews, tenrecs and primates and are widely distributed through the world (North and South America, Africa, Madagascar, the Oriental region, New Guinea and Australia). Extensive reviews of the genera and subgenera of *Listrophoroides* have been published by Fain (1972*a*,*b*, 1976, 1981).

The subgenus *Marquesania* Womersley is revised here. It included until now only six species and two subspecies, mostly associated with rats from the Oriental region, Australia and New Guinea (Fain 1981). As mentioned above, the atopomelid mites are highly specialised permanent parasites and they show co-evolution relationships with hosts (Fain 1994). Therefore, knowledge of the phylogeny and host ranges of the *Marquesania* species could provide indirect data on the phylogeny of their hosts (rats) and help to reconstruct the process of their dispersal from the Oriental region to Australia and New Guinea.

After the present revision, this subgenus includes 13 species. In this paper, a new definition of *Marquesania* is proposed, all the known species are redescribed, and keys for males and females are provided. Moreover, phylogenetic analysis of this subgenus is performed using a cladistic approach. The distributions of the species and their host-parasite relationships are discussed and summarised.

Materials and methods

This study is based on examination of more than 500 specimens of *Marquesania* spp., including almost all the type specimens. Most of this material belongs to the Institut royal des Sciences naturelles de

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Belgique, Bruxelles. Material depositories are cited using the following codes:

Abbreviations

BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii
BMNH	The Natural History Museum, London, UK
FMNH	Field Museum of Natural History, Chicago, USA
IRSNB	The Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium
MNHN	Museum d'Histoire Naturelle, Paris, France
SAM	South Australian Museum, Adelaide, Australia
SMF	Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt, Germany
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

In the descriptions, all measurements are given in micrometers (µm) and were taken as follows: length of the body = total length from posterior border of idiosoma to the anterior extremity of the gnathosoma; width of the body = maximum width taken at whatever level it occurs; length of the dorsal shields = maximum length, measured in the median line of the shields; length/width of the incisions of the hysteronotal shield = maximum length/width taken at whatever level it occurs; length of the posterior legs = from the most basal point of the trochanter to the apex of the tarsus (excluding the ambulacrum); length of the tibio-tarsi = from most basal point of this segment to the apex of the tarsus (excluding the ambulacrum).

All specimens were measured, but in the species descriptions we used only the measurements of the type series or of the specially indicated series. When the measurements of some specimens considerably differed from those for the respective type series, these data were also mentioned.

We have used here the standard nomenclature of the idiosomal chaetotaxy for Listrophoroidea (Fain 1972*b*). Host systematics is based on Wilson and Reader (1993).

A cladistic analysis based on numerical parsimony was used for the study of the phylogenetic relationships between the species of the subgenus *Marquesania*. This analysis included all the valid species of the subgenus.

We estimated ancestral states using an outgroup analysis (Maddison *et al.* 1984). The species of the subgenus *Listrophoroides*, *L. rajah* Fain inhabiting rats *Maxomys rajah* (Thomas) and *M. surifer* (Miller) from Thailand was used as a close outgroup. This outgroup was not specified in our analysis. ~~At the same time,~~ the species of the African subgenus *Olistrophoroides* Fain, 1972, *L. lemniscomys* Radford inhabiting the mice of the genus *Lemniscomys* Trouessart was chosen as a distant outgroup and it was specified in the analysis. Multistate characters were unordered.

In total, the 15 taxa and 21 characters were included in the analysis. The data matrix was done using NEXUS Data Editor 0.5.0 (Page 2001). The reconstruction of phylogenetic relationships of mites under study was performed with PAUP 4.0 beta version (Swofford 1998) for Windows. The maximum parsimony analysis was used for estimation of phylogeny.

The exact search algorithm (branch and bound) was used owing to the small number of taxa involved in this analysis. Successive weighting was performed according to the rescaled consistency index (*RC*) (Farris 1969) for finding maximally consistent trees (Platnick *et al.* 1996). After the multiple equally parsimonious trees were found, strict consensus was applied because this type of consensus seems preferable for a relatively small number of obtained trees. Support for the branches of trees was estimated by the standard bootstrap procedure with 100 replications using a heuristic searching strategy. However, we take into consideration that working with relatively scanty morphological characters, the bootstrapping results are of only approximate confidence (Kitching *et al.* 1998). The permutation tail probability (PTP) test (Faith and Cranston 1991) was used for the evaluation of our cladogram. For *a posteriori* optimisation of the character state distribution we used the DELTRAN (delayed transformation) option, which favours parallelisms over reversals when the choice is equally parsimonious. Drawing and editing of the trees was done with TreeView 1.5.2 (Page 1998).

The list of characters and the data matrix are given in Tables 1 and 2, respectively.

Table 1. List of apomorphies

(1)	Retrorse process of femur I present
(2)	Process of genu I present
(3)	Coxal membranes II reaching the lateral borders of the body
(4)	Coxal membranes II wide
(5)	Furrow of coxae III present
(6)	Ornamentation of postscapular shield lacking
(7)	In male, ornamentation of hysteronotal shield present
(8)	In male, lateral incisions of hysteronotal shield present
(9)	In male, lateral incisions of hysteronotal shield well developed
(10)	In male, scales behind setae *l3* present
(11)	In female, distance *d3*–*d3* longer than distance between *d3* and posterior margin of hysteronotal shield (1), shorter (2)
(12)	In female, setae *ai* longer than other hysterosomal setae, excluding *ae*
(13)	In male, genital shield with very deep median incision
(14)	In male, genital shield in shape as an inverted U
(15)	In male, anal shield present
(16)	Minimal observed body length more than 450 µm in female and 410 µm in male
(17)	In female, opisthogaster at least slightly sclerotised, without lateral bands (1), well sclerotised, with lateral bands (2)
(18)	In male, opisthosomal lobes divided
Characters for outgroup comparison	
(19)	Scutal organs present
(20)	Epimeres II fused
(21)	In female, copulatory papilla present

Table 2. Data matrix

Species	Character states			
			11	1111111122
	12345	67	8901	2345678901
L. cucullatus	11110	10/1	1110	0111011000
L. papuanus	11111	01	1100	0101111000
L. obliquelineatus	10101	01	1000	0101111000
L. mordax	11111	01	1110	0101111000
L. crenatus	11111	01	1010	0101011000
L. interpolatus	11111	01	1111	0111011000
L. melomys	11111	01	1000	0101011000
L. queenslandicus	11110/1	01	1110/1	0101111000
L. australiae	11110	10	1111	0101111000
L. postscuamatus	11111	01	1110	1101011000
L. lativentris	11110	00	1101	0101011000
L. sculpturatus	11111	00	1001	0101011000
L. dominator	11100	10	1001	1101011000
L. rajah	100-0	00	0-02	00-0021000
L. lemniscomys	000-0	00	0-00	00-0000111

Genus *Listrophoroides* Hirst

Subgenus *Marquesania* Womersley

Marquesania Womersley, 1943: 13.
Listrophoroides (*Marquesania*), Fain, 1977: 292.
Type species: *Listrophorus cucullatus* Trouessart.

Diagnosis

Body dorso-ventrally inflated. Legs III and IV inserted laterally. Coxae II widely separated from each other, with large clasping membranes, reaching the lateral borders of the body. Genu I with a spoon-like dorso-apical process, except in *L. obliquelineatus* Fain, comb. nov. Femur I with a small retrorse process. Postscapular shield undivided. Scutal organs lacking. Hysteronotal shield well developed.

Female. Epigynium normally developed. Copulatory papilla lacking. Opisthogaster without lateral sclerotised bands. Opisthogastric shield variable in shape, without distinct margins.

Male. Hysteronotal shield with a pair of incisions between levels of setae *l3* and *d3*. Penis shorter than postgenital shield. Postgenital shield well developed, in an inverted V or U. Anus with well-developed postanal V-shaped sclerite. Legs III and IV subequal or legs IV distinctly thickened.

Remarks

Based on this revision, the subgenus *Marquesania* includes at present 13 species associated with rats of the genus *Rattus* Fisher and allied genera in the Oriental region, New Guinea and Australia. Initially, the genus *Marquesania* was described by Womersley (1943) for *Listrophorus expansus* Ferris, but Domrow (1958) synonymised this genus with *Listrophoroides* Hirst. Fain (1972*a*) synonymised *L. expansus* and *L. tragardhi* Radford with *Listrophoroides cucullatus* (Trouessart). He also redescribed and redepicted this species and designated a lectotype male for it. In 1977, Fain restored the taxon *Marquesania*, but as a subgenus of *Listrophoroides*.

Among the 16 subgenera of *Listrophoroides*, *Marquesania* is closest to the nominative subgenus. The subgenus *Listrophoroides* includes at present 47 species, all associated with tropical rodents of the families Muridae and Cricetidae (Fain 1981, Bochkov and Mironov 2001). The subgenus *Marquesania* clearly differs from it mainly by the much larger size of the clasping membranes covering the coxae II and reaching the lateral margin of the body, while in *Listrophoroides* s. str. they are always separated from these margins by a finely punctate area. In addition, in most species of *Marquesania* the genu I in both sexes bears a dorso-apical process (absent in *Listrophoroides* s. str. and in *L.* (*M.*) *obliquelineatus*). The male differs by the shape of the postgenital shield and by the presence of a postanal sclerite.

Listrophoroides (Marquesania) cucullatus (Trouessart)

(Figs 1–6)

Listrophorus cucullatus Trouessart, 1893: 699. Complete bibliography in Domrow (1992).

Material examined

Lectotype. 1♂ from *Rattus norvegicus* (Berkenhout): Asia: unknown locality, coll. E. L. Trouessart (MNHN), designated by Fain (1972*a*).

Paralectotype. 1♀, same data as lectotype (MNHN).

Non-type specimens (all in IRSNB). **Seychelles Islands:** 3♂, 1♀ from *Rattus rattus* (L.) (BMNH 78.3055–3058), Praslin. **South America: Surinam:** 1♂, 4♀ from *R. rattus*, Paramaribo, 5.xii.1969, coll. F. Lukoschus; 7♂, 2♀ from *Rattus norvegicus* (Berkenhout), other data as previous, 15.i.1970; 1♂, 3♀ from *R. rattus*, Lelydorp, 11.xii.1960, F. Lukoschus. **New Guinea:** 2♂ from *R. rattus* (BPBM 67951), Sentani Irian; 7♂, 13♀ from *Rattus exulans* (Peale) (BPBM 67948), same locality as previous, 20.iii.1973; 6♂, 4♀ from *Melomys* sp., same locality as previous, 18.iii.1973; 2♀ from *R. exulans* (BPBM 716), Vogelkop, 4.i.1962, coll. S. Quate; 1♂, 1♀ from *R. exulans* (BMNH 97.8.7.84), Kapa Kapa; 1♂ from *Rattus* sp. (BPBM 21250), Coviak, 19.ii.1963, coll. H. Clissold; 1♂ from *Stenomys niobe* (Thomas) (BPBM 61318), Ertsberg, 1.v.1973. **Solomon Islands:** 1♀ from *Rattus* sp. (BPBM 61418), Bougainville Island, Tinputz; 10.iv.1968; 7♂, 6♀ from *Rattus* sp., Santa Isabel Island, Boala, 21.viii.1964, coll. P. Shanahan. **Hong Kong:** 2♂, 1♀ from *Rattus tanezumi* Temminck (BPBM 312), Tai Tam Reservation, 31.x.1964. **Malaysia: Selangor:** 2♂, 2♀ from *Rattus annandalei* (Bonhote), Subang Forest, 7.v.1979, coll. M. Nadchatram; 2♂, 3♀ from *R. exulans*, Ulu Jenderam, 31.v.1979, coll. M. Nadchatram; 2♂, 1♀ from *Rattus argentiventer* (Robinson *et* Kloss), same locality as previous, 30.v.1979, coll. M. Nadchatram; 3♂, 5♀ from *Rattus tiomanicus* (Miller), Bukit Langan, 4.v.1979, coll. M. Nadchatram. **The Philippines:** 2♂, 3♀, from *Rattus mindorensis* (Thomas), Leyte Island, vii.1964, coll. F. Lukoschus; 1♂ from *R. exulans*, Mindanao, Mt Katanglad, coll. F. Lukoschus; 1♂ from *Apomys insignis* Mearns, same locality as previous, coll. F. Lukoschus. **Indonesia:** 1♂, 4♀ from *Rattus hoffmanni* (Matschie) (USNM 502095), F. Lukoschus. **Celebes:** 1♂, 15♀ from *Rattus xanthurus* (Gray) (BMNH 87.7.15.2), Menado, Saputan, Mt Keledondi; 1♂, 5♀ from *Bunomys coelestes* (Thomas) (BMNH 97.1.3.26–27), Mt Bonthain. **Labuan:** 5♂, 8♀ from *R. tanezumi* (BMNH 94.7.2.77). **Archipelago Chagos:** 3♂, 9♀ from *R. rattus* (BMNH 70.353), Diego Garcia Atoll.

Diagnosis

Female. Postscapular shield with six transverse interrupted lines, hysteronotal shield with 9–10 straight transverse lines, three posterior lines short, distances *d3*–*d3* and *d3*–posterior margin of hysteronotal shield subequal.

Male. Postgenital shield in an inverted V, its anterior part forming a median sclerotised band immediately behind genital organ (Fig. 6).

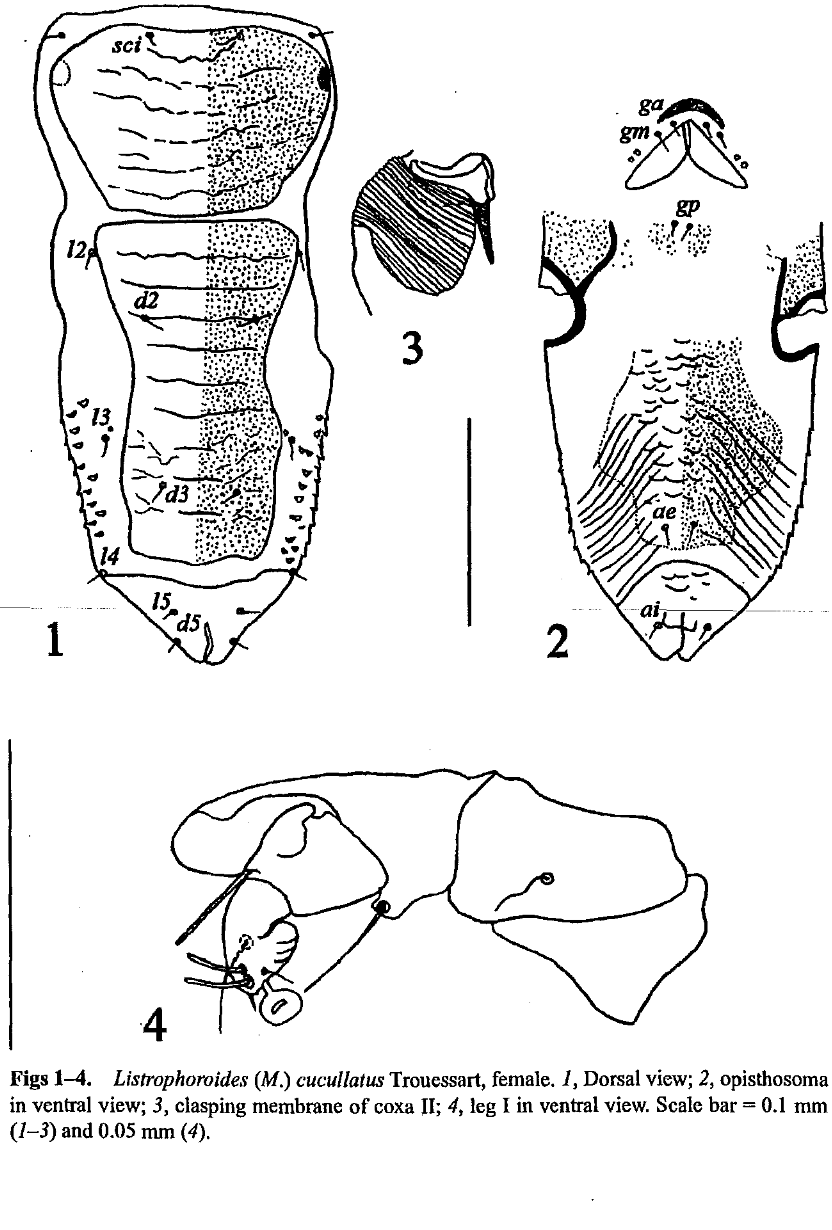
Description (*based on specimens from* R. norvegicus *and* R. rattus *in Surinam*)

Female (Figs 1–4)

Body 415–430 long and 145–150 wide. *Dorsum.* Post-scapular shield about 85 long, completely covered with 5–6 transverse lines. Hysteronotal shield 180 long, completely covered with 9–10 straight transverse lines, three posterior lines short. Width of this shield at level of setae *d2* 80–90 and at level of setae *d3* 75–90. Distances *d3–d3* and *d3*–posterior margin of hysteronotal shield subequal, 35–40. *Venter.* Striated membranes of coxae II reaching the lateral margins of the body. Coxae III with a poorly distinct transverse line. Opisthosoma 165 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma with widely rounded scales spreading from level of setae *gp* to level of setae *ae*. Legs III and IV about 115 long. Solenidia *phi* of legs III and IV 15 and 5 long, respectively.

Male (Figs 5–6)

Body 360–375 long and 140–160 wide (375 × 160 in lectotype). ***Dorsum.*** Postscapular shield about 70 long, similar to those of female, bearing six transverse lines. Hysteronotal shield about 155 long, covered with transverse lines extending from the anterior margin to level of setae *d3*. Incisions of hysteronotal shield 20–25 long and 25–30 wide. Their minimal distance between each other 35–40. Setae *l3* variable in position, either on or off hysteronotal shield, soft cuticle behind these setae usually with 1–3 scales or without ones. Setae *d3* situated on hysteronotal shield, distance *d3–d3* 1.4–1.5× shorter than distance between incisions of hysteronotal shield, 25–30. Setae *l5* about 50 long. *Venter.* Striated membranes of coxae II as in female. Coxae III with poorly distinct transverse line or without one. Postgenital shield in an inverted V, its anterior part forming a median sclerotised band immediately behind genital organ and 25–35 long; its lateral projections 60–75 long (90 long in the lectotype, Fig. 5*A*) distance between these projections at level of setae *gp* 14–15. Distance between postgenital shield and the postanal sclerite about 3×



Figs 1–4. *Listrophoroides* (*M.*) *cucullatus* Trouessart, female. *1*, Dorsal view; *2*, opisthosoma in ventral view; *3*, clasping membrane of coxa II; *4*, leg I in ventral view. Scale bar = 0.1 mm (*1–3*) and 0.05 mm (*4*).

shorter than the projections of postgenital shield, 20–25. Legs III and IV 115 and 130 long, respectively. Tibio-tarsi III and IV subequal 40 long. Solenidia *phi* of legs III and IV 15 and 45 long, respectively.

Remarks

This species was described from *R. norvegicus* in an undetermined region of Asia (Trouessart 1893). Fain (1972*a*) redescribed and figured this species from the type series, designated its lectotype and discussed synonymy.

Listrophoroides cucullatus is widely distributed among numerous endemic rats of the Oriental region and New Guinea. It is also common on the cosmopolitan *R. norvegicus* and *R. rattus*, but apparently only in warm countries (e.g. Surinam). Its findings on *Lemniscomys striatus* (L.) from Uganda, *Tatera indica* (Hardwicke) from Ceylon (Radford 1940) and *Echymipera* sp. in New Guinea (Fain 1972*b*) were, probably, accidental.

There are some morphological differences between the New Guinean–Solomon Islands populations and the other populations of *L. cucullatus*. In the New Guinean-Solomon Islands specimens the body is 335–350 long in males and 380–420 long in females. Moreover, in the males the scales behind setae *l3* are usually lacking.

Listrophoroides (Marquesania) papuanus Fain

(Figs 7–10)

Listrophoroides papuanus Fain, 1970: 284; 1972*b*: 175–178, figs 206–208.

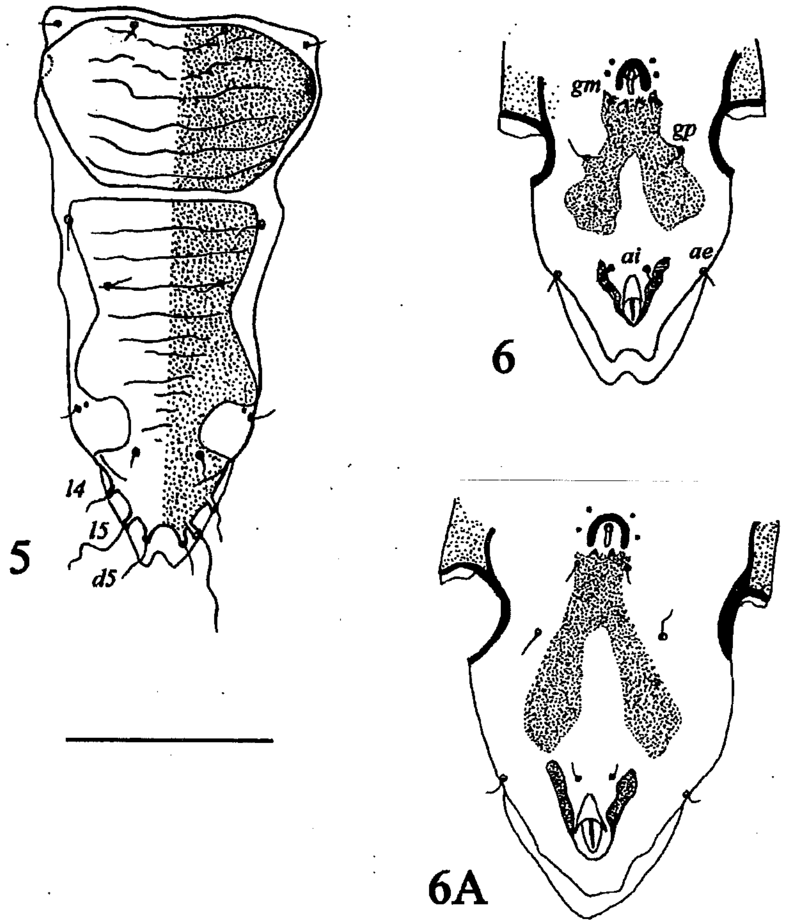
Listrophoroides (*Marquesania*) *papuanus*. – Fain, 1977: 293.

Material examined

Holotype. ♂ from *Conilurus penicillatus* (Gould) (BMNH 26.3.11.245–248): N. Australia: Groote Eylandt (BMNH).

Paratypes. 2♂, 3♀, same data as holotype (IRSNB).

Non-type specimens (all in IRSNB). **Australia:** 11♂, 12♀ from *C. penicillatus* (FMNH 3111), Port Warrender (14°30′S, 125°50′E), 29.x.1976; 3♂, 2♀ from *Pseudomys nanus* (Gould) (FMNH 3050), Mitchell Plateau (14°50′S, 125°49′E), 21.x.1976.



Figs 5–6. *Listrophoroides* (*M.*) *cucullatus* Trouessart, male. *5*, Dorsal view; *6*, opisthosoma in ventral view; *6A*, opisthosoma of lectotype in ventral view. Scale bar = 0.1 mm.

Diagnosis

Large mites.

Female. Ornamentation of postscapular shield strongly marked, transverse lines in anterior part of hysteronotal shield curved laterally, distances *d3–d3* and *d3*–posterior margin of hysteronotal shield subequal.

Male. Postscapular shield completely covered with short curved lines, arranged into six transverse rows, hysteronotal shield with transverse lines extending from the anterior margin to level of setae *d3*, incisions of hysteronotal shield well developed, scales behind setae *l3* lacking.

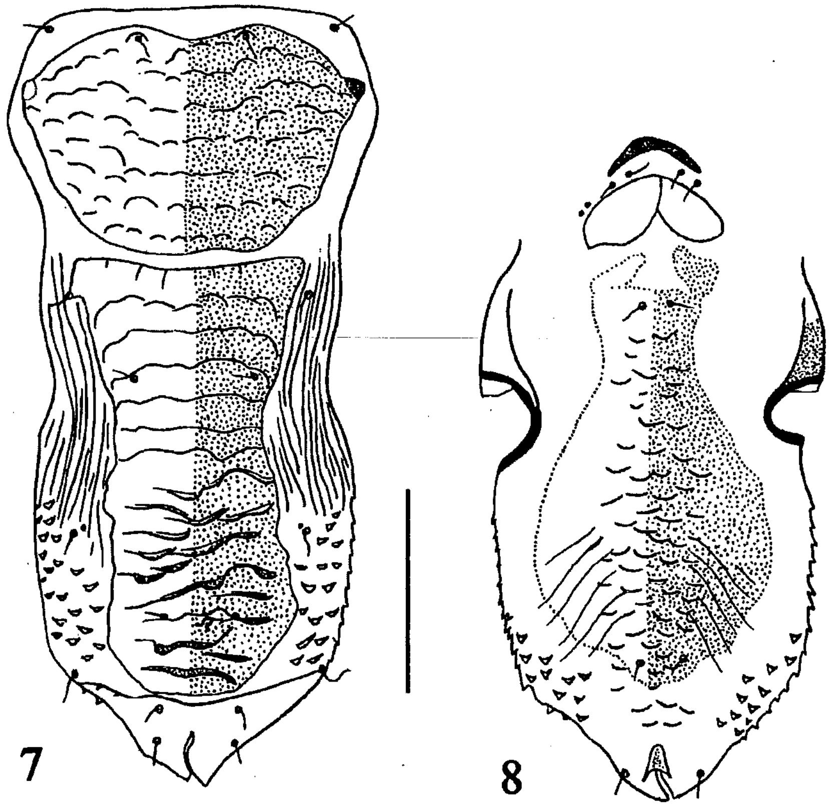
Description (*based on specimens from type host*)

Female (Figs 7, 8)

Body 465–500 long and 165–185 wide. *Dorsum*. Postscapular shield about 105 long, completely covered with short curved lines arranged into six transverse rows. Hysteronotal shield 200 long, completely covered with 12–15 strong transverse lines, some from them folder-like; 2–3 of these lines situated behind level of setae *d3*. The 3–4 first anterior lines curved in their lateral parts. Width of this shield at level of setae *d2* 75–100 and at level of setae *d3* 75–85. Distances *d3–d3* and *d3*–posterior margin of hysteronotal shield subequal, 35–40. *Venter*. Striated membranes of coxae II wide. Coxae III with a poorly developed transverse line. Opisthosoma 105 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma densely covered with well-developed widely rounded scales spreading from level of setae *gp* to level of setae *ae*. Legs III and IV about 140 long. Solenidia *phi* of legs III and IV 14 and 8 long, respectively.

Male (holotype, Figs 9, 10)

Body 425 long (450–480) and 150 wide (175–180). *Dorsum*. Postscapular shield 95 long, bearing 6–7 transverse lines, similar to those in female. Hysteronotal shield about 205 long, covered with transverse lines extending from the anterior margin to level of setae *d3*. These lines less developed in posterior half of this shield. Incisions of hysteronotal shield 30–45 long and 30–40 wide, and their minimal distance between each other 40–60. Setae *l3* variable in position, either on or off hysteronotal shield, soft cuticle behind these setae without scales. Setae *d3* situated on hysteronotal shield, distance *d3–d3* 35–45, about 1.1–1.3× shorter than minimal distance between incisions of hysteronotal shield. Setae *l5* about 65 long. *Venter*. Striated membranes of coxae II as in female. Coxae III with poorly distinct transverse line. Postgenital shield shaped in an



Figs 7–8. *Listrophoroides* (*M.*) *papuanus* Fain, female. *7*, Dorsal view; *8*, opisthosoma in ventral view. Scale bar = 0.1 mm.

inverted U, with projections 95–100 long, distance between these projections at level of setae *gp* 25–30. Distance between postgenital shield and the postanal sclerite 4–5× shorter than the projections of postgenital shield, 18–25. Legs III and IV 140 and 155 long, respectively. Tibio-tarsi III and IV subequal, 55 long. Solenidia *phi* of legs III and IV 20 and 70 long, respectively.

Remarks

This species was briefly described from *Conilurus penicillatus* in N. Australia (Fain 1970). Later on, it was described in detail and figured (Fain 1972*b*).

The specimens from *Pseudomys nanus* differ from those from the type host by the smaller body: 400–415 long and 135–145 wide in males and 430–435 long and 155–160 wide in females.

The records of this species from other hosts were probably results of misidentification. The specimens from *Rattus leucopus* (Gray) in N. Queensland (Fain 1972*b*) actually belong to *L. crenator* Fain, stat. nov., those from *R. leucopus* in New Guinea (Fain 1981) belong to *L. obliquelineatus* Fain and those from *Rattus tunneyi* (Thomas) (Fain and Lukoschus 1981) belong to *L. queenslandicus*.

Listrophoroides (Marquesania) obliquelineatus **Fain, comb. nov.**

(Figs 11–15)

Listrophoroides papuanus obliquelineatus Fain, 1975: 185.
Listrophoroides (*Listrophoroides*) *obliquelineatus*. – Fain, 1977: 292–293, figs 18–19; 1981: 80–81, figs 95–96.

Material examined

Holotype. ♀ from *Rattus* sp. (BPBM 60283-60285): New Guinea: Javarere, 20 km E. of Sogeri, 4.xi.1968, coll. N. Wilson and M. Nadchatram.

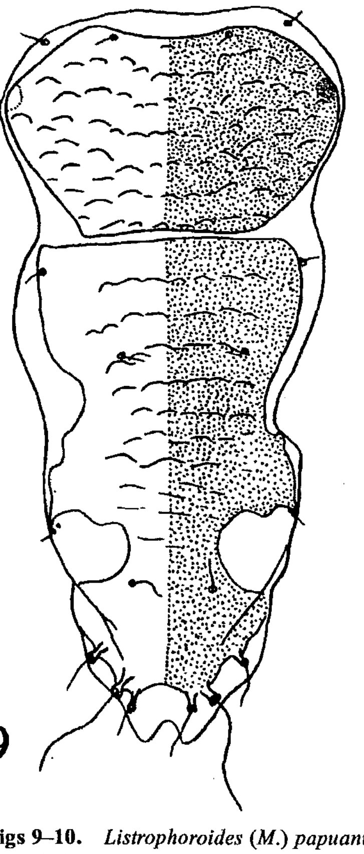
Paratypes. 2♂, 2♀; same data as holotype (IRSNB)

Non-type specimens (all in IRSNB). **New Guinea:** 2♂, 2♀ from *R. leucopus* (BPBM 25178), Mt Lamington, vic. Amboga R., 4.vii.1966, coll. P. Shanahan.

Diagnosis

Process of genu I lacking, clasping membranes of coxae II reaching the lateral margin of the body only in their anterior half. Postscapular shield ornamented only in lateral parts.

Male. Incisions of hysteronotal shield small, scales behind setae *l3* lacking.



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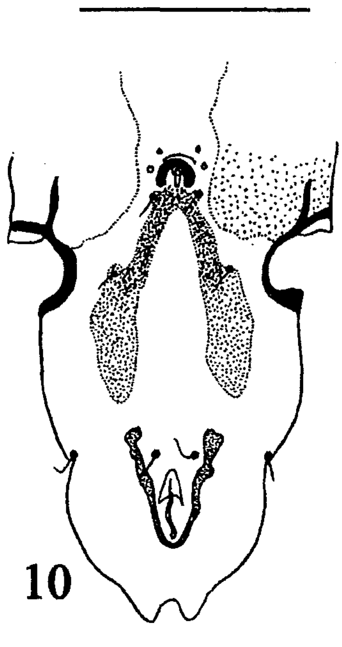

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Figs 9–10. *Listrophoroides* (*M.*) *papuanus* Fain, male. *9*, Dorsal view; *10*, opisthosoma in ventral view. Scale bar = 0.1 mm.

Description (based on type series)

Female (holotype, Figs 11–13)

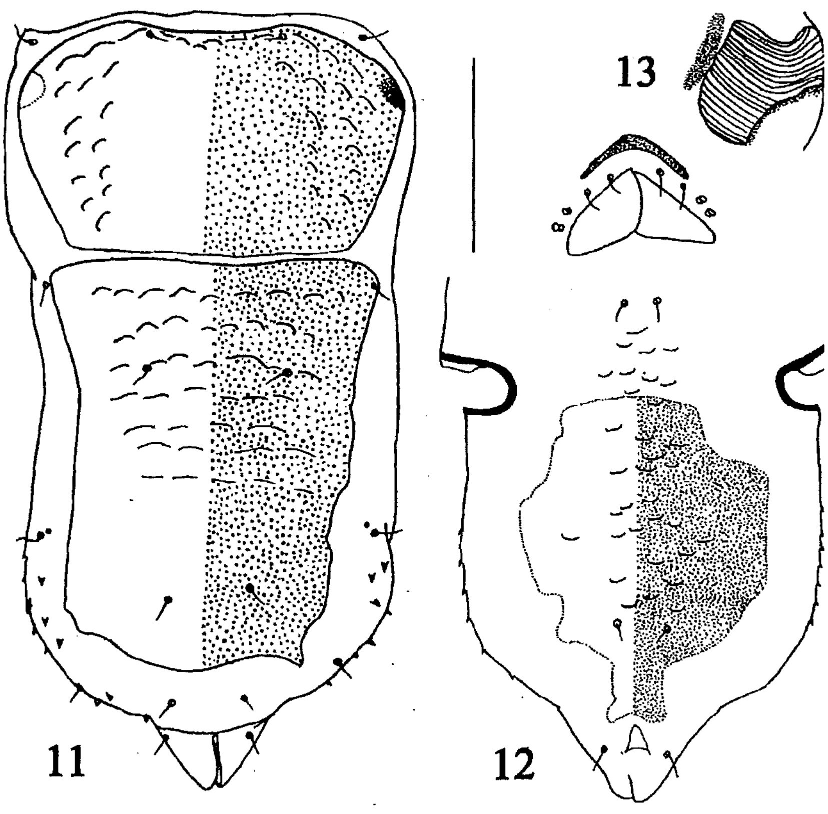
Body 495 long (490–500) and 205 wide (200–215). *Dorsum.* Postscapular shield 125 long, covered with short curved lines in its lateral parts. Hysteronotal shield 205 long, bearing six rows of short curved lines, the most posterior row remains far from level of setae *d3*. Width of this shield at level of setae *d2* 130–135 and at level of setae *d3* 115–120. Distances *d3–d3* and *d3*–posterior margin of hysteronotal shield subequal, 40–50. *Venter.* Striated membrane of coxae II reaching the lateral margins of the body only in their anterior half. Coxae III with a transverse line. Opisthosoma 200 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma with widely rounded and poorly distinct scales spreading from level of setae *gp* to level of setae *ae*. Legs III and IV about 150 long. Solenidia *phi* of legs III and IV 15 and 8 long, respectively.

Male (Figs 14, 15)

Body 465–480 long and 195–210 wide. *Dorsum.* Postscapular shield about 105 long, covered with short curved lines in lateral parts as in female. Hysteronotal shield about 225 long, bearing the same pattern as postscapular shield and spreading from the anterior margin to level of setae *d3*. Incisions of hysteronotal shield 25–30 long and about 15 wide, and their minimal distance between each other 85–90. Setae *l3* variable in position, either on or off hysteronotal shield, soft cuticle behind these setae without scales. Setae *d3* situated on hysteronotal shield, distance *d3–d3* 35–40, about 2.2–2.4× shorter than minimal distance between incisions of hysteronotal shield. Setae *l5* about 65 long. *Venter.* Striated membranes of coxae II as in female. Coxae III with a transverse line. Postgenital shield in an inverted U, with projections 80–85 long, distance between these projections at level of setae *gp* 35–40. Distance between postgenital shield and the postanal sclerite more than 2× shorter than the projections of postgenital shield, about 35. Legs III and IV 150 and 175 long, respectively. Tibio-tarsi III and IV subequal 55 long. Process of genu I not developed (reduced?). Solenidia *phi* of legs III and IV 10 and 50 long, respectively.

Remarks

This species was briefly described as a subspecies of *L. papuanus* from *Rattus* sp. in Javarere (New Guinea) (Fain 1975). Later on, Fain (1977) raised this subspecies to the species rank, he depicted this species and transferred it into the subgenus *Listrophoroides*. In a subsequent publication



Figs 11–13. *Listrophoroides* (*M.*) *obliquelineatus* Fain, comb. nov., female. *11*, Dorsal view; *12*, opisthosoma in ventral view; *13*, clasping membrane of coxa II. Scale bar = 0.1 mm.

Fain (1981) completed the figures of this species and discussed its taxonomical position. According to this author (Fain 1981), *L. obliquelineatus* like the species from the subgenus *Listrophoroides*, has poorly developed membranes of the coxae II. We re-investigated the type series of *L. obliquelineatus* and observed that in all specimens the coxal membranes reach the lateral margin of the body, but only in their anterior half. Furthermore, this species possesses other characters of the subgenus *Marquesania*, i.e. the specific shape of the postgenital shield and the well sclerotised anal membrane in the male. Therefore, we include this species into the subgenus *Marquesania*.

Listrophoroides mordax, sp. nov.

(Figs 16–19)

Material examined

Holotype. ♂ from *Rattus mordax* (Thomas) (BMNH 13.6.18.128–135): New Guinea: R. Utakwa (IRSNB).

Paratypes. 5♂, 5♀, same data as holotype (IRSNB).

Non-type specimens (all in IRSNB). **New Guinea:** 6♂, 12♀ from ?*Rattus ruber* (BMNH 13.6.18), Utakwa R.; 9♀ from ?*R. ruber* (BMNH 22.3.23), Kloof Bivak; 4♀ from ?*R. ruber* (BPBM 25124), Mt Lamington, vic. Amboga R., 29.vii.1966, coll. P. Shanahan; 1♂, 1♀ from *R. leucopus* (BPBM 25278), same locality as previous, 9.vii.1966; 1♂, 10♀ from *Rattus* sp. (BPBM 21483), Enarotali, 31.vii,1962, coll. N. Wilson; 1♀ from *Rattus* sp. (BPBM 60138), Brown R.,19.x.1968, coll. F. Radovsky.

Diagnosis

Large mites.

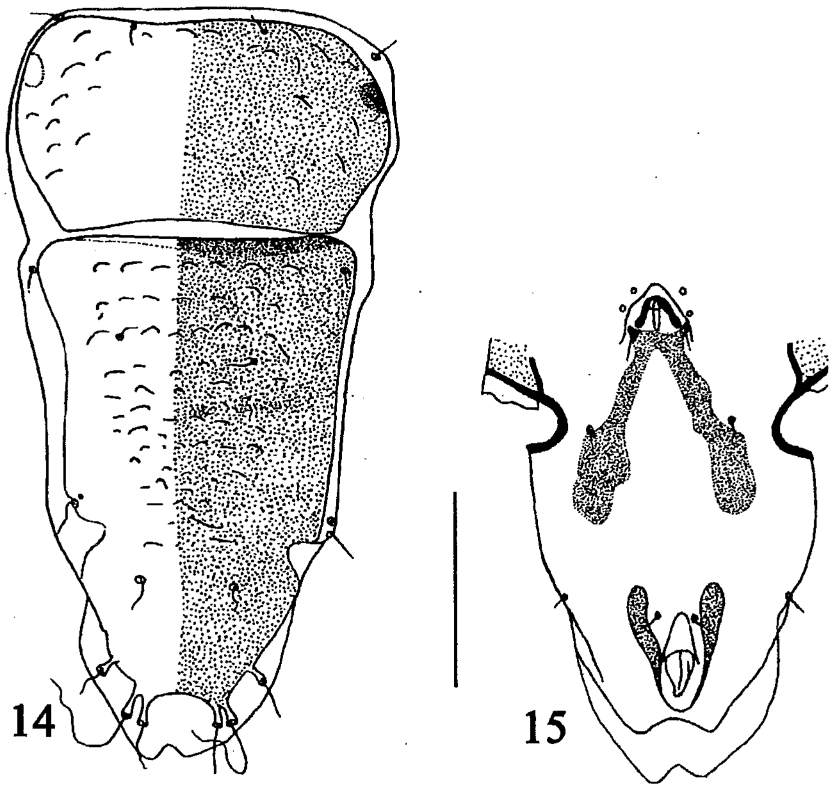
Female. Postscapular shield with short curved lines, transverse lines in anterior part of hysteronotal shield straight, distances *d3–d3* and *d3*–posterior margin of hysteronotal shield subequal.

Male. Postscapular shield ornamented only in anterior third, hysteronotal shield ornamented between the anterior margin and level of setae *d2*, incisions of hysteronotal shield well developed, scales behind setae *l3* present.

Description (*based on type series*)

Female (Figs 16–17)

Body 440–460 long and 170–205 wide. *Dorsum.* Postscapular shield 110 long, covered with six (seven in one specimen) transverse rows of short curved lines in anterior third. Hysteronotal shield 185 long, covered with 8–11 strong transverse lines from anterior margin to level of setae *d3* or to the posterior margin (in two specimens). Width of this shield at level of setae *d2* 95–105 and at level of setae *d3* 75–95. Distances *d3–d3* and *d3*–posterior r margin of hysteronotal shield subequal, 35–45. *Venter.* Striated mem-



Figs 14–15. *Listrophoroides* (*M.*) *obliquelineatus* Fain, comb. nov., male. *14*, Dorsal view; *15*, opisthosoma in ventral view. Scale bar = 0.1 mm.

branes of coxae II wide. Coxae III with a transverse line. Opisthosoma 175 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma with widely rounded and poorly distinct scales spreading from level of setae *gp* to level of setae *ae*. Legs III and IV about 140 long. Solenidia *phi* of legs III and IV 15 and 8 long, respectively.

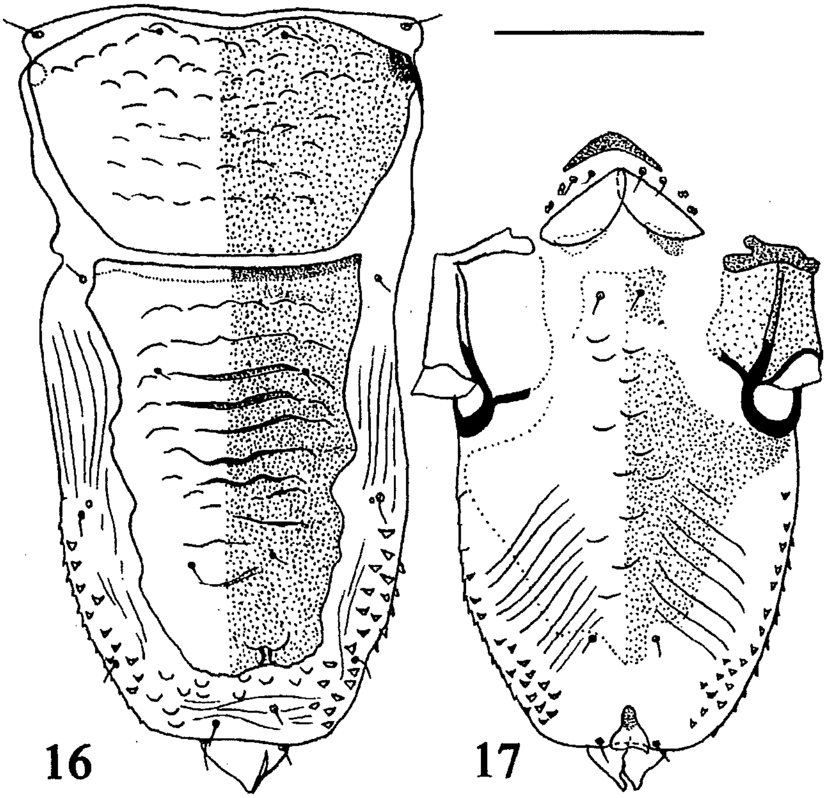
Male (holotype, Figs 18, 19)

Body 420 long (410–470) and 175 wide (165–205). *Dorsum*. Postscapular shield 100 long, covered with short curved lines in anterior third. Hysteronotal shield about 200 long, covered with the same pattern as postscapular shield, spreading from the anterior margin to level of setae *d2*. Incisions of hysterosomal shield 35–40 long and 33–46 wide, their minimal distance between each other 45–55. Setae *l3* variable in position, either on or off hysteronotal shield, soft cuticle behind these setae with 2–5 small scales. Setae *d3* situated on hysteronotal shield, distance *d3–d3* 38–45, about 1.2× shorter than minimal distance between incisions of hysteronotal shield. Setae *l5* about 45 long. *Venter*. Striated membranes of coxae II as in female. Coxae III with a transverse line. Postgenital shield in an inverted U, with projections 65–85 long, distance between these projections at level of setae *gp* 35–40. Distance between postgenital shield and the postanal sclerite 2–2.4× shorter than the projections of postgenital shield, 30–35. Legs III and IV 130 and 150 long, respectively. Tibio-tarsi III and IV subequal 50 long. Solenidia *phi* of legs III and IV 15 and 60 long, respectively.

Remarks

This species is closest to *L. obliquelineatus* but clearly differs from it by the following characters. In both sexes of *L. mordax*, sp. nov. the clasping membranes of coxae II reach the lateral margins of the body in their posterior as well as anterior half, the process of the genu I is well developed. In the male the postscapular shield is ornamented only in anterior third, the hysteronotal shield is ornamented between the anterior margin and the level of setae *d2*, the incisions of the hysteronotal shield are well developed; the scales behind setae *l3* are present. In the female the postscapular shield is completely covered with short curved lines, the hysterosomal shield bears 8–11 strong transverse lines.

In both sexes of *L. obliquelineatus* the clasping membranes of the coxae II reach the lateral margins of the body only in their anterior half, the process of the genu I is lacking, the postscapular shield is ornamented only in the lateral part. In the male the hysteronotal shield is ornamented from the anterior margin to the level of setae *d3*, the incisions



Figs 16–17. *Listrophoroides* (*M.*) *mordax*, sp. nov., female. *16*, Dorsal view; *17*, opisthosoma in ventral view. Scale bar = 0.1 mm.

of the hysteronotal shield are small and the scales behind setae *l3* are lacking. In the female the hysteronotal shield bears 6 rows of short curved lines.

The holotype of *Rattus ruber*, second host of this species, is, actually, a specimen of the introduced *Rattus nitidus* (Hogson) (Wilson and Reader 1993). These rats are distributed in the South-east Asia but they are absent from New Guinea. The three valid New Guinean species, *Rattus steini* Rummler, *R. praetor* (Thomas) and *R. mordax*, were initially described as three different subspecies of *R. ruber*. Therefore, the mites collected from ?*R. ruber*, actually, can originate from every one of these hosts.

Listrophoroides (Marquesania) crenatus Fain, stat. nov.

(Figs 20–23)

Listrophoroides papuanus crenatus Fain, 1975: 185; 1977: 294–295, figs 21–22.

Material examined

Holotype. ♀ from ?*R. ruber* (BPBM 54706–54709): New Guinea: N. E. of Wau, base of Mt Missim, 24.x.1967, coll. P. Colman (BM).

Paratypes (all in IRSNB). Same host and locality as holotype: 7♂, 6♀ from host (BPBM 54710–54711), 29.x.1967; 4♂, 2♀ from host (BPBM 54724–54725), 26.x.1967; 4♂, 4♀ from host (BPBM 54661), 21.x. 1967; 2♂, 2♀ from host (BPBM 54669), 21.x.1967; 2♀ from host (BPBM 54706–54709), 29.x.1967; 2♀ from host (BPBM 54717), 25.x.1967, coll. A. Mirza.

Non-type specimens (all in IRSNB). **New Guinea: Wau:** 5♀ from *Melomys rufescens* (Alston) (BPBM 21063), Mt Missim, 9.i.1963, coll. H. Clissold; 1♀ from *Melomys moncktoni* (Thomas) (BPBM 52205), Mt Kaindi, 19 km SW of Wau, 24.i.1966, coll. R. Mitchell. **Morobe District:** 2♂ from ?*R. ruber* (BPBM 95157), 17.iii.1967; 2♀ from ?*R. ruber* (BPBM 61523), 9.v.1965; 3♂ from ?*R. ruber*, 15.ix.1967. **Mara Punga:** 2♂, 3♀ from *St. niobe* (BPBM 81630), 1967, coll. F. Radovsky; 3♀ from *St. niobe* (BPBM 81632), same data as previous. **Solomon Islands, Bougainville Island:** 8♂, 6♀ from *Rattus* sp. (BPBM 61081–61082), Pokapa, 6 km WSW of Tinputz, 29.iii.1968; 6♂, 8♀ from *Rattus* sp. (BPBM 61319), Tinputz, Patrol Post, 29.iii.1968; 10♂, 4♀ from *Rattus* sp. Wakunai, Mt Balbi, 10.iv.1968, **Isabel Island:** 2♂, 4♀, Boala, 21.viii.1969, coll. P. Shanahan. **Australia: N. Queensland:** 14♂, 4♀ from *R. leucopus*, Deyman, point near Mossman, 10.v.1971, coll. R. Domrow and Campbell.

Diagnosis

Postscapular shield with short and deep interrupted transverse crenel-like lines.

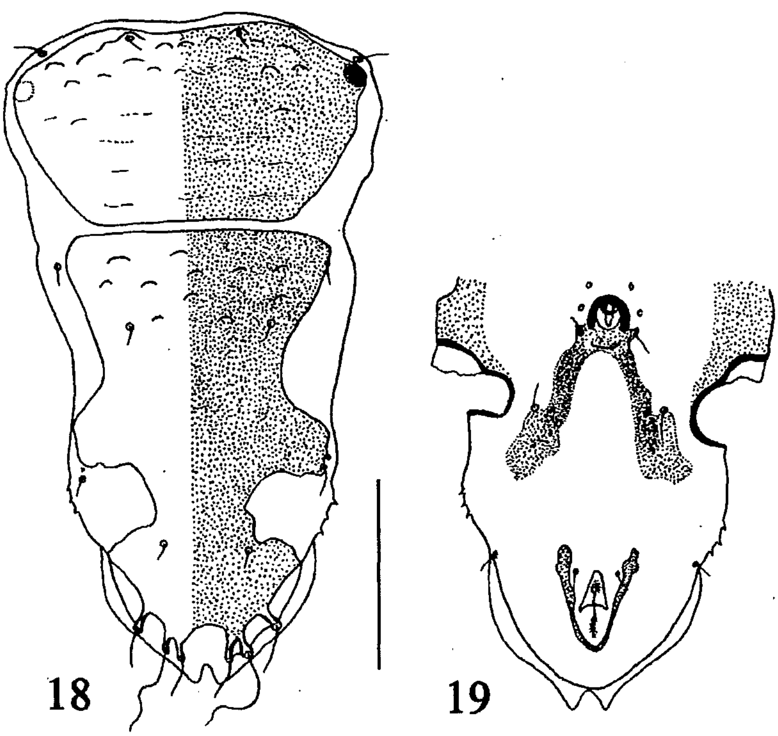
Female. Hysteronotal shield with transverse lines prolonged by short line directed back wards, distances *d3–d3* and *d3*–posterior margin of hysteronotal shield subequal.

Male. Incisions of hysteronotal shield small, scales behind setae *l3* present.

Description (*based on type series*)

Female (holotype, Figs 20, 21)

Body 420 long (400–430 in paratypes) and 165 wide (156–175). *Dorsum.* Postscapular shield 110 long, covered

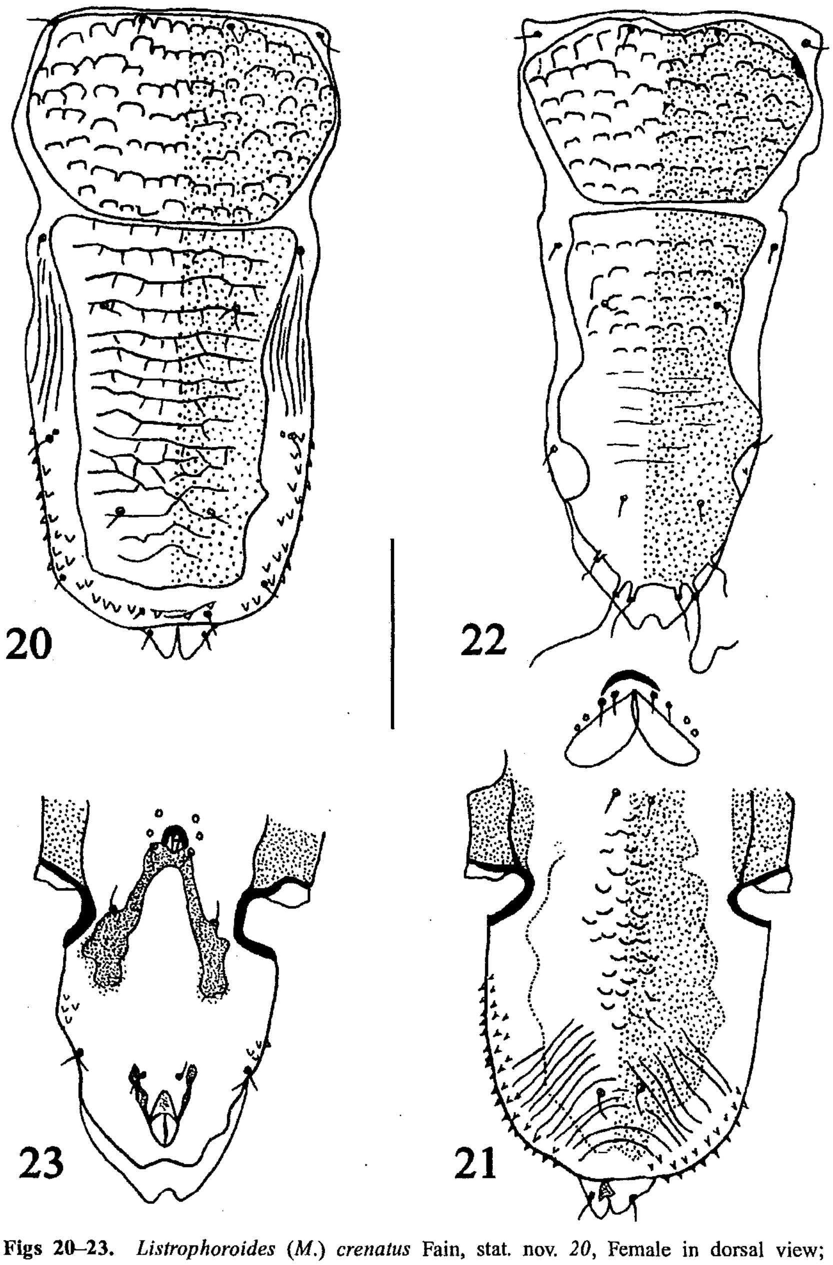


Figs 18–19. *Listrophoroides* (*M.*) *mordax*, sp. nov., male. *18*, Dorsal view; *19*, opisthosoma in ventral view. Scale bar = 0.1 mm.

with seven transverse rows of lines shaped as inverted squared-off U's (crenel-like, Fig. 20). Hysteronotal shield 180 long, almost completely covered with 12–15 transverse furrows. Transverse lines connected by short longitudinal lines in the anterior half of this shield. Width of this shield at level of setae *d2* 95–100 and at level of setae *d3* 75–85. Distances *d3–d3* 35–50 and *d3*–posterior margin of hysteronotal shield subequal, 35–50. *Venter.* Striated membranes of coxae II wide. Coxae III with a transverse line. Opisthosoma 160 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma with widely rounded scales spreading from level of setae *gp* to level of setae *ae*. Legs III and IV about 115 long. Solenidia *phi* of legs III and IV 13 and 8 long, respectively.

Male (Figs 22, 23)

Body 370–400 long and 145–170 wide. *Dorsum.* Postscapular shield 100 long, completely covered with short curved lines and arranged into 6–7 transverse rows of crenel-like lines, similar to those in female. Hysteronotal shield



Figs 20–23. *Listrophoroides* (*M.*) *crenatus* Fain, stat. nov. *20*, Female in dorsal view; *21*, opisthosoma of female in ventral view; *22*, male in dorsal view; *23*, opisthosoma of male in ventral view. Scale bar = 0.1 mm.

about 190 long, covered with the same pattern as postscapular shield in anterior third and with weakly developed lines in median part. Incisions of hysteronotal shield small, 20–25 long and 11–17 wide. Their minimal distance between each other 65–90. Setae *l3* variable in position, either on or off hysteronotal shield, soft cuticle behind these setae with 2–5 small scales. Setae *d3* situated on hysteronotal shield, distance *d3–d3* 35–40, about 1.9–2× shorter than minimal distance between incisions of hysteronotal shield. Setae *l5* about 60 long. *Venter.* Striated membranes of coxae II as in female. Coxae III with a transverse line. Postgenital shield in an inverted U, with projections 75–85 long, distance between these projections at level of setae *gp* 25–30. Distance between postgenital shield and the postanal sclerite 2.5–3× shorter than the projections of postgenital shield, 25–33. Legs III and IV 120 and 135 long, respectively. Tibio-tarsi III and IV subequal 45 long. Solenidia *phi* of legs III and IV 15 and 60 long, respectively.

Remarks

This species was briefly described as a subspecies of *L. papuanus* from ?*R. ruber* in N. E. Wau (New Guinea) (Fain 1975). Later on, Fain (1977) illustrated this subspecies. We have re-examined a large series of these mites and consider now that *L. crenatus* is a separate species, clearly distinct from *L. papuanus* by the specific ornamentation of the postscapular shield in both sexes, the presence of scales behind the setae *l3*, the small incisions of the hysteronotal shield in male and by some other characters.

The discussion about the taxonomical status of its type host species, ? *R. ruber* has been given above (see *L. obliquelineatus*).

Listrophoroides (Marquesania) interpolatus Fain, stat. nov.

(Figs 24–27)

Listrophoroides papuanus interpolatus Fain, 1975: 184; 1977: 293–294, fig. 293.

Material examined

Holotype. ♂ from *St. niobe* (BPBM 68000): New Guinea: West Irian, Ertsberg, 29.iv.1973 (BM).

Paratypes. ♀, same data as holotype, from host (BPBM 67998); 2♂, 3♀, same data as holotype, from host (BPBM 1607) (IRSNB).

Non-type specimens (all in IRSNB). **New Guinea: West Irian:** 7♀ from *M. moncktoni* (BPBM 61318), Ertsberg, 4.v.1973; 1♂ from *Rattus* sp. (BPBM 61318), same locality as previous, 1.v.1973; 1♂, 1♀ from *St. niobe* (BPBM 54919–54930), Bulldog Road, Edie Ck, 5.xi.1967, coll. M. Nadchatram; 1♂, same data as previous, from host (BPBM 52272), 4.vii.1966, coll. R. Mitchell; 2♂, 3♀ from *St. niobe* (BPBM 52775), Saruwaged Range, 32 km S. W. of Kabwum, 7.viii.1966, coll. R. Mitchell; 1♂ from *St. niobe* (BPBM 55570), Marafunga, 11.xi.1968, coll. R. Traub; 3♀ from *St. niobe* (BPBM 97426), Murmur Pass, 1.x.1968, coll. R. Traub; 2♀ from *Stenomys verecundus* (Thomas) (BPBM 24635), Wau, Mt Missim, 21.iii.1966, coll. P. Shanahan; 1♂, 5♀ from *St. verecundus*, Mt Albert-Edward.

Diagnosis

Small mites.

Female. Postscapular shield covered with six transverse rows of lines, transverse lines in anterior part of hysteronotal shield straight, distance *d3–d3* 1.8–2.5× longer than distance between *d3* and posterior margin of hysteronotal shield.

Male. Postscapular shield completely covered with 5–6 interrupted transverse lines, hysteronotal shield ornamented between anterior margin and level of setae *d3*, incisions of hysteronotal shield well developed, scales behind setae *l3* present, projections behind genital organ in an inverted V (Fig. 27).

Description (based on specimens from type host)

Female (Figs 24, 25)

Body 360–380 long and 145–150 wide. *Dorsum.* Postscapular shield 90 long, completely covered with six interrupted transverse lines, the most anterior row represented by short curved lines in an inverted U, three most posterior lines poorly distinct. Hysteronotal shield 170 long, almost completely covered with 9–11 strong transverse lines. Width of this shield at level of setae *d2* 90–95 and at level of setae *d3* 65–80. Distance *d3–d3* 35–45, about 1.8–2.5× longer than distance between *d3* and posterior margin of hysteronotal shield, 15–25. *Venter.* Striated membranes of coxae II wide. Coxae III with a transverse line. Opisthosoma 155 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma with widely rounded scales spreading from level of setae *gp* to level of setae *ae*. Legs III and IV about 100 long. Solenidia *phi* of legs III and IV 11 and 5 long, respectively.

Male (holotype, Figs 26, 27)

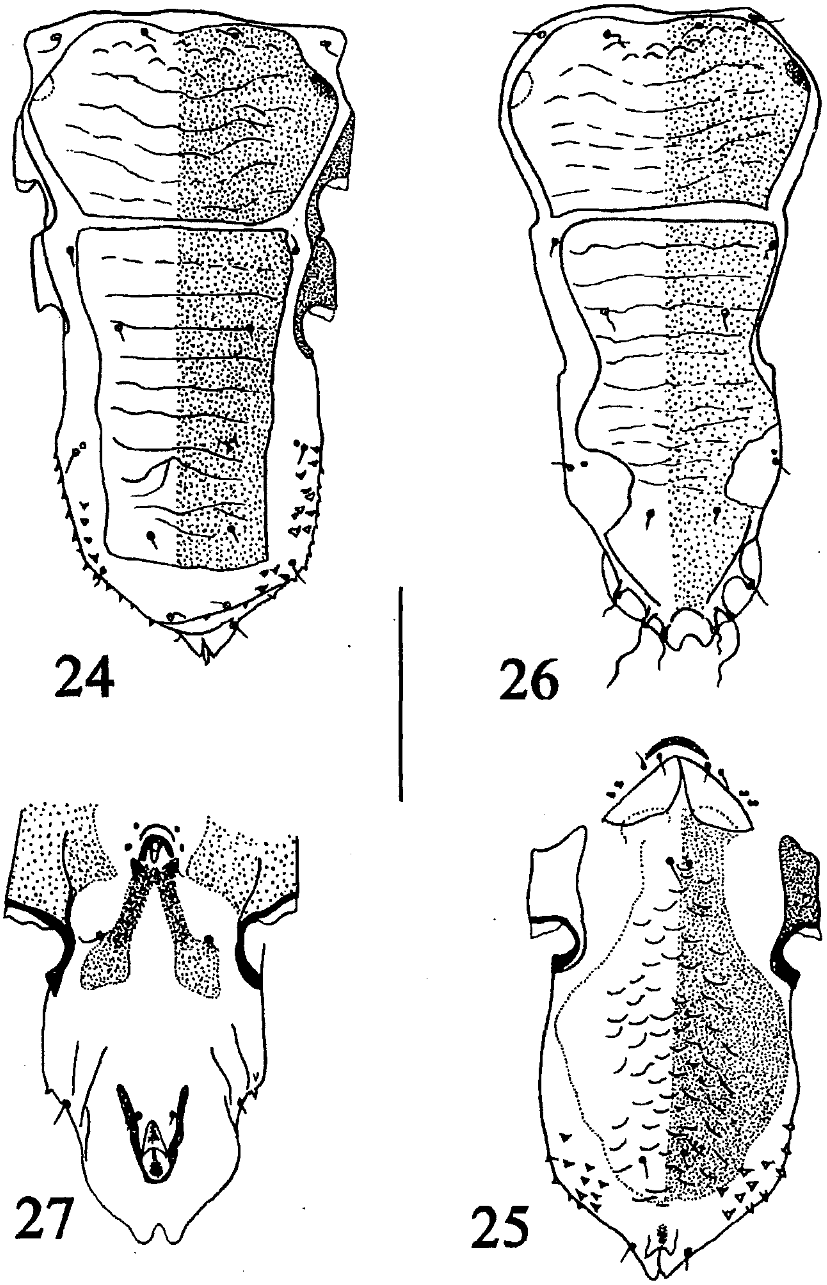
Body 375 long (345–380) and 140 wide (133–150). *Dorsum.* Postscapular shield 75 long, completely covered with 5–6 interrupted transverse lines, similar to those in female. Hysteronotal shield about 160 long, covered with transverse lines extending from the anterior margin to level of setae *d3*. These lines poorly distinct in posterior half of this shield. Incisions of hysteronotal shield 28–35 long and 25–35 wide. Their minimal distance between each other 35–55. Setae *l3* variable in position, either on or off hysteronotal shield, soft cuticle behind these setae with 1–4 small scales or without scales in some specimens. Setae *d3* situated on the hysteronotal shield, distance *d3–d3* 30–40, about 1.2–1.4× shorter than minimal distance between incisions of hysteronotal shield. Setae *l5* about 45 long. *Venter.* Striated membranes of coxae II as in female. Coxae III with a transverse line. Postgenital shield in an inverted V, with projections 60–65 long, distance between these projections at level of setae *gp* 16–25. Distance between postgenital shield and the postanal sclerite 1.7–1.8× shorter than the projections of postgenital shield, 33–38 long. Legs

III and IV 100 and 115 long, respectively. Tibio-tarsi III and IV subequal 35 long. Solenidia *phi* of legs III and IV 13 and 40 long, respectively.

Remarks

This species was described as a subspecies of *L. papuanus* from *Stenomys niobe* in West Irian (New Guinea) (Fain 1975). We have re-examined a large series of these mites and believe now that *L. interpolatus* is a separate species, clearly distinct from *L. papuanus* mostly by the small body sizes in both sexes, the ratio *d3–d3* and *d3*–posterior margin of hysteronotal shield distances in female and by the presence of scales behind the setae *l3* in male.

Several specimens (2♂, 7♀) collected from *St. niobe* and *Rattus* sp. in Ertsberg (New Guinea) differ from the other specimens from the same locality, including the type series,



Figs 24–27. *Listrophoroides* (*M.*) *interpolatus* Fain, stat. nov. *24*, Female in dorsal view; *25*, opisthosoma of female in ventral view; *26*, male in dorsal view; *27*, opisthosoma of male in ventral view. Scale bar = 0.1 mm.

by a larger body: 380–400 long and 155–160 wide in males and 430–440 long and 155–165 wide in females.

The specimens from *Rattus annandalei* (Bonhote) in Selangor (Malaysia) identified by Fain (1981) as *L. papuanus interpolatus*, actually belong to *L. cucullatus*.

Listrophoroides (Marquesania) melomys, sp. nov.

(Figs 28–31)

Material examined

Holotype. ♂ from *M. moncktoni* (BPBM 52217): New Guinea: West Wau, Mt Kaindi, 26.vi.1966, coll. R. Mitchell (IRSNB).

Paratypes. 3♂, 2♀, same as holotype (IRSNB).

Diagnosis

Small mites.

Female. Postscapular shield with seven transverse lines, the transverse lines in the anterior half of hysteronotal shield curved in their lateral parts, the first line connected with the anterior margin of this shield by a pair of short longitudinal lateral lines (Fig. 28), distances *d3–d3* and *d3*–posterior margin of hysteronotal shield subequal.

Male. Incisions of hysteronotal shield small, scales behind setae *l3* lacking.

Description

Female (Figs 28, 29)

Body 390–395 long and 140–150 wide. *Dorsum*. Postscapular shield 85 long, covered with seven transverse furrows, the most posterior line poorly distinct. Hysteronotal shield 180 long, covered with nine strong transverse furrows situated from the anterior margin to level of setae *d3*, first line connected with anterior margin of this shield by a pair of short longitudinal lateral lines; five anterior lines curved in their lateral parts. Width of this shield at level of setae *d2* 100–105 and at level of setae *d3* 75–85. Distances *d3–d3* and *d3*–posterior margin of hysteronotal shield subequal, about 40. *Venter*. Striated membranes of coxae II wide. Coxae III with a strong transverse line. Opisthosoma 155 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma with widely rounded scales spreading from level of setae *gp* to level of setae *ae*. Legs III and IV about 105 long. Solenidia *phi* of legs III and IV 8 and 3 long, respectively.

Male (holotype, Figs 30, 31)

Body 355 long (335–350 in paratypes) and 140 wide (125–145). *Dorsum*. Postscapular shield 85 long, covered with seven transverse furrows, similar to those in female. Hysteronotal shield about 170 long, covered with transverse furrows from the anterior margin to level of setae *d3*. Incisions of hysteronotal shield small, 29–35 long and 8–15 wide. Their minimal distance between each other 65–80. Setae *l3* variable in position, either on or off hysteronotal shield, soft cuticle behind these setae without scales. Setae *d3* situated on hysteronotal shield, distance *d3–d3* 40–45, about 1.6–1.7× shorter than minimal distance between incisions of hysteronotal shield. Setae *l5* about 35 long. *Venter*. Striated membranes of coxae II as in female. Coxae III with a strong transverse line. Postgenital shield in an inverted U, with projections 75–85 long, distance between these projections at level of setae *gp* 13–15. Distance between postgenital shield and the postanal sclerite 5–6× shorter than the projections of postgenital shield, 12–15 long. Legs III and IV 105 and 120 long, respectively. Tibiotarsi III and IV subequal 35 long. Solenidia *phi* of legs III and IV 5 and 40 long, respectively.

Remarks

This species is closest to *L. interpolatus* but differs from it by the following characters. In the male of *L. melomys*, sp. nov. the incisions of the hysteronotal shield are small and the scales behind setae *l3* are lacking. In the female the distances *d3–d3* and *d3*–posterior margin of the hysteronotal shield are subequal.

In the male of *L. interpolatus* the incisions of the hysteronotal shield are well developed and scales behind setae *l3* are present. In the female the distance *d3–d3* is 1.8–2.5× longer than distance *d3*–posterior margin of the hysteronotal shield.

Listrophoroides (Marquesania) queenslandicus (Womersley)

(Figs 32–35)

Marquesania expansa var. *queenslandica* Womersley, 1943: 15. Complete bibliography in Domrow (1992).

Material examined

Lectotype. ♀ from *Rattus sordidus* (Gould): Australia: Queensland, Cowan Cowan, ix.1938 (SAM).

Paralectotype. ♂, same data as holotype (SAM).

Non-type specimens (all in IRSNB). **Australia:** 9♂, 10♀ from *Rattus fuscipes* (Waterhouse) (RMNH 20359), 1869; 6♂, 4♀ from *R. fuscipes* (BMNH 22.12.18.36–39), Ravenhoc; 1♂ from *Rattus villosissimus* (Waite) (BMNH 85.7.4.1), Kimberley; 8♂, 15♀ from *R. fuscipes* (BMNH 23.3.28.4–5), Peason Island;. 4♂ from *R. fuscipes* (BMNH 36.12.8.4–5), Portlend; 4♀ from *R. fuscipes* (BMHN 36.12.8.1–3), Eakdale; 1♂, 1♀ from *R. fuscipes* (BMNH 26.3.11.241–242), Guy Fautis; 10♂, 2♀ from *R. tunneyi*, Port Warrender (14°30′S, 125°50′E), 30.x.1976. **New Guinea:** 1♂ from *Rattus leucopus* (BMNH 97.8.7.34), Astrolabe, Gerekonumi, Mt Loria.

Diagnosis

Large mites.

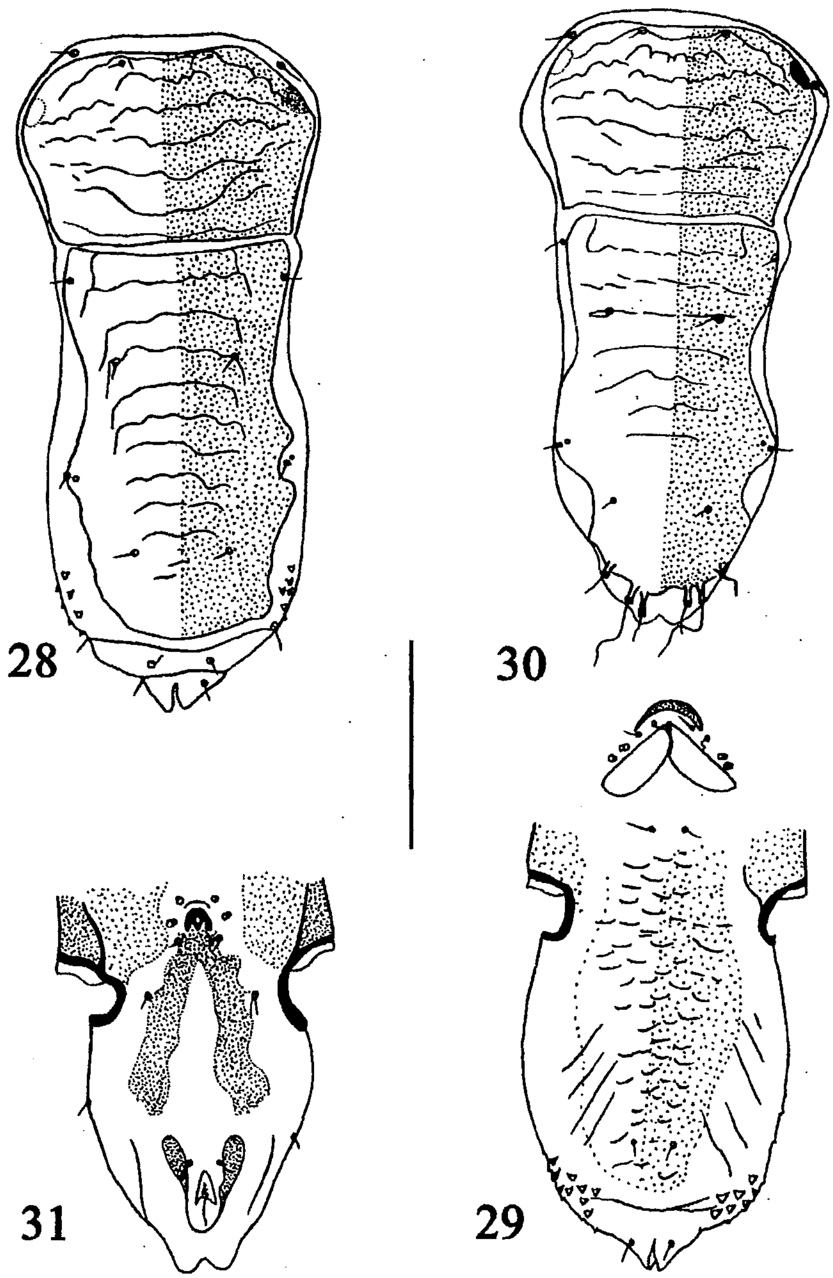
Female. Postscapular shield with six poorly distinct transverse lines, ratio between distances *d3–d3* and *d3*–posterior margin of hysteronotal shield variable, from 1:1 to 1:2.

Male. Dorsal shields completely covered with very poorly distinct transverse lines, incisions of hysteronotal shield well developed, scales behind setae *l3* present.

Description (based on specimens from R. fuscipes)

Female (Figs 32, 33)

Body 425–460 long and 175–85 wide (450 × 180 in lectotype). *Dorsum.* Postscapular shield 100 long, covered with six transverse poorly distinct lines, in the lectotype and some specimens these rows almost invisible, but always present. Hysteronotal shield 175 long, completely covered with 10–13 straight transverse lines. Width of this shield at level of setae *d2* 90–105 and at level of setae *d3* 75–85. Distance *d3–d3* 30–50; distance *d3*–posterior margin of hysteronotal shield variable, 15–40. *Venter.* Striated membranes of coxae II wide. Coxae III devoid of lines or



Figs 28–31. *Listrophoroides* (*M.*) *melomys*, sp. nov. *28*, Female in dorsal view; *29*, opisthosoma of female in ventral view; *30*, male in dorsal view; *31*, opisthosoma of male in ventral view. Scale bar = 0.1 mm.

with a poorly distinct transverse line. Opisthosoma 155 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma with widely rounded scales spreading from level of setae *gp* to level of setae *ae*. Legs III and IV about 130 long. Solenidia *phi* of legs III and IV 15 and 8 long, respectively.

Male (Figs 34, 35)

Body 405–410 long and 175–185 wide. *Dorsum*. Postscapular shield 85 long, completely covered with six poorly distinct transverse lines, similar to those in female. Hysteronotal shield about 175 long, covered with transverse lines extending from the anterior margin to level of setae *d3*. Incisions of hysteronotal shield 40–50 long and 30–40 wide. Their minimal distance between each other 30–50. Setae *l3* variable in position, either on or off hysteronotal shield, soft cuticle behind these setae with 5–8 scales; in some specimens these scales rounded. Setae *d3* situated on hysteronotal shield, distance *d3–d3* subequal to distance between incisions of hysteronotal shield, 35–40. Setae *l5* about 58 long. *Venter*. Striated membranes of coxae II as in female. Coxae III devoid of lines or with a poorly distinct transverse line. Postgenital shield in an inverted U, with projections 65–75 long, distance between these projections at level of setae *gp* 30–35. Distance between postgenital shield and the postanal sclerite variable, 1.5–2.5× shorter than the projections of postgenital shield, 25–45 long. Legs III and IV 125 and 140 long, respectively. Tibio-tarsi III and IV subequal 50 long. Solenidia *phi* of legs III and IV 15 and 50 long, respectively.

Remarks

This species was described from *R. sordidus* (= *youngi*) in Queensland (Womersley 1943). Fain (1972*b*) redescribed *L. queenslandicus* from the type series and designated lectotype.

Domrow (1958) collected it from *Uromys caudimaculatus* (Krefft) in North Queensland. However, this record requires a confirmation. The record of this species from the marsupial *Cercartetus concinnus* (Gould) in Australia (Fain and Lukoschus 1981) is, obviously, accidental.

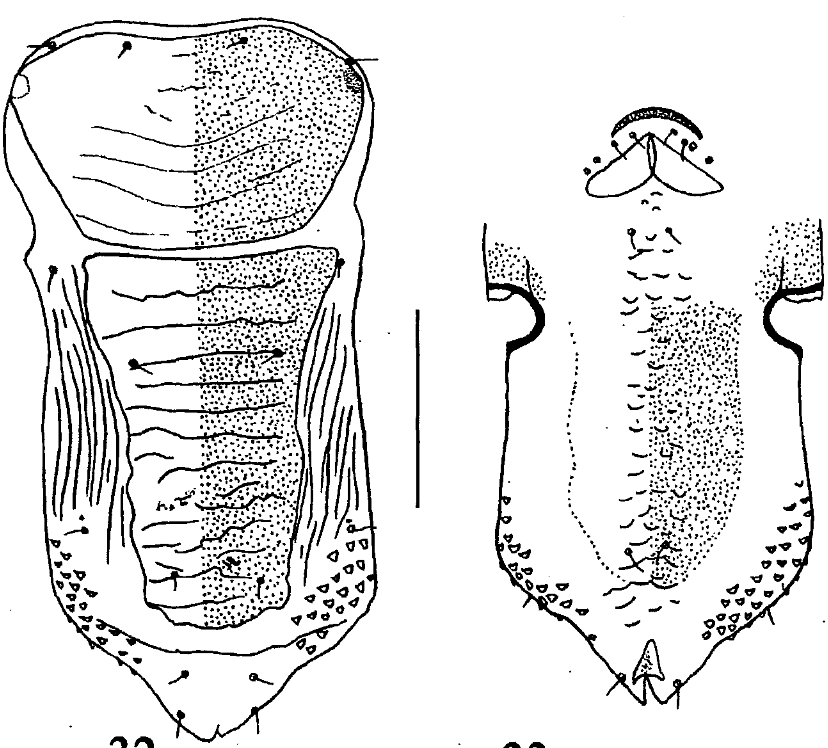
Listrophoroides (Marquesania) australiae Fain

(Figs 36–39)

Listrophoroides australiae Fain, 1970: 283.

Material examined

Holotype. ♂ from *Antechinus stuartii* Macleay (= *Phascogale unicolor*) (BMNH 26.3.11.268.76): Australia: New South Wales, Guy Fawkes (IRSNB).



32 33

Figs 32–33. *Listrophoroides* (*M.*) *queenslandicus* (Womersley), female. *32*, Dorsal view; *33*, opisthosoma in ventral view. Scale bar = 0.1 mm.

Paratypes. 1♂, 1♀, same data as holotype (IRSNB).

Non-type specimens (all in IRSNB). **Australia:** 4♂, 7♀ from *Rattus lutreolus* (Gray) (BMNH 26.3.11.229–236), New South Wales, Guy Fawkes; 1♂ from *R. fuscipes* (BMNH 23.3.28.1–5), Peasson Island; 3♀ from *R. fuscipes* (BMNH 36.12.8.1–3), Eskdale; 2♀ from *R. fuscipes*, Tidal R., 6.v.1970, 2♂, 1♀ from *R. fuscipes* (BMNH 26.3.11.241–242), Guy Fautis.

Diagnosis

Large mites. Ornamentation of postscapular shield completely lacking.

Male. Hysteronotal shield without ornamentation, incisions of hysterosomal shield well developed, scales behind setae *l3* present.

Description (*based on holotype and other specimens*)

Female (Figs 36, 37)

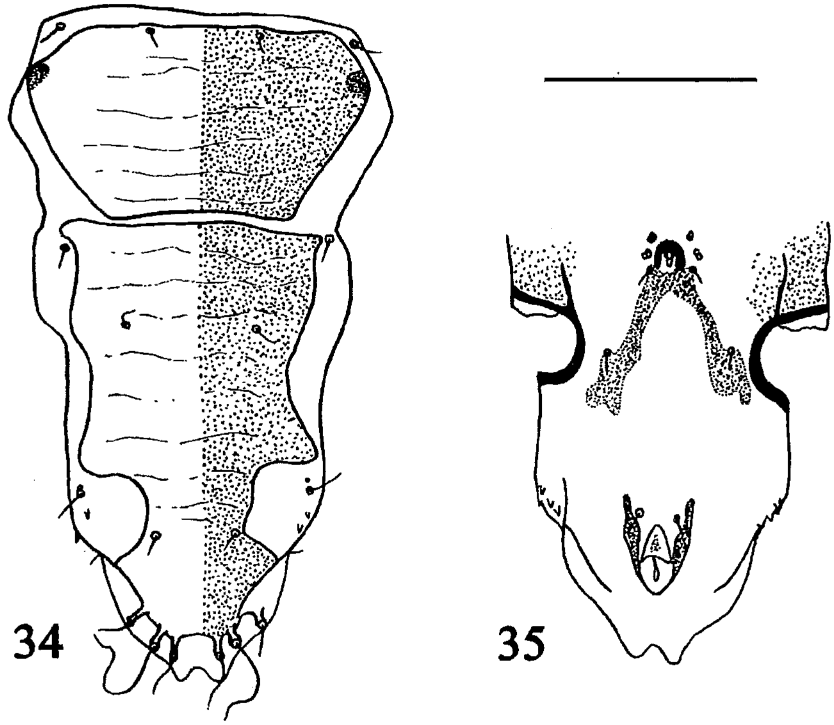
Body 430–450 long and 175–185 wide. *Dorsum.* Postscapular shield 100 long, without ornamentation. Hysteronotal shield 175 long, covered with 10–15 strong transverse lines, 2–3 from them situated behind level of setae *d3*. Width of this shield at level of setae *d2* 90–105 and at level of setae *d3* 60–70. Distance *d3–d3* 40–45, about 1.5–2× longer than the distance between *d3* and posterior margin of hysteronotal shield, 25–30. *Venter.* Striated membranes of coxae II wide. Coxae III devoid of lines. Opisthosoma 165 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma with widely rounded scales spreading from level of setae *gp* to level of setae *ae*. Legs III and IV about 130 long. Solenidia *phi* of legs III and IV 18 and 7 long, respectively.

Male (holotype, Figs 38, 39)

Body 400 long (390–415) and 165 wide (175–190). *Dorsum.* Postscapular shield 185 long, hysteronotal shield about 335 long, both without ornamentation. Incisions of hysteronotal shield 35–40 long and 30–40 wide. Their minimal distance between each other 25–35. Setae *l3* variable in position, either on or off hysteronotal shield, soft cuticle behind these setae with scales. Setae *d3* situated off or on margin of hysteronotal shield, distance *d3–d3* 35–40, subequal to minimal distance between incisions of hysteronotal shield. Setae *l5* about 70 long. *Venter.* Striated membranes of coxae II as in female. Coxae III devoid of lines. Postgenital shield in an inverted U, with projections 75–85 long, distance between these projections at level of setae *gp* 25–35. Distance between postgenital shield and the postanal sclerite 2–2.5× shorter than the projections of postgenital shield, 30–40. Legs III and IV 125 and 150 long, respectively. Tibio-tarsi III and IV subequal 50 long. Solenidia *phi* of legs III and IV 17 and 35 long, respectively.

Remarks

This species was briefly described from *Antechinus stuartii* in Australia (Fain 1970). Later on, Fain (1972*b*)



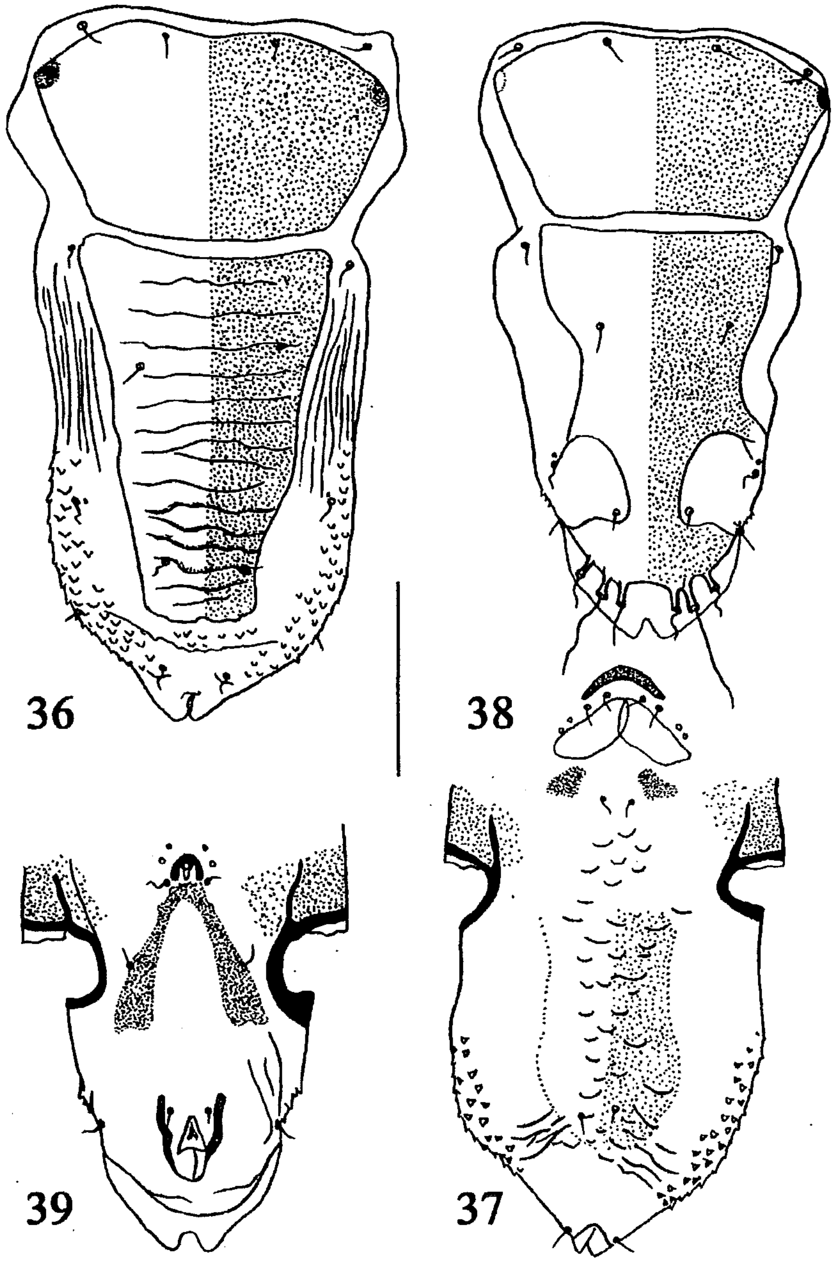
Figs 34–35. *Listrophoroides* (*M.*) *queenslandicus* (Womersley), male. *34*, Dorsal view; *35*, opisthosoma in ventral view. Scale bar = 0.1 mm.

synonymised this species with *L. queenslandicus*. However, *L. australiae* is distinguished from the latter by the lack of ornamentation on the postscapular shield in both sexes and on the hysterosomal shield in the male. Both species may occur in the same locality (for example, Victoria, Australia) and from the same host species (*R. fuscipes*), therefore the differences between them are not in relation with their geographical distribution. Thus, we think now that *L. australiae* is a distinct species.

Antechinus stuartii in Australia (Fain 1970) was, probably, an accidental host for this species.

Listrophoroides (Marquesania) postsquamatus Fain
(Figs 40–43)

Listrophoroides (*Marquesania*) *postsquamatus* Fain, 1976: 63; 1981: 107–108, figs 137–140.



Figs 36–39. *Listrophoroides* (*M.*) *australiae* Fain. *36*, Female in dorsal view; *37*, opisthosoma of female in ventral view; *38*, male in dorsal view; *39*, opisthosoma of male in ventral view. Scale bar = 0.1 mm.

Material examined

Holotype. ♂ from *Rattus everetti* (Gunther) (BMNH ♂ M566): The Philippines: Leyte Tambis Island, Burauen, Mt Lobi Range, 5.vi.1964 (BMNH).
Paratype. ♀ same data as holotype (BMNH).
Non-type specimens. **The Philippines:** 3♂, 1♀ from *R. everetti* (SMF 30943), Mindanao, Mt Katanglad (IRSNB).

Diagnosis

Female. Posterior half of opisthonotum covered with numerous scales, setae *ai* long.
Male. Lateral margins of hysteronotal shield unclear and its incisions not distinct, scales behind setae *l3* numerous.

Description (*based on specimens from type host*)

Female (Figs 40, 41)

Body 425–450 long and 175–185 wide. *Dorsum.* Postscapular shield 85 long, covered with six transverse rows of short lines. Hysteronotal shield 165 long, covered with 8–9 furrows from the anterior margin to level of setae *d3*. Width of this shield at level of setae *d2* 90–95 and at level of setae *d3* 85–90. Distances *d3–d3* and *d3*–posterior margin of hysteronotal shield subequal, 25–35. Posterior half of opisthonotum covered with numerous scales. *Venter.* Striated membranes of coxae II wide. Coxae with a transverse line. Opisthosoma 155 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma with widely rounded scales spreading from level of setae *gp* to level of setae *ae*. Setae *ai* about 40 long. Legs III and IV about 125 long. Solenidia *phi* of legs III and IV 15 and 7 long, respectively.

Male (holotype, Figs 42, 43)

Body 345 long (355–400) and 165 wide (150–180). *Dorsum.* Postscapular shield 75 long, completely covered with 5–6 transverse lines, similar to those in female. Hysteronotal shield about 154 long, covered with transverse lines extending from the anterior margin to level of setae *d3*. Lateral margins of hysteronotal shield at level of setae *l3* poorly distinct, and therefore lateral incisions not visible. Setae *l3* situated off hysteronotal shield, soft cuticle behind these setae usually with numerous, more 30, scales. Setae *l5* about 90 long. *Venter.* Striated membranes of coxae II as in female. Coxae III with a transverse line. Postgenital shield in an inverted U, its projections 70–75 long, distance between these projections at level of setae *gp* 30–35. Distance between postgenital shield and the postanal sclerite about 2.6–2.8× shorter than the projections of postgenital shield, 25–30. Legs III and IV 115 and 130 long, respectively. Tibiotarsi III and IV subequal 40 long. Solenidia *phi* of legs III and IV 15 and 50 long, respectively.

Remarks

This species was briefly described from *R. everetti* in the Philippines (Fain 1976). Later on, Fain (1981) described in detail and depicted this species.

Listrophoroides (Marquesania) lativentris Fain

(Figs 44–47)

Listrophoroides (Marquesania) lativentris Fain, 1981: 108–111, figs 141–144.

Material examined

Holotype. ♂ from *Sundamys muelleri* (Jentink) (BMNH 75.1348–1349): Malaysia: Trengganu (BMNH).
Paratypes (all in IRSNB). 1♂, same data as holotype; 3♀ from *S. muelleri*, Combak Forest, 15.v.1979, 1♀ from *S. muelleri*, Selangor, Bukit Lanjar, 7.v.1979.

Diagnosis

Female. Postscapular shield with a few straight short lines, situated in disorder, hysteronotal shield with 8–9 furrows, extending from the anterior margin to level of setae *d3*, distance *d3–d3* 1.5–1.7× longer than distance between *d3* and posterior margin of hysteronotal shield.
Male. Postscapular shield with a few short straight lines in lateral parts, hysteronotal shield without ornamentation, incisions of hysteronotal shield well developed, scales behind setae *l3* lacking.

Description

Female (Figs 44, 45)

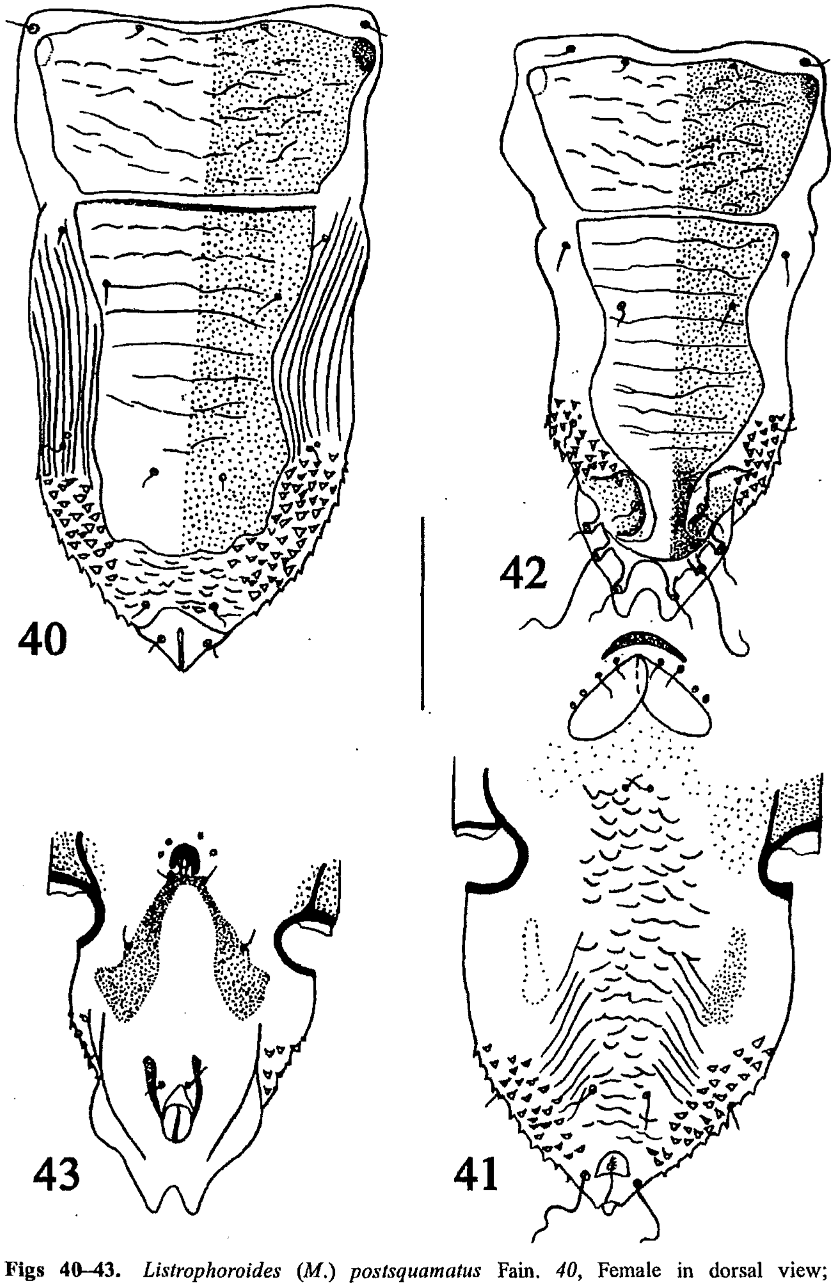
Body 375–415 long and 165–200 wide. *Dorsum.* Postscapular shield 85 long, covered with a few short straight lines, situated in disorder. Hysteronotal shield 165 long, covered with 9–10 straight transverse lines extending from the anterior margin to level of setae *d3*, 1–3 posterior lines short. Width of this shield at level of setae *d2* and at level of setae *d3* subequal 85–90. Distance *d3–d3* 40–45, 1.5–1.7× longer than distance between *d3* and posterior margin of hysteronotal shield, 25–35. *Venter.* Striated membranes of coxae II wide. Coxae III without lines. Opisthosoma 140 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma with widely rounded scales spreading from level of setae *gp* to level of setae *ae*. Legs III and IV about 130 long. Solenidia *phi* of legs III and IV 15 and 3 long, respectively.

Male (holotype, Figs 46, 47)

Body 320 long (335–340) and 160 wide (160–165). *Dorsum.* Postscapular shield 70 long, covered with a few straight short lines in lateral parts. Hysteronotal shield about 130 long, devoid of ornamentation. Incisions of hysteronotal shield 35–40 long and 30–35 wide. Their minimal distance between each other 50–55. Setae *l3* situated off hysteronotal shield, soft cuticle behind these setae without scales. Setae *d3* situated on hysteronotal shield, distance *d3–d3* 30–35, 1.6–1.7× shorter than minimal distance between incisions of hysteronotal shield. Setae *l5* about 50 long. *Venter.* Striated membranes of coxae II as in female. Coxae III without lines. Postgenital shield in an inverted U, its projections about 65 long, distance between these projections at level of setae *gp* 25. Distance between postgenital shield and the postanal sclerite about 2.6–2.9× shorter than the projections of postgenital shield, 20–25. Legs III and IV 115 and 130 long, respectively. Tibio-tarsi III and IV subequal 40 long. Solenidia *phi* of legs III and IV 10 and 25 long, respectively.

Remarks

This species was described from *S. muelleri* in Malaysia (Fain 1981).



Figs 40–43. *Listrophoroides* (*M.*) *postsquamatus* Fain. *40*, Female in dorsal view; *41*, opisthosoma of female in ventral view; *42*, male in dorsal view; *43*, opisthosoma of male in ventral view. Scale bar = 0.1 mm.

Listrophoroides (Marquesania) sculpturatus Fain, Nadchatram & Lukoschus

(Figs 48–51)

Listrophoroides (*Marquesania*) *sculpturatus* Fain, Nadchatram & Lukoschus, 1981. – Fain, 1981: 111–114, figs 145–148.

Material examined

Holotype. ♂ from *S. muelleri*: Malaysia: near the road Kuala-Lumpur-Selangor (35 km), 28.v.1979, coll. M. Nadchatram (BMNH).

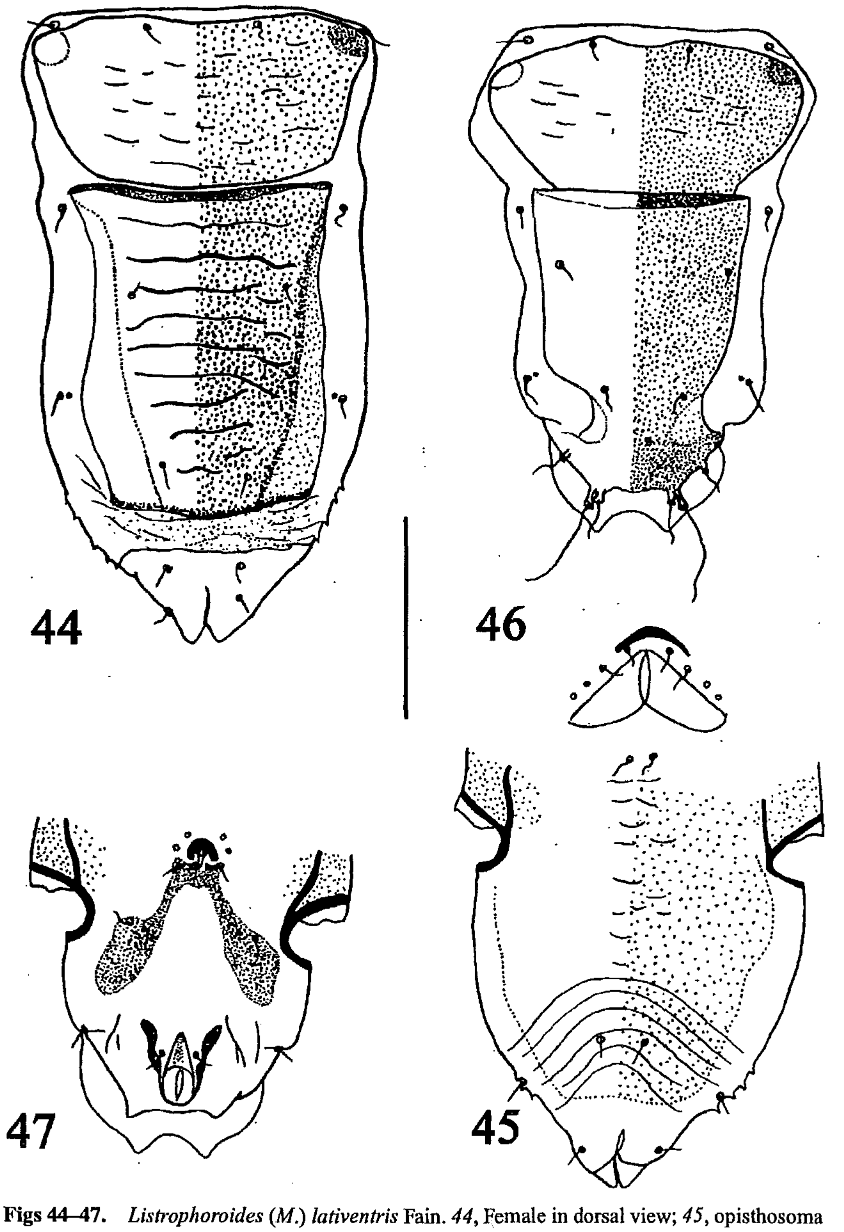
Paratype. ♀, same as holotype.

Non-type specimens. **The Philippines:** 1 ♀ from *Maxomys rajah* (Thomas) (BMNH 94.7.2.66), Palawan (IRSNB).

Diagnosis

Female. Postscapular shield with strong curved lines in lateral parts and five poorly distinct transverse lines in median part, hysteronotal shield with 7–8-transverse lines, curved in their lateral parts, this ornamentation does not reach level of setae *d3*, distance *d3–d3* 1.5× longer than distance *d3* and posterior margin of hysteronotal shield, opisthogaster without median scales.

Male. Postscapular shield with same ornamentation as in female, hysteronotal shield without ornamentation, incisions of hysteronotal shield small, scales behind setae *l3* lacking.



Figs 44–47. *Listrophoroides* (*M.*) *lativentris* Fain. *44*, Female in dorsal view; *45*, opisthosoma of female in ventral view; *46*, male in dorsal view; *47*, opisthosoma of male in ventral view. Scale bar = 0.1 mm.

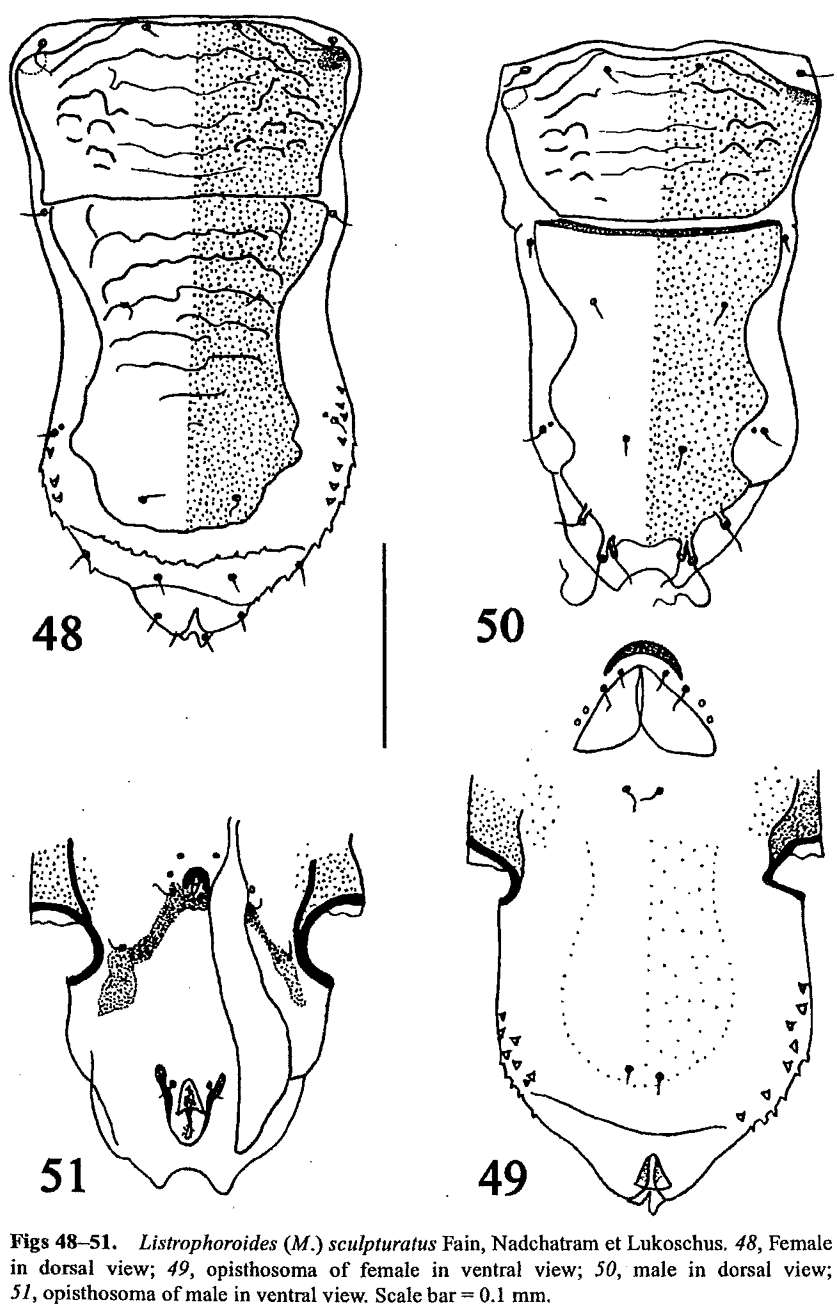
Description (based on type series)

Female (Figs 48, 49)

Body 385–400 long and 155–170 wide. *Dorsum*. Postscapular shield 85 long, covered with strong ornamentation (curved lines) in its lateral parts and five poorly distinct transverse lines in median part. Hysteronotal shield 165 long, covered with 7–8-transverse lines, curved in their lateral parts, this ornamentation not reach level of setae *d3*. Width of this shield at level of setae *d2* and at level of setae *d3* subequal, 85–90. Distance *d3*–*d3* about 40, 1.5× longer than distance between *d3* and posterior margin of hysteronotal shield, 25–28. *Venter*. Striated membranes of coxae II wide. Coxae III with a strong transverse line. Opisthosoma 150 long. Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma without scales. Opisthogastric shield poorly sclerotised. Legs III and IV about 130 long. Solenidia *phi* of legs III and IV 10 and 3 long, respectively.

Male (holotype, Figs 50, 51)

Body 325 long and 155 wide. *Dorsum*. Postscapular shield 85 long, ornamented as in female. Hysteronotal shield about



Figs 48–51. *Listrophoroides* (*M.*) *sculpturatus* Fain, Nadchatram et Lukoschus. *48*, Female in dorsal view; *49*, opisthosoma of female in ventral view; *50*, male in dorsal view; *51*, opisthosoma of male in ventral view. Scale bar = 0.1 mm.

165 long, devoid of ornamentation. Incisions of hysteronotal shield 30 long and 15 wide. Their minimal distance between each other 75. Setae *l3* situated off hysteronotal shield, soft cuticle behind these setae without scales. Setae *d3* situated on hysteronotal shield, distance *d3–d3* 25, 3× shorter than minimal distance between incisions of hysteronotal shield. Setae *l5* 40 long. *Venter.* Striated membranes of coxae II as in female. Coxae III with a strong transverse line. Postgenital shield in an inverted U, its projections 65 long. Distance between postgenital shield and the postanal sclerite 2× shorter than the projections of postgenital shield, 30. Legs III and IV 115 and 130 long, respectively. Tibio-tarsi III and IV subequal 40 long. Solenidia *phi* of legs III and IV 15 and 35 long, respectively.

Remarks

This species was described from *S. muelleri* in Malaysia (type series) and from *M. rajah* in the Philippines by Fain, Nadchatram and Lukoschus in monograph of Fain (1981).

Listrophoroides (Marquesania) dominator Fain, comb. nov.

(Figs 52–56)

Listrophoroides (Listrophoroides) dominator Fain, 1981: 83–85, figs 101–104.
Listrophoroides (Listrophoroides) compactus, Fain, 1981: 85–86, fig. 105, **syn. nov.**

Material examined

Holotype. ♂ from *Paruromys dominator* (Thomas) (BMHN 12.4.12.4): N. Celebes: Menado (BMNH).

Paratypes. 5♂, 13♀, same data as holotype (IRSNB).

Non-type specimens. Type series of *L. compactus*: ♂ holotype (BMNH), 4♂ and 5♀ paratypes (IRSNB) from *R. xanthurus* (BMHN 12.4.12.4)), N. Celebes: Menado.

Diagnosis

Process of genu I weakly developed, clasping membranes of coxae II reaching the lateral margins of the body only in their anterior half.

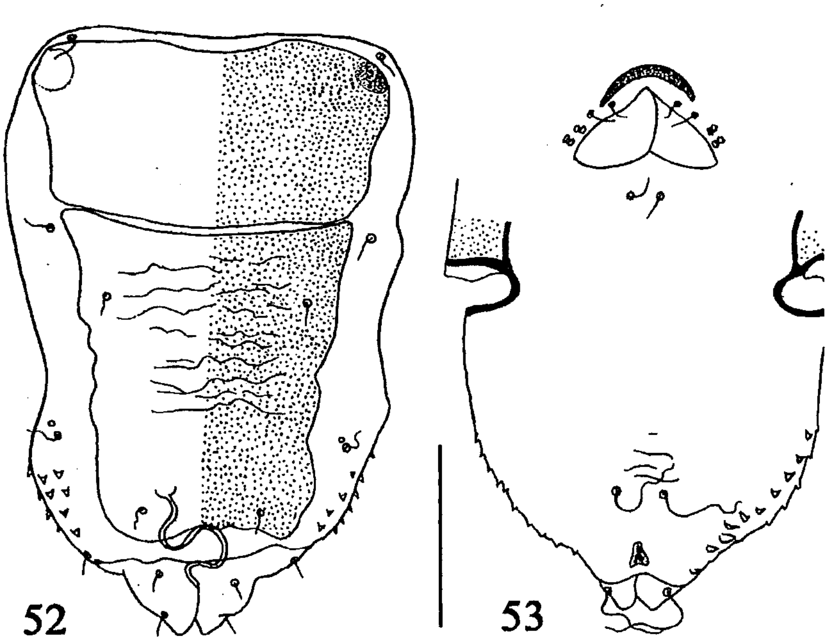
Female. Postscapular shield without ornamentation, hysteronotal shield with poorly distinct ornamentation, distance *d3–d3* 4× longer than distance between *d3* and posterior margin of hysteronotal shield, setae *ae* and *ai* longer than other opisthosomal setae.

Male. Dorsal shields without ornamentation, incisions of hysteronotal shield well developed, scales behind setae *l3* lacking.

Description (based on type series)

Female (Figs 52, 53)

Body 400–430 long and 195–220 wide. *Dorsum.* Postscapular shield 90 long, without ornamentation. Hysteronotal shield 165 long, covered with poorly distinct ornamentation, this ornamentation not reach level of setae *d3*. Width of this shield at level of setae *d2* 125–130 and at level of setae *d3* 100–105. Distance *d3–d3* about 60, 4× longer than distance between *d3* and posterior margin of hysteronotal shield, about 15. *Venter.* Striated membranes of coxae II reaching the lateral margins of the body only in their anterior half. Coxae III without lines. Opisthosoma 155 long.



Figs 52–53. *Listrophoroides (M.) dominator* Fain, comb. nov., female. *52*, Dorsal view; *53*, opisthosoma in ventral view. Scale bar = 0.1 mm.

Lateral parts of opisthosoma covered with numerous scales. Median part of opisthosoma without scales. Opisthogastric shield very poorly sclerotised, variable in shape, without distinct margins. Legs III and IV about 155 long. Solenidia *phi* of legs III and IV 15 and 8 long, respectively.

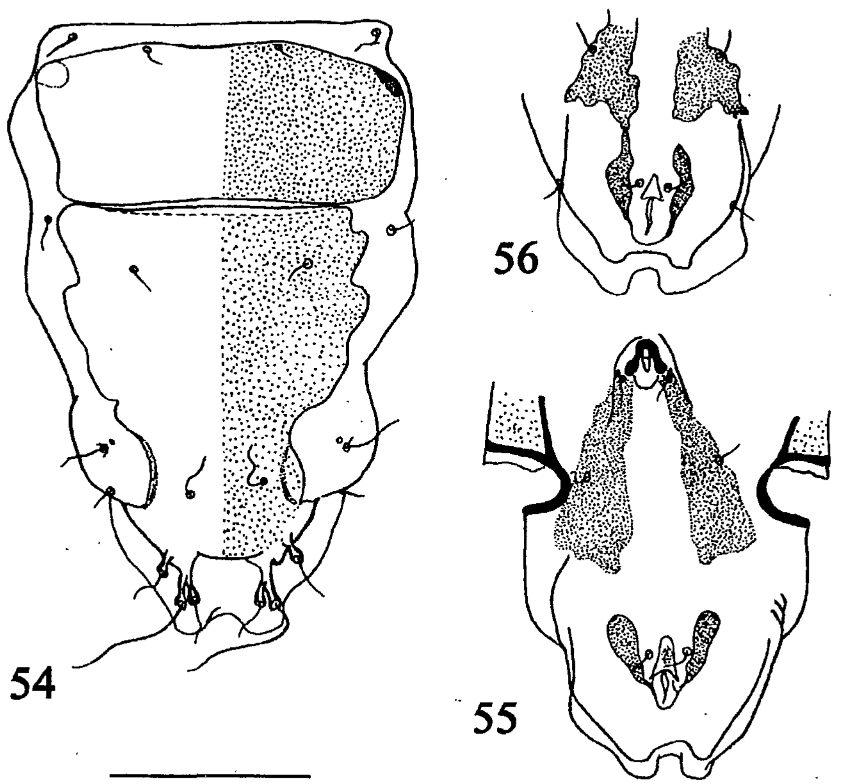
Male (holotype, Figs 54–56)

Body 370 long (370–415) and 195 wide (190–200). *Dorsum*. Dorsal shields without ornamentation. Postscapular shield 80 long. Hysteronotal shield about 190 long. Incisions of hysteronotal shield 40–50 long and 35–40 wide. Their minimal distance between each other about 65. Setae *l3* situated off hysteronotal shield, soft cuticle behind these setae without scales. Setae *d3* situated on hysteronotal shield, distance *d3–d3* about 35, 1.8× shorter than minimal distance between incisions of hysteronotal shield. Setae *l5* 65 long. *Venter*. Striated membranes of coxae II as in female. Coxae III without lines. Postgenital shield in an inverted U, its projections 90–100 long, distance between these projections at level of setae *gm* 20–25. Distance between postgenital shield and the postanal sclerite 5–6× shorter than the projections of postgenital shield, 15–20. Legs III and IV 110 and 125 long, respectively. Tibio-tarsi III and IV subequal 50 long. Process of genu I poorly developed. Solenidia *phi* of legs III and IV 15 and 40 long, respectively.

Remarks

This species has been described within the subgenus *Listrophoroides* s. str. from *Paruromys dominator* in N. Celebes (Fain 1981). However, the clasping membranes of coxae II in *L. dominator* are well developed as in the other species of the subgenus *Marquesania*, moreover the genua I of this species have the process. These processes are lacking in all the other species of the nominative subgenus but are characteristic of the latter subgenus. Therefore, we here transfer this species into the subgenus *Marquesania*.

The species *Listrophoroides compactus* Fain was described from the same locality as *L. dominator* but from another host, *R. xanthurus* (Fain 1981). According to Fain (1981), there is only a single difference between these species: the projections of the postgenital shield, which are fused with the anal sclerite in *L. compactus*. However, in some males from the type series these projections are separated from the anal sclerite, and hence, this character is variable. All the other characters, including measurements, are similar in these two species. We consider, therefore that *L. compactus*, syn. nov. is a junior synonym of *L. dominator*.



Figs 54–56. *Listrophoroides (M.) dominator* Fain, comb. nov., male. *54*, Dorsal view; *55*, opisthosoma in ventral view (specimen from *Paruromys dominator*), *56*, same species (specimen from *Rattus xanthurus*). Scale bar = 0.1 mm.

Key to the females of the subgenus *Marquesania*

1. Setae *ai* short, not longer than other opisthogastric setae, excluding *ae* 3
   Setae *ai* 35–50 long, more than 2× longer than other opisthogastric setae 2
2. Process of genu I poorly developed. Postscapular shield without ornamentation. Hysteronotal shield with poorly distinct ornamentation. Clasping membranes of coxae II reaching the lateral margins of the body only in their anterior half. Coxae III without lines. Opisthogastric poorly sclerotised and without scales in median part. Setae *ae* as long as *ai*. . . . . *L. dominator* Fain, comb. nov. (Figs 52, 53)
   Process of genu I well developed. Postscapular shield with ornamentation. Hysteronotal shield covered with well developed transverse furrows. Clasping membranes of coxae II reaching the lateral margins of the body along their entire lengths. Coxae III with a transverse line. Opisthogastric well sclerotised, with scales in its median part. Setae *ae* 2× shorter than *ai* . . . . *L. postsquamatus* Fain (Figs 40, 41)
3. Postscapular shield clearly ornamented 5
   Postscapular shield without ornamentation or with very poorly distinct ornamentation. 4
4. Ornamentation of postscapular shield completely lacking. . . . . *L. australiae* Fain (Figs 36, 37)
   Ornamentation of postscapular shield present, but very poorly distinct. . . . . . *L. queenslandicus* (Womersley) (Figs 32, 33)
5. Postscapular shield covered with dense crenel-like pattern, hysteronotal shield covered in anterior third with numerous short longitudinal lines connected with transverse furrows . . . . *L. crenatus* Fain, 1975 stat. nov. (Figs 20, 21)
   Dorsal shields covered with another pattern. 6
6. Distance *d3–d3* 1.5–4× longer than distance between *d3* and posterior margin of hysteronotal shield. 10
   Distances *d3–d3* and *d3*–posterior margin of hysteronotal shield subequal 7
7. Body 430–500 long, postscapular shield covered only with short and curved lines 8
   Body 345–430 long, postscapular shield covered with transverse, sometimes interrupted, lines 9
8. Postscapular shield covered with a dense ornamentation, hysteronotal shield with well developed furrows behind level of setae *d3* . . . . *L. papuanus* Fain (Figs 7, 8)
   Postscapular shield covered with poorly developed ornamentation, hysteronotal shield either with or without a poor ornamentation behind level of setae *d3* . . . . *L. mordax*, sp. nov. (Figs 18, 19)
9. Postscapular shield covered with deep and almost uninterrupted transverse furrows. Transverse furrows of hysteronotal shield curved in their lateral parts. First anterior line of hysteronotal shield connected with anterior margin by a pair of short longitudinal lateral furrows . . . . *L. melomys*, sp. nov. (Figs 28, 29)
   Postscapular shield covered with superficial and interrupted transverse lines. Hysteronotal shield with only straight transverse furrows. . . .*L. cucullatus* (Trouessart) (Figs 1–4)
10. Genu I with process. Median part of postscapular shield with ornamentation. Body length 375–415 11
    Genu I without process. Median part of postscapular shield without ornamentation. Body length 490–500 . . . . *L. obliquelineatus* Fain, comb. nov. (Figs 11–13)
11. Postscapular shield covered with uniform pattern of straight lines, sometimes poorly visible or short, hysteronotal shield covered with ornamentation from anterior margin to level of setae *d3* 12
    Postscapular shield covered with strong curved lines in lateral parts and with poorly distinct transverse lines in median part, ornamentation of hysteronotal shield not reach far level of setae *d3* . . . *L. sculpturatus* Fain, Nadchatram & Lukoschus . . . . (Figs 48, 49)
12. Postscapular shield covered with six interrupted transverse lines. Distances *d3–d3* 1.8–2.5× longer than distance between *d3* and posterior margin of hysteronotal shield. Coxae III without lines. Opisthogaster poorly sclerotised. . . . .*L. lativentris* Fain (Figs 44, 45)
    Postscapular shield covered with a few separate short lines. Distances *d3–d3* 1.5–1.7× longer than distance between *d3* and posterior margin of hysteronotal shield. Coxae III with a transverse line. Opisthogaster normally sclerotised. . . . . *L. interpolatus* Fain, stat. nov. (Figs 24, 25)

Key to the males of the subgenus *Marquesania*

1. Soft cuticle of hysteronotum behind setae *l3* without scales or with a few scales (less than 10) 2
   Soft cuticle of hysteronotum behind setae *l3* with numerous scales (more 30). . . . . . *L. postsquamatus* Fain (Figs 42, 43)
2. Incisions of hysteronotal shield well developed. Distance *d3–d3* subequal or 1.1–1.4× shorter then minimal distance between these incisions 6
   Incisions of hysteronotal shield poorly developed. Distance *d3–d3* 1.6–2× shorter than minimal distance between these incisions 3
3. Ornamentation of postscapular shield not crenel like. Scales behind setae *l3* lacking. 4
   Ornamentation of postscapular shield crenel-like. Scales behind setae *l3* present. . . . *L. crenatus* Fain, stat. nov. (Figs 22, 23)
4. Postscapular shield with ornamentation in median part. Body length 325–350 5
   Postscapular shield without ornamentation in median part. Body length 410–470 . . . . . *L. obliquelineatus* Fain (Figs 14, 15)
5. Postscapular shield covered with strong curved lines in its lateral parts and with poorly distinct transverse lines in median part. Hysteronotal shield without ornamentation. . . . . *L. sculpturatus* Fain, Nadchatram & Lukoschus . . . . (Figs 50, 51)
   Postscapular shield covered with uniform ornamentation (strong transverse furrows). Hysterosomal shield with ornamentation . . . .*L. melomys*, sp. nov. (Figs 30, 31)
6. Median sclerotised band of postgenital shield not developed. 7
   Median sclerotised band of postgenital shield well developed, 25–35 long . . . . *L. cucullatus* (Trouessart) (Figs 5, 6)
7. Postscapular shield covered with strong ornamentation. 11
   Postscapular shield without or with poorly distinct ornamentation 8
8. Ornamentation of dorsal shields present 9
   Ornamentation of dorsal shields completely lacking 10
9. Scales behind setae *l3* present. Body length 390–415. . . . . *L. queenslandicus* (Womersley) (Figs 34, 35)
   Scales behind setae *l3* lacking. Body length 320–340 . . . . *L. lativentris* Fain (Figs 46, 47)
10. Scales behind setae *l3* present. . . . . *L. australiae* Fain (Figs 38, 39)
    Scales behind setae *l3* lacking. . *L. dominator* Fain, comb. nov. . . . . (Figs 54–56)
11. Dorsal shields covered with ornamentation only in anterior third . . . .*L. mordax*, sp. nov. (Figs 18, 19)
    Dorsal shields completely ornamented 12

12. Postscapular shield covered with short curved lines. Scales behind setae *l3* absent. Postgenital shield in an inverted U. Body length 400–480 ...... *L. papuanus* Fain (Figs 9, 10)
Postscapular shield covered with transverse interrupted lines. Scales behind setae *l3* present. Postgenital shield in an inverted V. Body length 345–380 .... *L. interpolatus* Fain, stat. nov. (Figs 26, 27)

Results of the cladistic analysis

The initial parsimony analysis produced 82 equally parsimonious trees (tree length = 34, consistency index (*CI*), excluding uninformative characters = 0.5926, homoplasy index (*HI*), excluding uninformative characters = 0.4074, retention index (*RI*) = 0.7027 and rescaled consistency index (*RC*) = 0.4754). The strict consensus of these trees (Fig. 57) supports the monophyly of the subgenus *Marquesania*. The node joining all species of this subgenus is marked by the eight synapomorphies: 2 (process of genu I present), ♂ (coxal membranes II reaching the lateral borders of the body), 5 (furrow of coxae III present), 7 (ornamentation of hysteronotal shield present in male), 8 (lateral incisions of hysteronotal shield present in male), 13 (genital shield with very deep median incision in male), 15 (anal shield present in male) and 17.2 (opisthogaster of female well sclerotised, with lateral bands). Within the the *Marquesania* clade, the *L. cucullatus* and *L. interpolatus* are sister species, while the other ones form an unresolved polytomy. The node joining these two species is supported by two male characters: 10 (scales behind setae *l3* present) and 14 (genital shield shape as inverted U). Among the characters chosen for the analysis, 2, 4, 5, 7 and 9 undergo reversion in different species, and six characters (5, 7, 9, 10, 11, 16) have the *CI* indices less than 0.5.

Successive weighting showed that the weight of the character 12 (setae *ai* longer than other hysterosomal setae in female) is 0, and the weights of four characters 9 (lateral incisions of hysteronotal shield well developed in male), 10 (scales behind setae *l3* present in male), 11 (distance *d3*–*d3* longer than distance between *d3* and posterior margin of hysteronotal shield in female) and 16 (minimal observed body length more than 450 μm in female and 410 μm in male) are 0.375, 0.417, 0.5 and 0.375 respectively. The weight of all the other characters is 1. The search after re-weighting yielded only six most parsimonious trees (tree length = 24.45833, *CI* = 0.6969, *HI* = 0.3031, *RI* = 0.7925 and *RC* = 0.6210. The structure of the strict consensus for the re-weighted trees (Fig. 58) allows us to recognise the same general pattern as in the initial analysis. It should be noted that the most of the Oriental species, such as *L. lativentris*, *L. sculpturatus* and *L. dominator* are at base of the *Marquesania* cluster.

The small set of characters explains the relatively weak support of most branches by the Bootstrap analysis. However, the node marking the *Marquesania* cluster has 100% support and the node joining the species *L. cucullatus* and *L. interpolatus* has 67% support. The PTP test showed

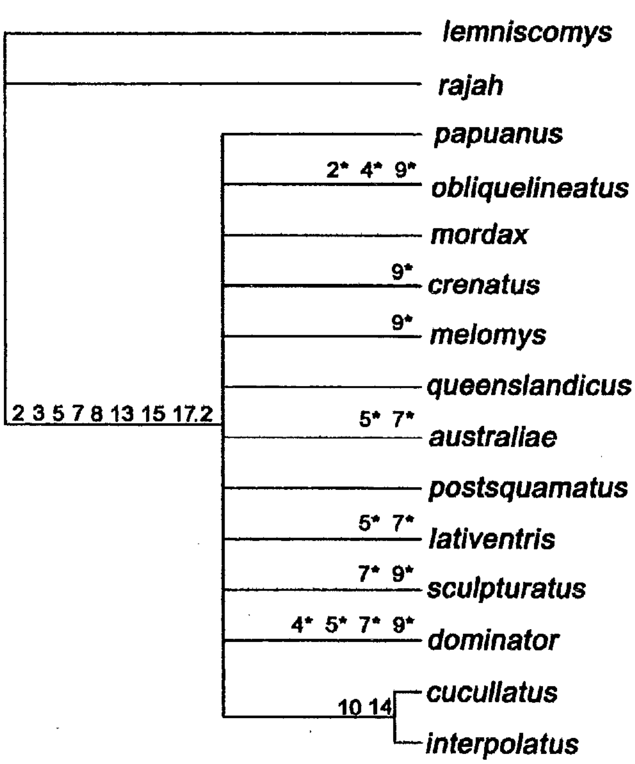


Fig. 57. Strict consensus of 82 equally parsimonious trees (tree length = 34, *CI* = 0.5926, *HI* = 0.4074, *RI* = 0.7027 and *RC* = 0.4754). All characters are unordered and not weighted. *, Reversion.

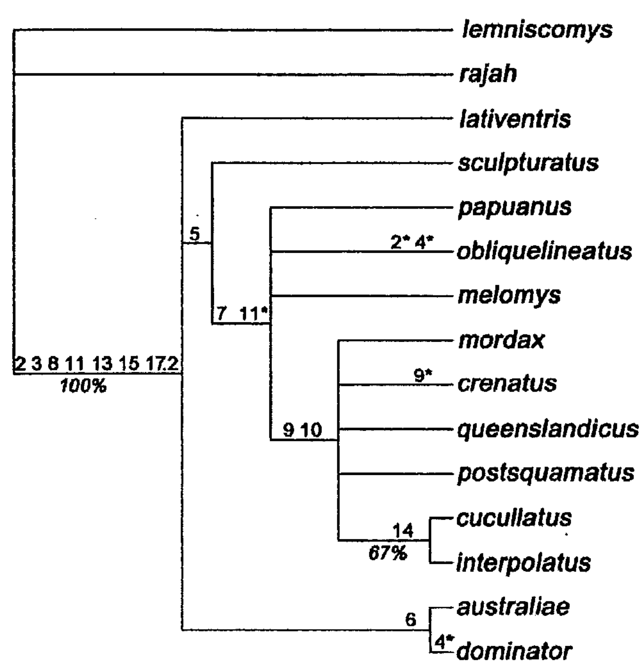


Fig. 58. Strict consensus of six equally parsimonious trees (tree length = 24.45833, *CI* = 0.6969, *HI* = 0.3031, *RI* = 0.7925 and *RC* = 0.6210). All characters are unordered and re-weighted according to *RC* index. *, Reversion; %, bootstrap value.

that the null hypothesis (absence of the cladistic covariation) could be rejected at the high significant level ($P < 0.001$).

Discussion

Pilicolous specialisation has induced a strong specificity in mites, especially in Listrophoroidea (Astigmata) (Fain 1994). This high specificity may be explained, at least in part, by the mode of life of these mites, which are permanent parasites and achieve their entire development on the same host. However, atopomelid species, and especially *Listrophoroides*, are generally more oligoxenous than monoxenous in their host range and they are regularly encountered on several closely allied hosts. Specificity and host-parasite parallel-evolution in Atopomelidae are well marked at the generic level. Most of the genera of this family are associated with a well-defined taxonomical group of hosts (Fain 1981; Fain and Hyland 1985). The subgenus *Marquesania* is restricted to Murinae from the Oriental, New Guinean and Australian regions with the exception of the two cosmopolitan host species *R. rattus* and *R. norvegicus* (see Table 3). The records of these mites from Gerbillinae (Domrow 1958) or marsupials (Fain and Lukoschus 1981) were probably accidental and could be explained by mechanical contamination during collecting in the field or by contaminations in the museums where the rats are housed. Furthermore, atopomelids are well-sclerotised mites and like some other ectoparasites, e.g. feather mites (Acari: Astigmata) (Vasyukova and Mironov 1990) may be able to

Table 3. Distribution of species of the subgenus *Marquesania* on hosts (Rodentia: Muridae)

Mite species	Host species	Locality
L. (M.) cucullatus (Trouessart)	**Rattus norvegicus*	Cosmopolitan
	Rattus rattus	"
	Rattus tanezumi	Hong Kong, Labuan, Borneo
	Rattus hoffmanni	Indonesia
	Rattus xanthurus	Celebes
	Bunomys coelestes	"
	Rattus annandalei	Malaysia
	Rattus argentiventer	"
	Rattus tiomanicus	"
	Rattus mindorensis	The Philippines
	Apomys insignis	"
	Rattus exulans	The Philippines, New Guinea
	Melomys sp.	New Guinea
	Stenomys niobe	"
L. (M.) papuanus Fain	**Conilurus penicillatus*	Australia
	Pseudomys nanus	"
L. (M.) obliquelineatus Fain, comb. nov.	**Rattus* sp.	New Guinea
	Rattus leucopus	Australia, New Guinea
L. (M.) mordax, sp. nov.	**Rattus mordax*	New Guinea
	R. leucopus	"
L. (M.) crenatus Fain, stat. nov.	**?Rattus ruber*	New Guinea
	Melomys rufescens	"
	Melomys moncktoni	"
L. (M.) interpolatus Fain, stat. nov.	**Stenomys niobe*	New Guinea
	Stenomys verecundus	"
	Melomys moncktoni	"
L. (M.) melomys, sp. nov.	**Melomys moncktoni*	New Guinea
L. (M.) queenslandicus (Womersley)	**Rattus sordidus*	Australia
	Rattus fuscipes	"
	Rattus villosissimus	"
	Rattus tunneyi	"
	Rattus leucopus	New Guinea
L. (M.) australiae Fain	*Rattus lutreolus*	Australia
	Rattus fuscipes	"
L. (M.) postsquamatus Fain	**Rattus everetti*	The Philippines
L. (M.) lativentris Fain	**Sundamys muelleri*	Malaysia
L. (M.) sculpturatus Fain, Nadchatram & Lukoschus	**Sundamys muelleri*	Malaysia
	Maxomys rajah	The Philippines
L. (M.) dominator Fain	**Paruromys dominator*	N. Celebes
	Rattus xanthurus	"

*, Type host

survive in the absence of their host for several days or weeks. During this time, the mites could have an opportunity to attach to another, sometimes atypical, host.

The mites of the subgenus *Marquesania* are represented in the Oriental region (five mite species were recorded from 16 species of rats) as well as in Australian–New Guinean region (nine species were recorded from 16 species of rats) (Table 3). As for the origin and historical distribution of hosts of the subgenus *Marquesania*, the assumption that Australian and New Guinean rats are the descendants of the Oriental rats is well accepted now (Watts 1983). Therefore, we think that the subgenus *Marquesania* originated on the ancestors of these rats in the Oriental region, before they migrated to the Australia-New Guinean region. This hypothesis is supported also by the cladistic analysis because most Oriental species are at the base of the *Marquesania* clade (Fig. 58). A polyphyletic origin for the Australian–New Guinean and Oriental species of *Marquesania* is groundless, since the monophyly of this subgenus is strongly supported by the cladistic analysis.

Among the Australian–New Guinean species, *L. papuanus* and *L. melomys* are associated with rats of the endemic genera, *Conilurus* Ogilby, *Pseudomys* Gray and *Melomys* Thomas. These mites are probably descendants from the first migration wave of murids to Australia. *L. interpolatus* is a parasite of rats of the genera *Stenomys* Thomas and *Melomys* in New Guinea. The genus *Stenomys* is also represented in Indonesia by one species, *Stenomys ceramicus* (Thomas). Therefore it is possible that *L. interpolatus* will be also found there. Other mites in Australia and New Guinea, i.e. *L. queenslandicus*, *L. australiae*, *L. crenatus*, *L. obliquelineatus* and *L. mordax*, are mostly associated with representatives of the genus *Rattus*, which penetrated into this region later (Watts 1983). The presence of these species on the hosts of the endemic genera, *Melomys* or *Stenomys*, is, probably, secondary. That was probably also the case for *L. cucullatus*, a species associated not only with the cosmopolitan species *R. norvegicus* and *R. rattus*, but also widely represented on other *Rattus* in the Oriental region. In New Guinea, *L. cucullatus* parasitises *R. exulans*, a species that is present in both the Oriental and New Guinean regions, and it could thus be transmitted to the representatives of the genera *Stenomys* and *Melomys*. Two other species of *Marquesania*, *L. crenatus* and *L. queenslandicus* are represented in Australia and New Guinea and associated with *R. leucopus*. This host and *R. sordidus* are the only two native *Rattus* occurring in both regions.

Thus, the descendants of the first wave of migrants, such as *L. papuanus*, *L. melomys* and *L. interpolatus*, are limited in their host distribution by few representatives of endemic Australian and New Guinean genera. These endemic rat genera diverged from the common murid stock a long time ago and mites inhabiting them were apparently unable to migrate to representatives of the genus *Rattus* because of their high specialisation to the hosts. In contrast, the other species of the subgenus that parasitise *Rattus* spp., such as *L. cucullatus*, *L. obliquelineatus*, *L. mordax*, *L. crenator*, *L. queenslandicus* and *L. australiae*, occupy a relatively wide range of closely allied hosts and sometimes they, apparently more ecologically plastic than migrants of the first wave, have been transmitted to the representatives of the endemic genera.

Unfortunately, it is impossible now to group the species of *Marquesania* according to their geographical distribution since the means of development of the *Marquesania* faunas in the Australian and New Guinean regions are noticeably complicated, reflecting the difficult settling history of their hosts (Watts 1983).

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