

Cladistic analysis of Malagasy pholcid spiders reveals generic level endemism: Revision of *Zatavua* n. gen. and *Paramicromerys* Millot (Pholcidae, Araneae)

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The six-eyed pholcid spiders of Madagascar are revised. Two genera are recognized: (1) *Paramicromerys* Millot, 1946, with 14 species described, 11 of them new, two transferred from *Spermophora*; (2) *Zatavua* n. gen., with 17 species described, 10 of them new, seven transferred from *Spermophora*. Both genera are widely distributed in Madagascar and are absent in large collections of East African and Comoran pholcids, suggesting that they are both endemic. A data matrix with 53 characters and 64 taxa (including 19 Malagasy species and 19 additional *Spermophora* and ‘*Spermophora*-like’ species) is cladistically analysed. Two conclusions are supported both by analyses using equally weighted characters and by two differential weighting schemes: (1) Malagasy taxa are not closely related to, and certainly not congeneric with, ‘true’ *Spermophora*; and (2), the island is inhabited by two taxa that are not closely related to each other and certainly not congeneric. Rather than that, *Zatavua* is seen as the sister clade of all other pholcines, whereas *Paramicromerys* is more distal and more closely related to (currently misplaced) ‘*Spermophora*’ species from East Africa and the Comoros. Two additional Malagasy species are described that are tentatively assigned to *Spermophora*. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, 137, 261–318.

ADDITIONAL KEYWORDS: Madagascar – *Spermophora*.

INTRODUCTION

When Nicolas Hentz created the genus *Spermophora* in 1841, it was to accommodate a single species that was unusual for having only six eyes and that Dugès had therefore named *Pholcus sexoculatus* five years earlier (Dugès, 1836). This species was also the smallest pholcid then known, and this combination of small size and six eyes was to become the primary criterion for assigning new species to *Spermophora*. Several new genera of small, six-eyed pholcids have been created since, but *Spermophora* continues as a wastebasket of widely distributed and widely disparate taxa (Huber, 2001). It was in this tradition that Millot (1946), in his revision of Malagasy pholcids, assigned most new species to *Spermophora*. This view, which suggests low endemism of Malagasy pholcids on a generic level, has never been challenged.

With 36 nominal species, *Spermophora* is currently only the sixth largest of 69 genera in Pholcidae, but it

is probably the most chaotic one taxonomically. This is especially true when considering its relationships with other genera and its distinction from genera with similar-looking representatives. The present paper is the first in a projected series dealing with this situation. Even though only Malagasy species are treated, this paper rests on the study of ‘*Spermophora*-like’ spiders from all over the world. This larger framework is not restricted to the inclusion of several non-Malagasy taxa in the cladistic analysis but is founded on a detailed investigation of about 100 additional species that will be treated in upcoming revisions of *Spermophora* and its potential relatives.

The history of pholcid taxonomy dealing with Malagasy taxa relevant in the present context is short and quickly outlined. It is essentially reflected in only three publications: Simon (1893) and Fage (1945) described a single species each, *Micromerys madagascariensis* and *Spermophora madagascariensis*. Millot (1946) added eight new *Spermophora* species, and transferred *Micromerys madagascariensis* Simon to the newly created genus *Paramicromerys*. A few other pholcids have been recorded from Madagascar, but

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these are evidently not relevant in this context. Most of them are widespread synanthropic species [*Artema atlanta* Walckenaer, 1837; *Crossopriza lyoni* (Blackwell, 1867); *Smeringopus pallidus* (Blackwell, 1858); *Micropholcus fauroti* (Simon, 1887); records in Strand, 1915, and Millot, 1946], others are apparently endemic species of widespread Old World genera (*Leptopholcus sakalavensis* Millot, 1946; *Smeringopus madagascariensis* Millot, 1946; *Pholcus lambertoni* Millot, 1946; *Crossopriza nigrescens* Millot, 1946). In the half century since Millot's paper, some names have been synonymized, but nothing has been added. The present paper adds 23 new species, more than doubling the number of known species to 41.

MATERIALS AND METHODS

This work is based primarily on material collected between 1992 and 1998 by Charles Griswold and colleagues and deposited in the California Academy of Sciences. However, pholcids resembling *Spermophora* were borrowed from more than 40 institutions and individuals, and the list below covers only those with material actually used in the present paper.

AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; CLD, Collection C. L. Deeleman-Reinhold, deposited in the National Museum of Natural History, Leiden; IES, Instituto de Ecología y Sistemática, La Habana; MCN, Museu de Ciências Naturais, Porto Alegre, Rio Grande do Sul; MCZ, Museum of Comparative Zoology, Cambridge; MHNG, Muséum d'Histoire Naturelle, Genève; MNHN, Muséum National d'Histoire Naturelle, Paris; MRAC, Africa Museum, Tervuren; NCP, National Collection, Pretoria; QMB, Queensland Museum, Brisbane; UCR, Universidad de Costa Rica, San José; USNM, National Museum of Natural History, Washington, D. C.; WAM, Western Australian Museum, Perth; ZFMK, Zoological Research Institute and Museum Alexander Koenig, Bonn; ZMUC Zoological Museum, Copenhagen.

Methods and terminology are as in Huber (2000). Measurements are in mm (± 0.02 mm) unless otherwise noted. Eye measurements are ± 5 μ m. Drawings were done with a camera lucida on a Nikon Labophot-2 compound microscope. Photos were made with a Nikon Coolpix 950 digital camera (1600 \times 1200 pixels) mounted on a Nikon SMZ-U dissecting scope. For SEM photos, specimens were cleaned ultrasonically, dried in HMDS (Brown, 1993), and photographed with a Hitachi S-2460 scanning electron microscope. The numerical cladistic analysis was done using NONA, version 1.8 (Goloboff, 1993) and PEE-WEE, version 2.8 (Goloboff, 1997). Cladogram analysis was done with

WINCLADA, version 0.9.9+ (Nixon, 1999). See Relationships for details of the analysis.

RELATIONSHIPS

Relationships were analysed by cladistic analysis, based on the data matrix in Appendix 3. The 64 taxa and 53 characters used for this matrix are listed in Appendices 1 and 2. The matrix is modified from Huber (2000, 2001) as follows. (1) Several taxa were added, with an emphasis on Malagasy taxa and following the maximum diversity approach with respect to other '*Spermophora*-like' species. (2) Some taxa were deleted, especially New World taxa and ninetines, which were heavily represented in the previous analyses but would not have contributed to the resolution of *Spermophora* and its relatives. (3) Several characters were added according to the new taxa included. (4) Several characters were deleted, either because they were uninformative resulting from the deletion of taxa (characters 5, 7, 18, 19, 25, 26, 30, 39, 42, 43, 48, 49, 58, 59 from Huber, 2000), or because it became obvious that unambiguous coding is impossible (characters 4, 17, 45, 51, 61), or because they are obviously uninformative at the present level of analysis (characters 41, 50).

Binary character coding was used as far as possible. Multistate characters were only used when coding as binary characters would not have represented independent evidence in support of a group (characters 4, 16, 35, 40, 42). All multistate characters were treated as unordered.

Using NONA with **hold/50**, **mult*100** and **amb** resulted in 15 most parsimonious cladograms (MPCs) of length 123 (CI = 47; RI = 82). These cladograms all supported the four subfamilies provisionally named pholcines, holocnemines, ninetines and New World clade in Huber (2000) (see that paper for arguments against using formal names before a stable and convincing cladogram is found). However, the relationships among these subfamilies varied considerably, allowing no new conclusion as to the basic topology of pholcid phylogeny. Therefore, the cladogram presented in Appendix 4 is a strict consensus of the 15 MPCs found by NONA. This is also justified by the fact that all Malagasy taxa treated herein (and in fact all potential relatives of *Spermophora*), are members of a single subfamily, the pholcines (node 1). Within pholcines, there were only two basic resolutions represented in the 15 MPCs (Appendix 5). These two topologies depended on only two characters, namely carapace sculpture and distance between posterior median eyes (characters 2 and 4 in Appendix 2). No topology seems preferable to the other. Apart from this, the only variation within pholcines was within *Zatavua*, where three MPCs resolved *Z. isalo* + *Z.*

madagascariensis as a monophylum. All other polytomies within pholcines shown in Appendix 4 are due to insufficient data (low number of characters in relation to taxa) rather than to character conflict.

Clade stability was estimated using the Bremer support function in NONA, which calculates the number of extra steps required before a clade is lost from the strict consensus of near-minimum length cladograms. Within pholcines, only three clades had a Bremer support of 3 (*Spermophorides*; *Metagonia*; '*Spermophora*' spp. 6 + 9 + 10); two clades had a support of 2 (*Spermophora peninsula* + *Spermophora* sp. 3; *Micromerys*); all other clades had a Bremer support of 1. Surprisingly, this was also true for *Zatavua* n. gen., a clade supported by three synapomorphies. The only higher values in the entire cladogram were for Pholcidae (4) and Ninetinae (5).

The two main conclusions from this cladogram are that (1) Malagasy taxa (nodes 2 and 6) are not closely related to, and certainly not congeneric with, 'true' *Spermophora* (node 4), and (2) the island is inhabited mainly by two taxa that are not closely related to each other and certainly not congeneric. Rather than that, *Zatavua* is seen as the sister clade of all other pholcines (nodes 2 and 3), whereas *Paramicromerys* (node 6) is more derived and more closely related to '*Spermophora*' species from East Africa and the Comoros (node 5) and other genera. The two main conclusions also hold when the data are analysed using character weighting. Successive weighting in NONA (with the consistency index as weighting function) resulted in 12 most parsimonious cladograms, stabilizing at the second iteration. The strict consensus of these MPCs was identical to the one shown in Appendix 4. Implied weighting in PEE-WEE (which resolves character conflict in favour of the characters that have less homoplasy) with all possible settings of the constant of concavity K (1–6) resulted in some interesting differences. However, with the exception of K = 1 (which weights most strongly against characters with homoplasy), all cladograms obtained resolved *Zatavua* and *Paramicromerys* as monophyletic groups, and no cladogram resolved the two genera as sister groups. The most remarkable difference obtained using PEE-WEE was that *Metagonia* was not nested within pholcines but was either the sister taxon of all other pholcines or branched off the basal polytomy (resulting in a pentachotomy instead of a tetrachotomy). This is noteworthy because *Metagonia* is the only pholcine genus present in the New World, with the exception of some mysterious *Pholcus* and *Leptopholcus* species on the Antilles and in the Eastern USA (Huber, 2000).

In conclusion, even though the analysis is preliminary for a number of reasons (see Appendix 2, characters 1, 12 and 28), it strongly suggests that Malagasy '*Spermophora*-like' pholcids are not congeneric with

Spermophora and that two endemic groups exist that are not sister taxa to each other but rather distantly related.

TAXONOMY

ZATAVUA, NEW GENUS

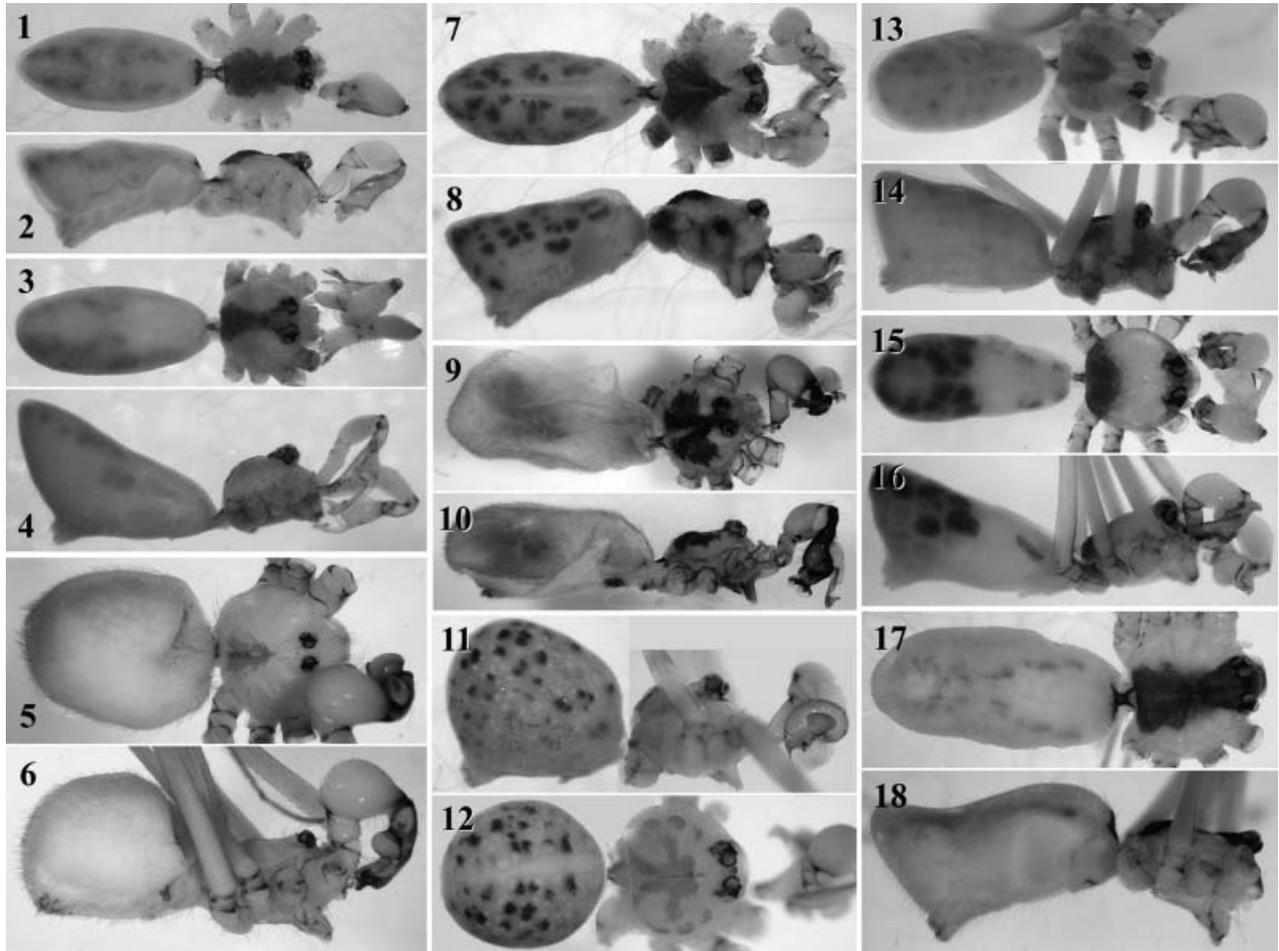
Type species. Zatavua griswoldi, new species.

Etymology. Named for Zatavu, a great magician in Malagasy mythology who created himself and was therefore allowed to marry a goddess. Gender feminine.

Note. Millot (1946) described several species belonging to this genus (under *Spermophora*). Unfortunately, most of the material studied by him has not been available to me (it could not be found at the MNHN in Paris; C. Rollard, pers. comm.). Therefore, the diagnosis and description given below may not perfectly cover all the species included. Nevertheless, judging by Millot's excellent illustrations, some of his species seem very closely related to some of the species newly described herein (see Specific Relationships below), so the diagnosis and description may in fact be tolerably accurate.

Diagnosis. Long-legged, six-eyed pholcids with globular or elongate opisthosoma and variable size (total length ~2–8 mm). Distinguished from *Paramicromerys* and other six-eyed genera by the lateral cheliceral apophyses pointing backwards (Figs 62, 84, 86 and 98), the presence of a retrolateral notch on the cymbium (Figs 34, 48 and 57), and by the shift of the tibia-tarsus joints, resulting in a dorsal position of the retrolateral joint and in a ventral position of the prolateral joint (Figs 29, 30, 33 and 34, etc.; two latter characters missing in *Z. kely*, *mahafaly*). Distinguished from *Paramicromerys* also by the closeness of the triads (e.g. Fig. 67; PME-PME <180% of PME diameter, vs. >230% in *Paramicromerys*), and by the presence of several spigots on the ALS in addition to the basic set of two (Figs 39, 40, 46, 74, 75 and 77).

Description. Total length in males usually ~3–5 mm; only *Z. zanahary* and *punctata* (Millot) up to 8 mm, *Z. kely* only ~1.5 mm. Carapace oval or round, with or without thoracic groove, often with dark pattern that may be distinctive (Figs 1–18). Six eyes in two triads, on moderately elevated ocular area; no trace of AME. Distance PME-ALE small (~20–40% of PME diameter), distance PME-PME also small (~90–180% of PME diameter). Clypeus in some species with paired unsclerotized projections at rim. Male chelicerae with pair of lateral apophyses pointing backwards (Figs 62, 84, 86 and 98), and frontal apophyses variable in position and shape; never with modified hairs, never with

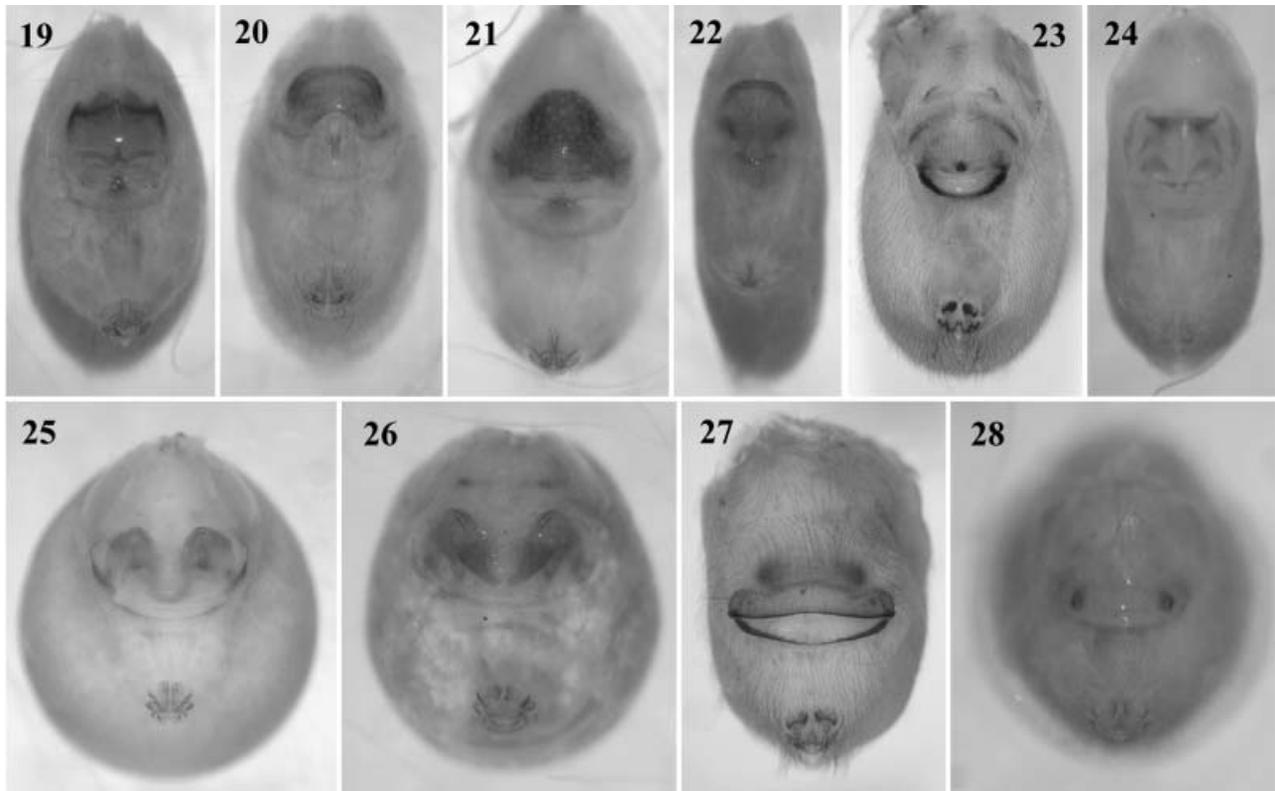


Figures 1–18. *Zatauvia* habitus, males in dorsal and lateral views. 1–2, *Z. griswoldi*. 3–4, *Z. analalava*. 5–6, *Z. mahafaly*. 7–8, *Z. vohiparara*. 9–10, *Z. zanahary*. 11–12, *Z. isalo*. 13–14, *Z. tamatave*. 15–16, *Z. voahangyae*. 17–18, *Z. talatakely*.

stridulatory ridges. Male palps moderately large in relation to overall size; coxa and trochanter without retrolateral apophyses, femur usually cylindrical, sometimes with small ventral apophysis proximally; tibia moderately to highly expanded, with two trichobothria; tibia-cymbium joints distinctively shifted (resulting in dorsal position of retrolateral joint and ventral position of prolateral joint); cymbium with distinctive notch on retrolateral side (Figs 34, 48 and 57); procurus usually complex but never with hinged process; with capsulate tarsal organ (Fig. 73), often in very distal position (Figs 30, 33, 47, 52, 56, 61 and 78); bulb consisting of proximal globular part and embolus that is partly sclerotized and often provided with sclerotized spine. Legs usually long (leg 1 about 8–11 × body length; in *Z. kely* only 6 ×), medium-thin (tibia 1 L/d ~40–90), leg 1 always longest, legs 2 and 4 about same length, leg 3 shortest. Legs usually without spines, with few vertical hairs, without curved

hairs; retrolateral trichobothrium of tibia 1 usually at 5–15%, in *Z. kely* at 27%. Prolateral trichobothrium missing on tibiae 1, present in all others. Tarsus 1 with over 20 pseudosegments, but only ~10–20 distal pseudosegments easily visible in dissecting microscope. Opisthosoma either globular or elongate, often with posterior elongation over spinnerets (Figs 4, 14 and 16). Male gonopore with four epiandrous spigots in all species examined (*Z. zanahary*, *griswoldi*, *voahangyae*; Figs 41 and 66); ALS with several spigots in addition to basic set of two (examined: *Z. griswoldi*, *vohiparara*, *voahangyae*, *isalo*, *kely*; Figs 39, 40, 46, 74, 75 and 77); other spinnerets typical for family (e.g. Fig. 38; cf. Huber, 2000).

Sexual dimorphism slight. In some species females with median conical elevation posteriorly on carapace; corresponding side of opisthosoma not visibly modified. Epigynum shape very variable, often with pair of pockets, in *Z. vohiparara* with short scape (Fig. 45);



Figures 19–28. *Zatauvia*, female opisthosomata, ventral views with epigynum. 19, *Z. griswoldi*. 20, *Z. vohiparara*. 21, *Z. tamatave*. 22, *Z. analalava*. 23, *Z. zana-hary*. 24, *Z. voahangyae*. 25, *Z. madagascariensis*. 26, *Z. isalo*. 27, *Z. mahafaly*. 28, *Z. kely*.

internally with pair of relatively large pore plates and complex system of sclerites and membranes of unknown function.

Monophyly. The monophyly of this genus is supported by the following three synapomorphies: the backward facing lateral cheliceral apophyses (shared by all species included), the shift of the tibia-cymbium joints, and the notch on the cymbium (the latter two characters are not shared by *Z. kely* and *Z. mahafaly*).

Generic relationships. As discussed above, *Zatauvia* is here considered the sister taxon of all other pholcines. The presence of lateral apophyses on the male chelicerae places the genus within the subfamily, but the genus lacks the retrolateral trochanter apophysis characteristic of other pholcines.

Specific relationships. Several synapomorphies support species groups within *Zatauvia*. A core group of species is characterized by the presence of a conical elevation on the female carapace [*Z. griswoldi*, *tamatave*, *vohiparara*, maybe including *andrei* (Millot) and *ankaranae* (Millot)]. This group shares with *Z. analalava* the projections on the male clypeus. The resulting group shares with several further species [*Z. zana-*

hary, *punctata* (Millot), *voahangyae*, *talatakely*, probably *impudica* (Millot)] the distal position of the male palpal tarsal organ. Within this latter group, *Z. zana-hary* and *punctata* share their unusual size and the unique pattern on the carapace (Fig. 9). All species listed so far share with *Z. isalo* and *madagascariensis* (Fage) the shift of the tibia-cymbium joints and the notch on the cymbium. The latter two species have almost identical palps (not coded) and are therefore seen as closely related. *Zatauvia fagei* (Millot) is only known from the female, but was collected near the type locality of *Z. madagascariensis* (Fage) and is either a junior synonym or a closely related species. Finally, *Z. mahafaly* and *kely* are very unusual in several aspects, but share with all other species the backward facing lateral cheliceral apophyses on the male chelicerae. Of these, *Z. kely* might be close to *imerinensis* (Millot), judging by the similar shapes of the palps.

Natural history. No species has ever been studied in any detail, and little can be inferred from notes on the collection labels. Several species have been collected in caves [*Z. andrei*, *ankaranae*, *impudica*, *madagascariensis* (Fage), *mahafaly*], two more were classified

as 'semi-cavernicole' by Millot (1946) (*Z. fagei*, *punctata*), and one as 'semi-domestique' (*Z. imerinensis*). All new species described below (except *Z. mahafaly*) were apparently collected in forests. *Zatavua vohiparara* was collected on *Pandanus*, an undescribed species from the AMNH was collected by beating vegetation.

Distribution. Known from Madagascar only. The genus is widely distributed in Madagascar (Map 1), and probably covered most of the island before human destruction of a large part of the primary vegetation. As in *Paramicromerys*, no species has been collected at two localities more than a few kilometres apart. A possible exception is *Z. punctata* (Millot), which has been recorded from the Antonibe Peninsula and on Nosy-Komba Island (about 200 km apart), but the latter record is based on a female and a juvenile specimen and should be checked.

Composition. The genus includes a total of 17 described species. Of these, six were described by Millot (1946), and are not treated below (*Z. andrei*, *ankaranae*, *fagei*, *imerinensis*, *impudica*, *punctata*). The remaining 11 species [10 new species and *Z. madagascariensis* (Fage)], are (re)described below. The collections studied contain four additional new species that are not described due to their poor state of preservation. Considering the facts that (1) most or all species seem to have small distributional ranges, and that (2) all areas that were subjected to intense collecting yielded between one and three species, it seems reasonable to expect several dozen additional species not yet discovered.

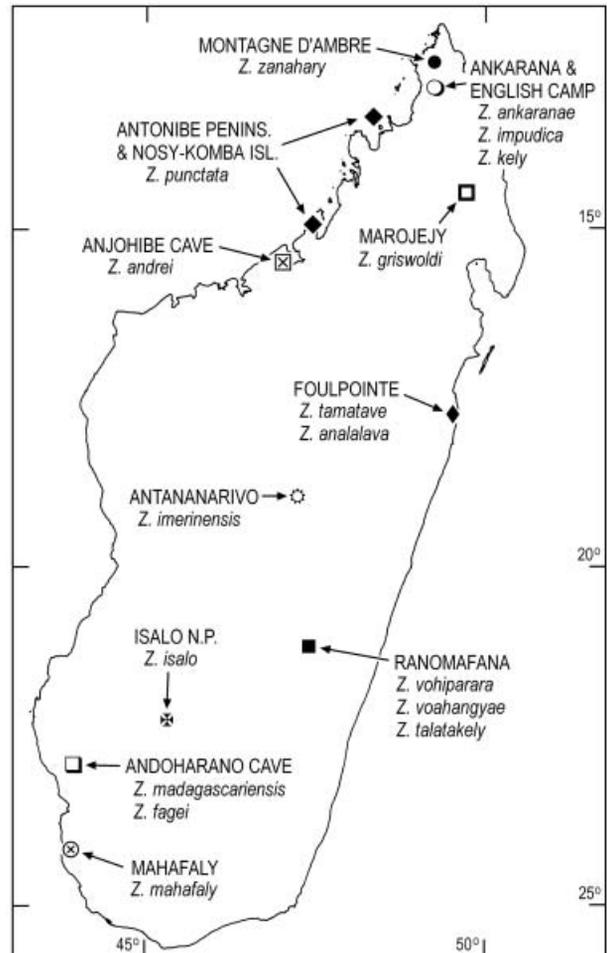
ZATAVUA GRISWOLDI, NEW SPECIES

(FIGS 1, 2, 19, 29–32, 38–44)

Type. Male holotype from Marojejy Res., 8.4 km NNW Manantenina (14°26'S, 49°45'E), 700 m a.s.l., Antsiranana, Madagascar; November 10–16, 1993 (C. E. Griswold, J. Coddington, N. Scharff, S. Larcher, R. Andriamasimanana); in CAS.

Etymology. Named for the first collector, Charles Griswold from the California Academy of Sciences, who kindly made his superb collection of Malagasy pholcids available to me.

Diagnosis. Medium size species with elongated opisthosoma, distinguished from known congeners by the shape of procurus and embolus (Figs 29, 30: overall shape and several unnamed details), and by the shape of the epigynum (Figs 19 and 31). The AMNH has a male from a nearby locality (10.5 km NW Manantenina) that differs slightly by having a shorter procurus and more profoundly by the shape of the embolus. The MRAC has a further close relative from



Map 1. Known distribution of *Zatavua*.

Vohibe (16°06'S, 49°08'E) that differs slightly with respect to procurus and embolus shape.

Male (holotype). Total length 3.5, carapace width 1.2. Leg 1: 37.9 (9.3 + 0.6 + 9.3 + 16.5 + 2.2), tibia 2: 6.0, tibia 3: 3.8, tibia 4: 6.3; tibia 1 L/d: 82. Habitus as in Figures 1 and 2. Carapace ochre-yellow with dark brown band medially; sternum whitish. Legs ochre-yellow with several darker rings: on femora at ~50% (faint) and subdistally, at patella area, on tibiae at ~40% and subdistally, on metatarsi proximally. Opisthosoma grey, with dark spots shining through cuticle; with dark brown plate above pedicel (cf. *Z. talatakely*); ventrally without marks. Ocular area elevated; distance PME-PME 120 µm; diameter PME 120 µm; distance PME-ALE 40 µm. Thoracic furrow absent, only short line behind ocular area. Clypeus with pair of unsclerotized projections at rim. Sternum wider than long (0.80/0.64). Chelicerae almost identical to *Z. analalava* (cf. Fig. 53), but apophyses minimally longer and (depending on view?) slightly more

distal. Palps as in Figures 29 and 30, trochanter with pair of small humps ventrally, femur with small projections proximo-ventrally, procurus with three distinctive sclerotized lamellae retrolaterally ('l' in Fig. 30). Embolus ('e' in Fig. 29) mostly sclerotized, with dark flattened spine winding partly around embolus ('s' in Fig. 29). Legs without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 7%; tarsus 1 with >20 pseudosegments (about 20 distally quite distinct). Epiandrous spigots and ALS spigots as in Figures 39 and 41.

Variation. Tibia 1 in two other males from type locality: 8.5, 8.7; palps and chelicerae identical.

Female. In general similar to male, but brown band on carapace excludes ocular area, with small conical median elevation on posterior half of carapace, plate above pedicel divided into two small plates, without clypeus projections, and sternum with light brown markings (especially frontally). Tibia 1 in 10 females: 7.0–7.8 (\bar{x} = 7.5). Epigynum with large frontal plate (Fig. 19) and tiny pockets lying close together ('p' in Figs 31 and 42). Dorsal view as in Figure 32. ALS spigots as in male (Fig. 40).

Distribution. Known only from type locality (Map 1).

Material examined. MADAGASCAR: *Antsiranana*: Marojejy Reserve: type above, together with 2♂ 6♀, same collection data; 1♂ 7♀ 1 juvenile, same collection data.

ZATAVUA VOHIPARARA, NEW SPECIES

(FIGS 7, 8, 20, 33–37, 45, 46)

Type. Male holotype from Vohiparara, Piste Touristique (21°13.6'S, 47°24.0'E), ~1000 m a.s.l., on *Pandanus*, Ranomafana National Park, Fianarantsoa, Madagascar; April 19, 1998 (C. E. Griswold & D. Ubick); in CAS.

Etymology. Named for the type locality. The specific name is a noun in apposition.

Diagnosis. Medium size species with elongated opisthosoma, distinguished from known congeners by the shape of the procurus (Fig. 34: overall shape, lamellae, distal elements), and the epigynum with long scape (Figs 20, 36 and 45).

Male (holotype). Total length 3.6, carapace width 1.2. Leg 1: 38.5 (9.3 + 0.6 + 9.3 + 17.1 + 2.2), tibia 2: 6.0, tibia 3: 3.8, tibia 4: 6.3; tibia 1 L/d: 78. Habitus as in Figures 7 and 8. Carapace ochre-yellow with dark brown mark posteriorly, clypeus light brown; sternum whitish. Legs ochre-yellow with dark rings subdistally on femora and tibiae and in patella area. Opisthosoma ochre-grey, with dark spots shining through cuticle;

ventrally pair of small brown spots in front of genital area. Ocular area elevated; distance PME-PME 140 µm; diameter PME 120 µm; distance PME-ALE 40 µm. Thoracic furrow absent, but with depression behind ocular area. Clypeus with pair of unsclerotized humps laterally on rim. Sternum wider than long (0.92/0.72). Chelicerae as in Figure 35, proximal apophyses in lateral view as in *Z. voahangyae* (Fig. 62). Palps as in Figures 33 and 34, trochanter with small humps pro- and retrolaterally, femur with hump proximo-ventrally, procurus relatively simple, with two sclerotized lamellae ('l' in Fig. 34; cf. *Z. griswoldi*). Embolus ('e' in Fig. 33) partly sclerotized, with strong sclerotized spine ('sp'). Legs probably without spines, without curved hairs, few vertical hairs (many hairs missing); retrolateral trichobothrium of tibia 1 at 6%; tarsus 1 with >15 pseudosegments (only distally fairly distinct).

Variation. Tibia 1 in males accompanying holotype: 9.0, 9.3; palps and chelicerae identical. The male from Mahira differs slightly with respect to the terminal structures of the procurus: process 'a' in Figure 34 is less pointed, process 'b' is not as wide as in the type.

Female. In general similar to male, but with conical median elevation on posterior half of carapace. This elevation is apparently not opposing a structure on the opisthosoma. Tibia 1 in 3 females: 7.5, 7.8, 8.0. Epigynum with large frontal and posterior plates, both weakly sclerotized; with distinctive scape ('s' in Figs 36 and 45). Dorsal view as in Figure 37. ALS spigots as in Figure 46.

Distribution. Known from two localities in Ranomafana National Park (Map 1).

Material examined. MADAGASCAR: *Fianarantsoa*: Ranomafana National Park: Vohiparara: type above, together with 2♂ 5♀, same collection data. Ranomafana N. P.: Mahira, camp, April 11, 1992 ('Pierre for Kariko & Roth'), 1♂ in MCZ (33.981).

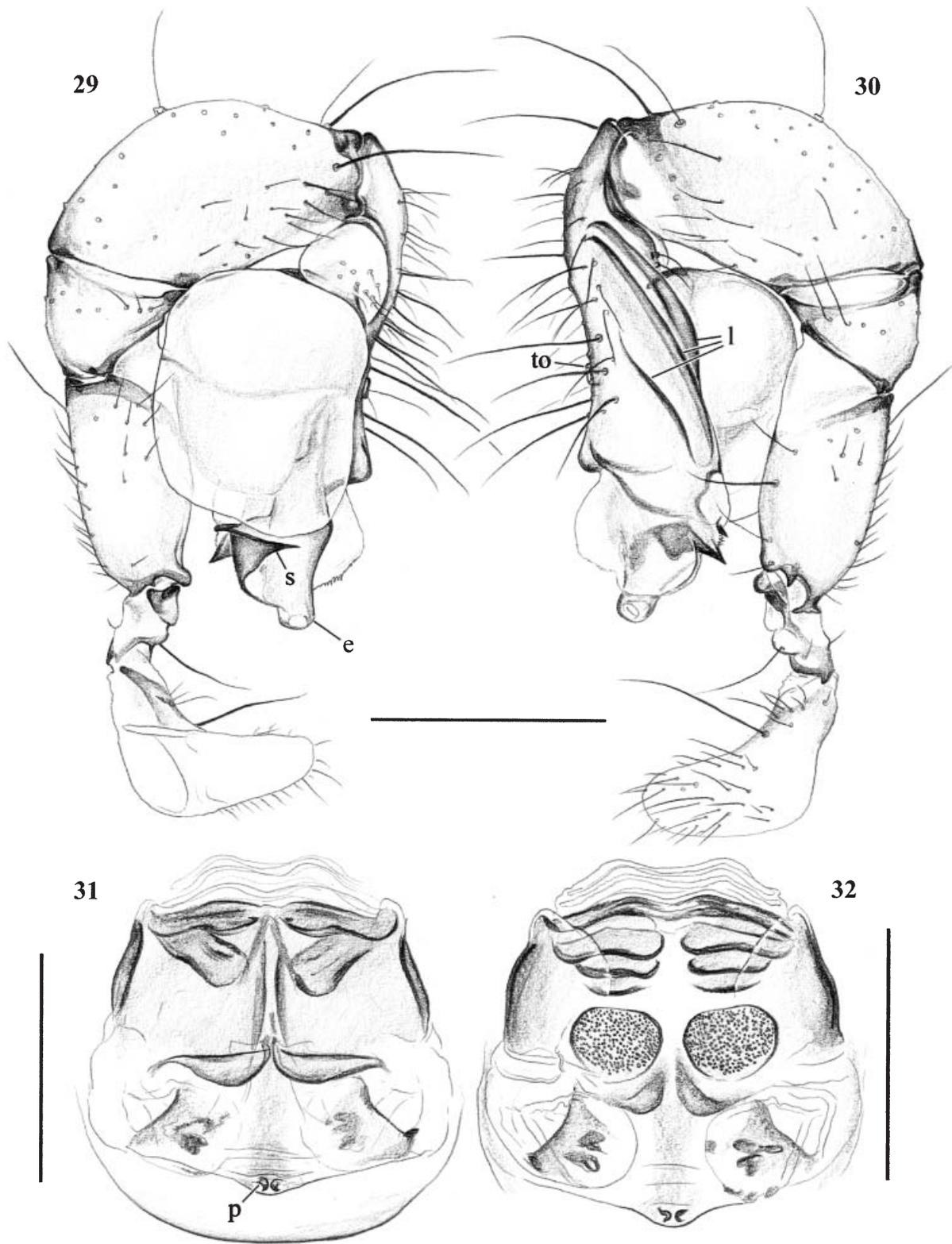
ZATAVUA TAMATAVE, NEW SPECIES

(FIGS 13, 14, 21, 47–50)

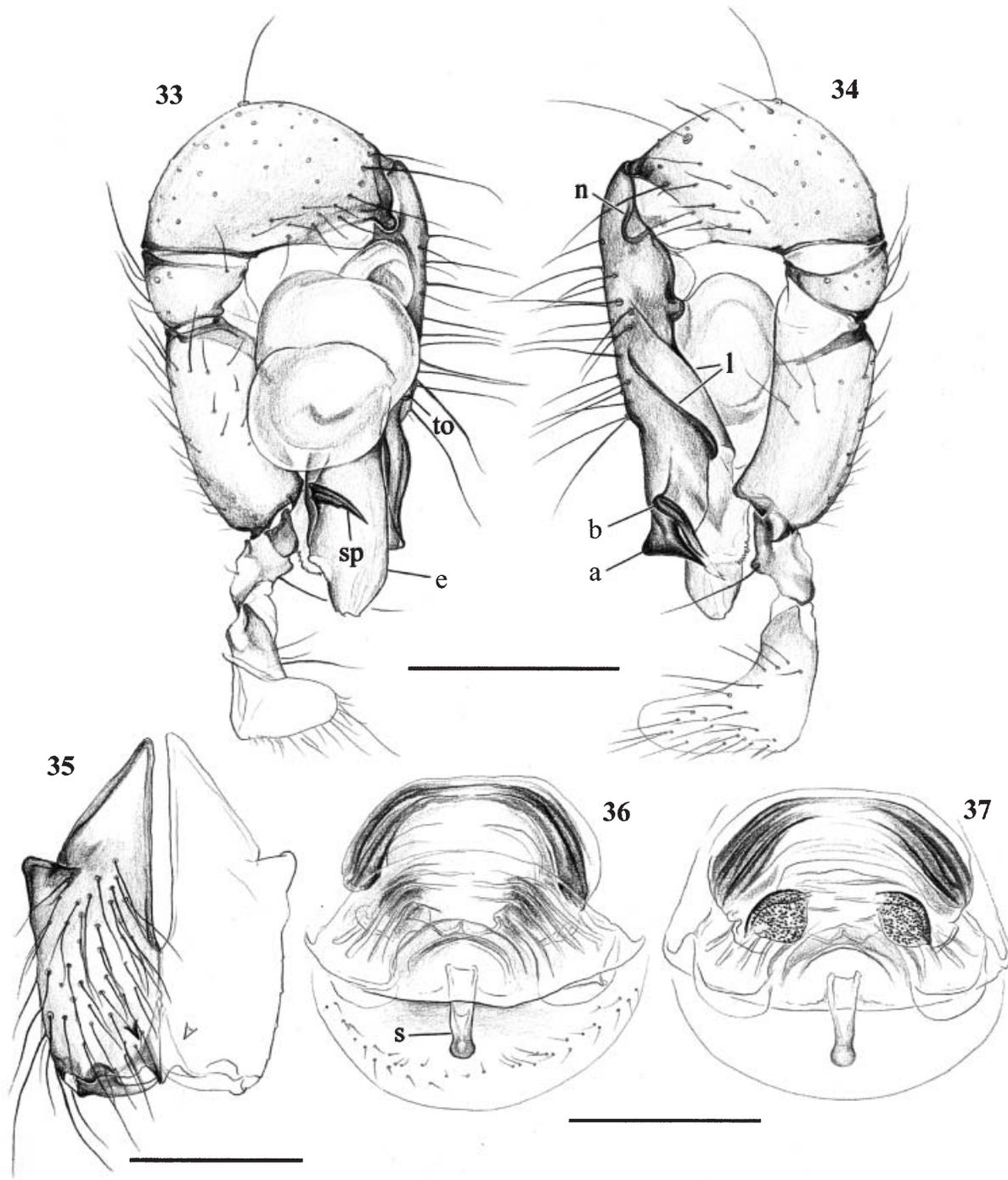
Type. Male holotype from Tamatave, Foulpointe, forêt Analalava (17°40'S, 49°31'E), Toamasina, Madagascar; May 1995 (A. Pauly); in MRAC (206.053).

Etymology. Named for the type locality. The specific name is a noun in apposition.

Diagnosis. Medium size species with elongated opisthosoma, distinguished from known congeners by the shape of the procurus (Fig. 48), and the epigynum with tiny pockets and short scape (Fig. 49).



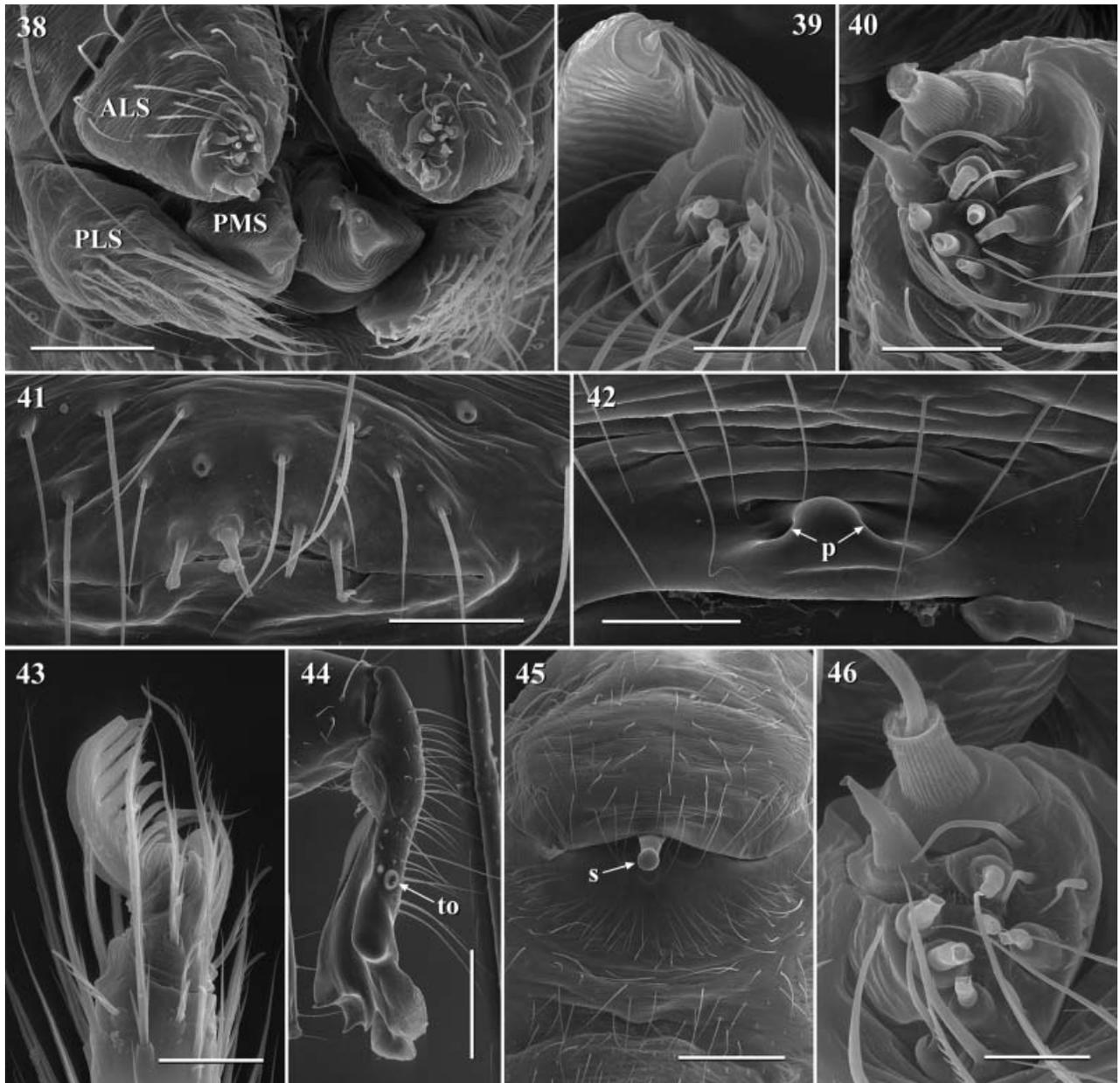
Figures 29–32. *Zatauvia griswoldi*. Left male palp in prolateral (29) and retrolateral (30) views, and cleared epigynum in ventral (31) and dorsal (32) views. ‘e’: embolus; ‘l’: lamellae on procurus; ‘p’: pocket; ‘s’: spine on embolus; ‘to’: tarsal organ. Scale lines: 0.5 mm.



Figures 33–37. *Zatauvua vohiparara*. Left male palp in prolateral (33) and retrolateral (34) views, male chelicerae in frontal view (35), and cleared epigynum in ventral (36) and dorsal (37) views. ‘a’, ‘b’: distal structures on procurus that differ in male from Mahira (see text); ‘e’: embolus; ‘l’: lamellae on procurus; ‘n’: notch on cymbium; ‘s’: scape; ‘sp’: spine on embolus; ‘to’: tarsal organ. Scale lines: 0.5 mm (33–34, 36–37), 0.3 mm (35).

Male (holotype). Total length 2.6, carapace width 1.0. Leg 1: 24.6 (5.8 + 0.4 + 5.9 + 10.8 + 1.7), tibia 2: 3.8, tibia 3: 2.4, tibia 4: 4.1; tibia 1 L/d: 69. Habitus as in Figures 13 and 14. Carapace ochre with light brown

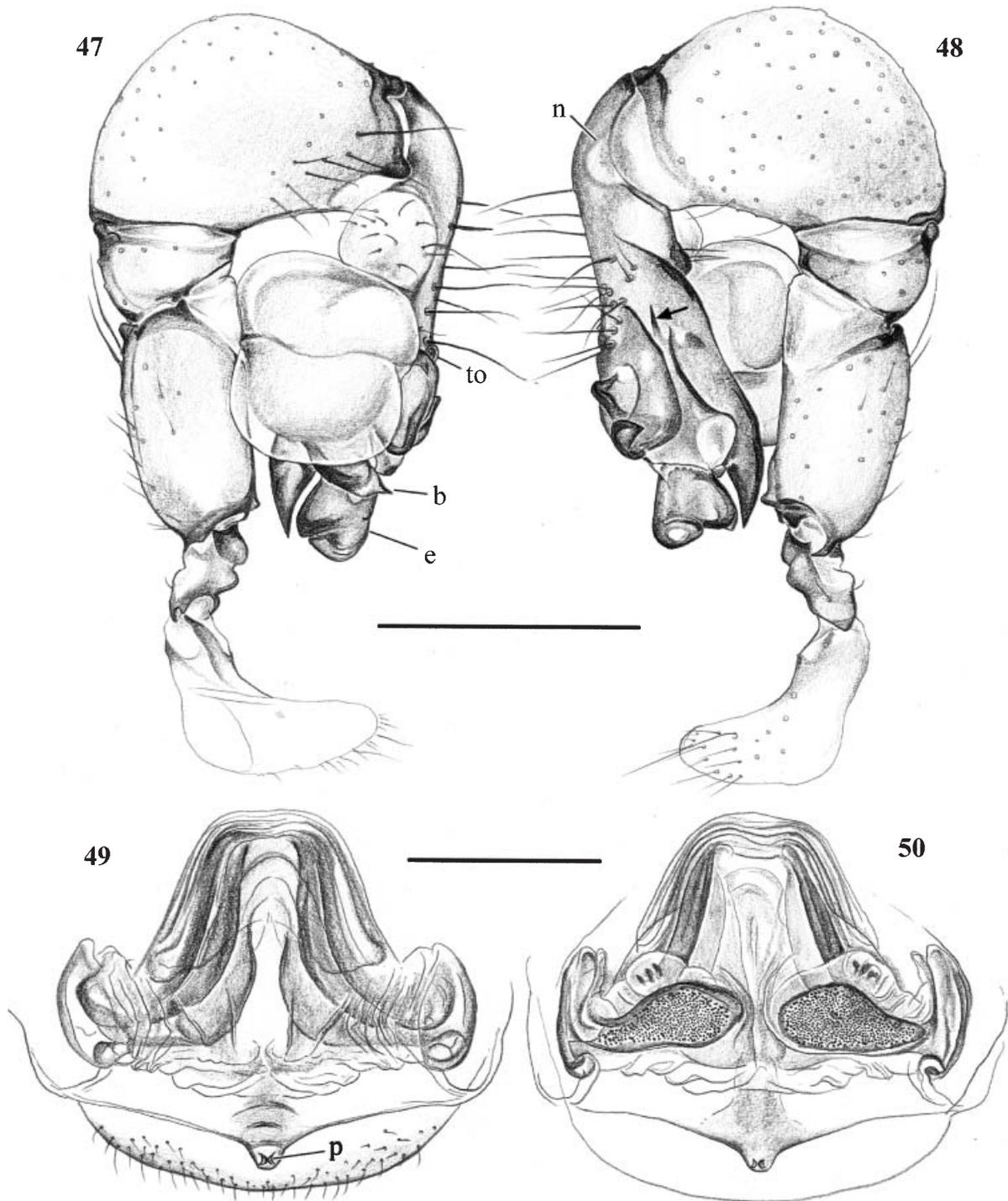
pattern; sternum pale ochre. Legs ochre-yellow with slightly darker rings on femora and tibiae (subdistally), and in patella area. Opisthosoma ochre-grey, with slightly darker spots shining through cuticle;



Figures 38–46. *Zatauvia griswoldi* (38–44) and *Z. vohiparara* (45–46). 38, Female spinnerets. 39, Male ALS and PMS. 40, Female ALS. 41, Male gonopore with epiandrous spigots. 42, Pockets ('p') on epigynum. 43, Claws of third male leg. 44, Procurus, showing position of tarsal organ ('to'). 45, Epigynum with scape ('s'). 46, Female ALS. Scale lines: 100 μ m (38), 30 μ m (39–40), 50 μ m (41), 80 μ m (42), 40 μ m (43), 300 μ m (44–45), 20 μ m (46).

ventrally no markings. Ocular area elevated, not clearly separated from carapace; distance PME-PME 140 μ m; diameter PME 100 μ m; distance PME-ALE 30 μ m. Thoracic furrow absent, only indistinct line behind ocular area. Clypeus with pair of unsclerotized projections above lateral cheliceral apophyses. Sternum wider than long (0.68/0.52). Chelicerae as in *Z. vohiparara* (cf. Fig. 35), with tiny apophyses near

fangs, proximal apophyses in lateral view as in *Z. voahangyae* (Fig. 62). Palps as in Figures 47 and 48, trochanter with pair of humps ventrally, femur with sclerotized ridge retrolatero-ventrally; procurus very complex, with distinctive spine visible in retrolateral view (arrow in Fig. 48) (cf. *Z. talatakely*: Fig. 79). Embolus ('e' in Fig. 47) with proximal branch ('b' in Fig. 47) and distal conical projection, both sclerotized.



Figures 47–50. *Zatauvia tamatave*. Left male palp in prolateral (47) and retrolateral (48) views, and cleared epigynum in ventral (49) and dorsal (50) views. 'b': branch of embolus; 'e': embolus; 'n': cymbium notch; 'p': pocket; 'to': tarsal organ; arrow points to distinctive spine on procurus. Scale lines: 0.5 mm.

Legs probably without spines, without curved hairs, few vertical hairs (most hairs missing); retrolateral trichobothrium of tibia 1 at 9%; tarsus 1 with >10 pseudosegments, but only about 7 distally fairly distinct.

Variation. Tibia 2 in other male seen: 3.9; palps and chelicerae identical.

Female (see Note below). In general similar to male, but with conical projection on carapace. Clypeus dark but unmodified. Tibia 1: 7.1 (missing in other female seen). Epigynum as in Figure 21, with tiny pockets on short scape ('p' in Fig. 49). Dorsal view as in Figure 50.

Note. The females might not be conspecific with the male type. Both are identical in colour pattern and habitus to the two males seen, but both are unusually larger than the males (compare tibia 1 lengths).

Distribution. Known only from type locality (Map 1).

Material examined. MADAGASCAR: Toamasina: Tamatave, Foulpointe: type above. Same locality and collector, January 1995: 1♂ (MRAC 207.093), 1♀ (separated from MRAC 206.971), 1♀ (separated from MRAC 207.013).

ZATAVUA ANALALAVA, NEW SPECIES

(FIGS 3, 4, 22, 51–55, 76, 77)

Type. Male holotype from Tamatave, Foulpointe, forêt Analalava (17°40'S, 49°31'E), Toamasina, Madagascar; January 1995 (A. Pauly); in MRAC (206.971).

Etymology. Named for the type locality. The specific name is a noun in apposition.

Diagnosis. Medium size species with elongated and posteriorly strongly elevated opisthosoma (Fig. 4), distinguished from known congeners by the slender procurus and its distal elements (Fig. 52), by the embolus with pair of subdistal teeth (Fig. 51), and by the shape of the epigynum (Figs 22 and 54).

Male (holotype). Total length 3.5, carapace width 1.2. Leg 1: 38.5 (9.3 + 0.4 + 9.1 + 17.7 + 2.0), tibia 2: 5.7, tibia 3 missing, tibia 4: 5.7; tibia 1 L/d: 91. Habitus as in Figures 3 and 4. Carapace ochre-yellow with brown median band; sternum whitish. Legs ochre-yellow with dark patellae and subdistal ring on tibiae. Opisthosoma ochre-grey, with slightly darker spots shining through cuticle; ventrally no markings. Ocular area elevated; distance PME-PME 180 µm; diameter PME 100 µm; distance PME-ALE 30 µm. Thoracic furrow absent. Clypeus with pair of transparent projections at rim. Sternum wider than long (0.72/0.60). Chelicerae as in Figure 53, proximal apophyses in lateral view as in *Z. voahangyae* (Fig. 62).

Palps as in Figures 51 and 52, trochanter with small hump retrolaterally, femur with ventral hump proximally; procurus long and slender, with medium-complex tip. Embolus ('e' in Fig. 51) with pair of little sclerotized teeth. Legs with short spines on tibiae 1 and 2 (these are just short normal hairs rather than real macrotrichia), probably without curved hairs and vertical hairs (most hairs missing); retrolateral trichobothrium of tibia 1 at 8%; tarsus 1 with >10 pseudosegments, but only about 5 distally fairly distinct.

Variation. Tibia 1 in 3 other males seen: 8.2, 8.3, 9.0. The MRAC has some extremely similar males from the same locality (1♂ separated from 206.971, 1♂ separated from 206.053, 1♂ in 205.929) that can only be distinguished by the tip of the procurus whose elements are shorter in the present material. More material needs to be studied to decide on the taxonomic status of these males.

Female (see Note below). In general similar to male, but dark band on carapace either absent or restricted to posterior half of carapace; opisthosoma longer and even more pointed than in male. Tibia 1 (N = 9) 6.3–7.0 (\bar{x} = 6.6). Epigynum as in Figure 22, with tiny pockets lying close together ('p' in Figs 54 and 76). Dorsal view as in Figure 55. ALS spigots as in Figure 77.

Note. The females assigned to the present species might partly belong to the males with uncertain status mentioned above. If this is the case, then the epigyna are not distinguishable externally.

Distribution. Known only from the Foulpointe area (Map 1).

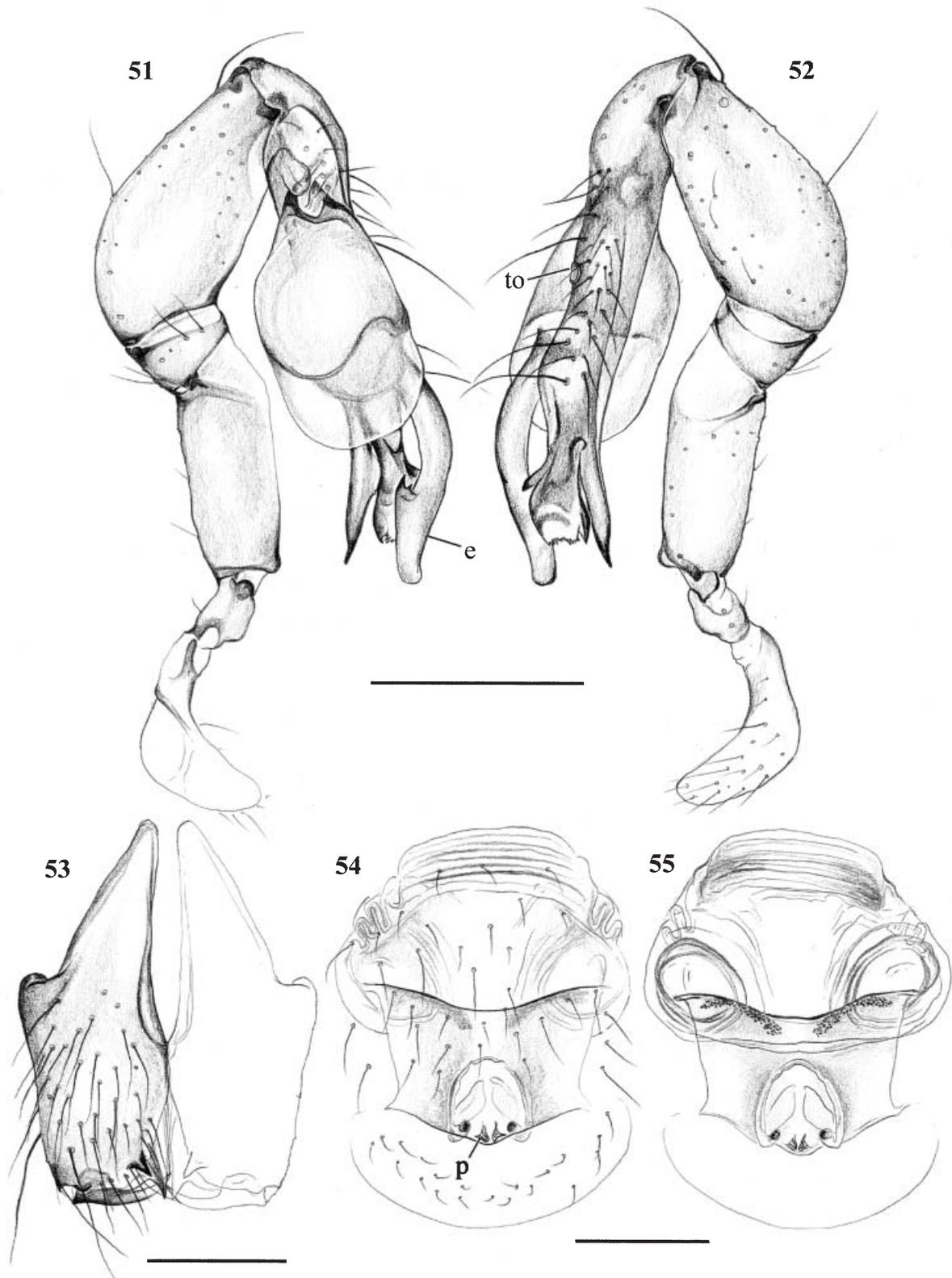
Material examined. MADAGASCAR: Toamasina: Tamatave, Foulpointe: forêt Analalava: type above, together with 2♂ 6♀ 1 juvenile; same collection data: 1♂ (MRAC 207.209), 3♀ (MRAC 206.970, 207.013, 207.234). Foulpointe: forêt sur table 'marais à Pandanus, dans toiles', November 10, 1993 (A. Pauly) 1♀ (MRAC 200.196). Foulpointe: 'tamisage litière forêt sur argile', December 9, 1993 (A. Pauly) 1♀ (MRAC 200.057).

ZATAVUA ZANAHARY, NEW SPECIES

(FIGS 9, 10, 23, 56–59)

Type. Male holotype from Montagne d'Ambre (12°30'57"S, 49°11'04"E), Antsiranana, Madagascar; August 12, 1992 (V. & B. Roth); in CAS.

Etymology. Named for Zanahary, the 'creator god' in Malagasy mythology, a terrifying god who speaks in thunder and lightning. The name is here used as noun in apposition.



Figures 51–55. *Zatauvia analalava*. Left male palp in prolateral (51) and retrolateral (52) views, male chelicerae in frontal view (53), and cleared epigynum in ventral (54) and dorsal (55) views. 'e': embolus; 'p': pocket; 'to': tarsal organ. Scale lines: 0.5 mm (51–52), 0.2 mm (53), 0.3 mm (54–55).

Diagnosis. Very large species with cylindrical opisthosoma. The only known species with comparable size and similar pattern on the carapace is *Z. punctata* (Millot) (cf. fig. 18A in Millot, 1946). These species also share epigynum shape and the armature on the male chelicerae. *Zatavua zanahary* differs from *punctata* and from other congeners by the shapes of procurus and bulb (Figs 56 and 57), from most species except *Z. punctata* also by the shape of the epigynum (Fig. 23).

Male (holotype). Total length 7.9, carapace width 2.6. Leg 1: 65.7 (16.8 + 1.0 + 15.8 + 28.8 + 3.3), tibia 2: 11.2, tibia 3: 7.8, tibia 4: 10.7; tibia 1 L/d: 63. Habitus as in Figures 9 and 10. Carapace ochre-grey with distinctive brown pattern; sternum brown. Legs light to dark brown, with dark rings subdistally on femora and tibiae and in patella area. Opisthosoma monochromatic grey. Ocular area slightly elevated, not clearly separated from carapace; distance PME-PME 240 µm; diameter PME 240 µm; distance PME-ALE 50 µm. Thoracic furrow absent, only slight depression behind ocular area. Clypeus not modified. Sternum wider than long (1.52/1.32). Chelicerae almost identical to *Z. analalava* (cf. Fig. 53), lateral view similar to *Z. voahangyae* (cf. Fig. 62) but not narrowing distally. Distance between tips of apophyses about 100 µm. Palps as in Figures 56 and 57; trochanter without apophysis, femur with unsclerotized hump retrolaterally, procurus complex and massive. Bulb with unsclerotized papilla ('pa' in Fig. 56). Embolus ('e' in Fig. 56) on one side only sclerotized, subterminal short branch with sclerotized spine. Legs without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 5%; pseudosegments on tarsus 1 very indistinct, but on other tarsi >15 pseudosegments quite distinct.

Female. In general similar to male. Tibia 1: 16.3, leg 2 missing, tibia 3: 8.3, tibia 4: 11.7. Epigynum as in Figures 23 and 58, with pair of pockets close together ('p' in Fig. 58; distance about 65 µm). Dorsal view as in Figure 59.

Distribution. Known only from type locality (Map 1).

Material examined. MADAGASCAR: *Antsiranana*: Montagne d'Ambre: type above, together with 1♀, same data.

ZATAVUA VOAHANGYAE, NEW SPECIES (FIGS 15, 16, 24, 60–75)

Type. Male holotype from Talatakely (21°15'S, 47°26'E), 900 m a.s.l., Ranomafana National Park, Fianarantsoa, Madagascar; December 5–7, 1993 (N. Scharff, S. Larcher, C. E. Griswold, R. Andriamasimanana); in CAS.

Etymology. Named for Marie-Voahangy Ramariavelo, outstanding painter of French-Malagasy descent.

Diagnosis. Medium size species with elongated and posteriorly elevated opisthosoma, distinguished from known congeners by the posterior mark on the carapace (Fig. 15), the shape of the procurus (Fig. 61), the long spine on the embolus ('s' in Fig. 60), and by the shape of the epigynum (Figs 24 and 64).

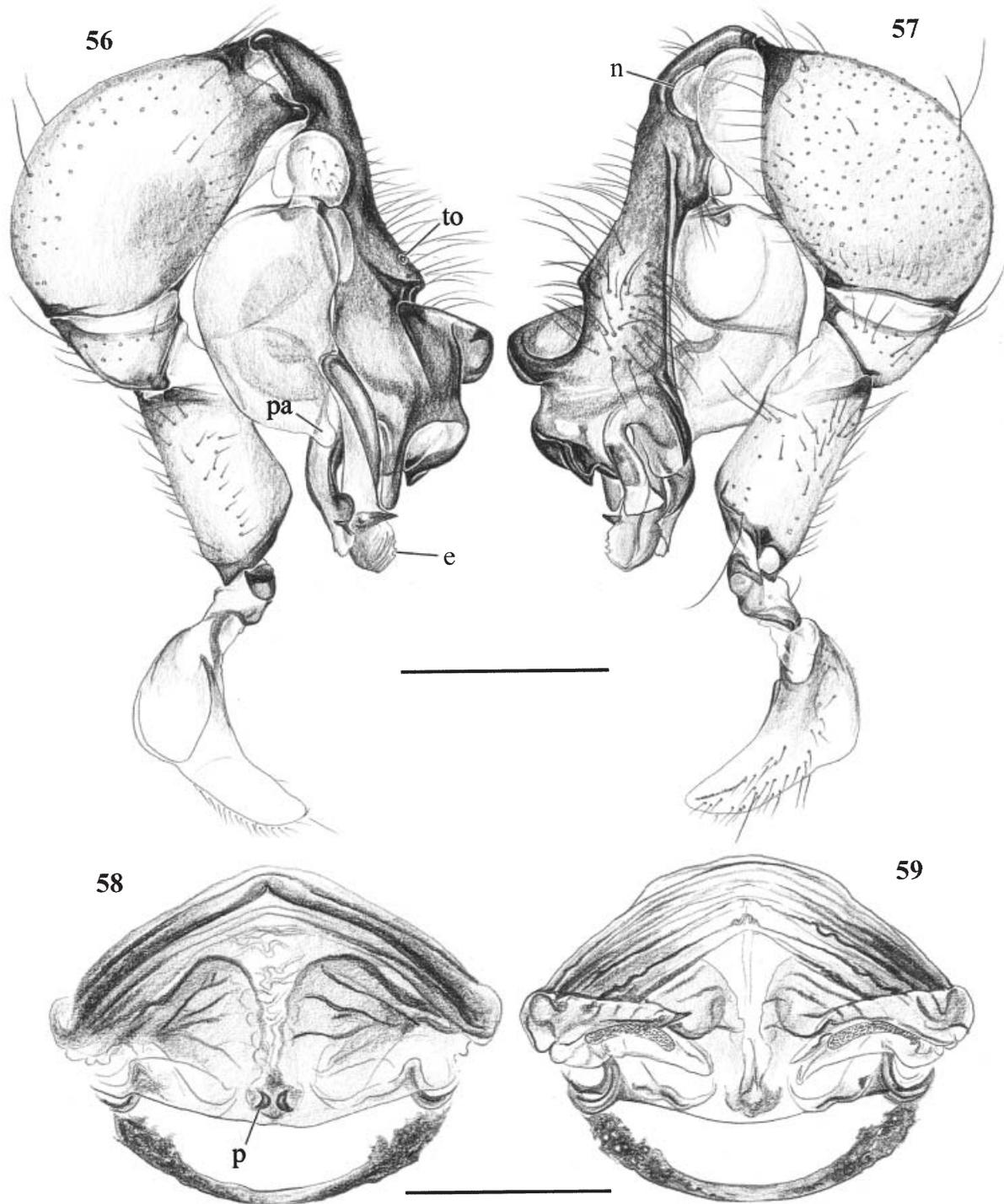
Male (holotype). Total length 2.8, carapace width 1.0. Leg 1 missing, tibia 2: 5.1, tibia 3: 3.1, tibia 4: 5.2. Habitus as in Figures 15 and 16. Carapace ochre-yellow with brown marks posteriorly and at ocular area and clypeus; sternum whitish. Legs ochre-yellow with dark rings at three-quarters of femora and tibiae, and in patella area and tibia-metatarsus joints. Opisthosoma ochre-grey, with dark spots shining through cuticle posteriorly and pair of lighter marks frontally; ventrally no marks. Ocular area slightly elevated, not clearly separated from carapace; distance PME-PME 130 µm; diameter PME 100 µm; distance PME-ALE 20 µm. Thoracic furrow absent, only indistinct line behind ocular area. Clypeus not modified. Sternum wider than long (0.64/0.52). Chelicerae as in Figures 62 and 63; distance between tips of apophyses 104 µm. Palps as in Figures 60 and 61, trochanter without apophysis, femur with rounded hump prolat-erally, procurus complex, with distinctive distal structures (Fig. 71). Embolus mostly sclerotized, with complex tip and long sclerotized spine ('s' in Figs 60 and 72). Legs probably without spines, curved hairs, and vertical hairs (most hairs missing); retrolateral trichobothrium of tibia 2 at 7%; tarsus 2 with >15 pseudosegments (only distally fairly distinct). Epiandrous spigots and ALS spigots as in Figures 66 and 75.

Variation. Measurements of male in MCZ (identical palps and chelicerae): tibia 1: 7.5, tibia 2: 4.7; tibia 1 L/d: 94, retrolateral trichobothrium of tibia 1 at 7%. Other males seen had identical genitalia but lacked legs 1.

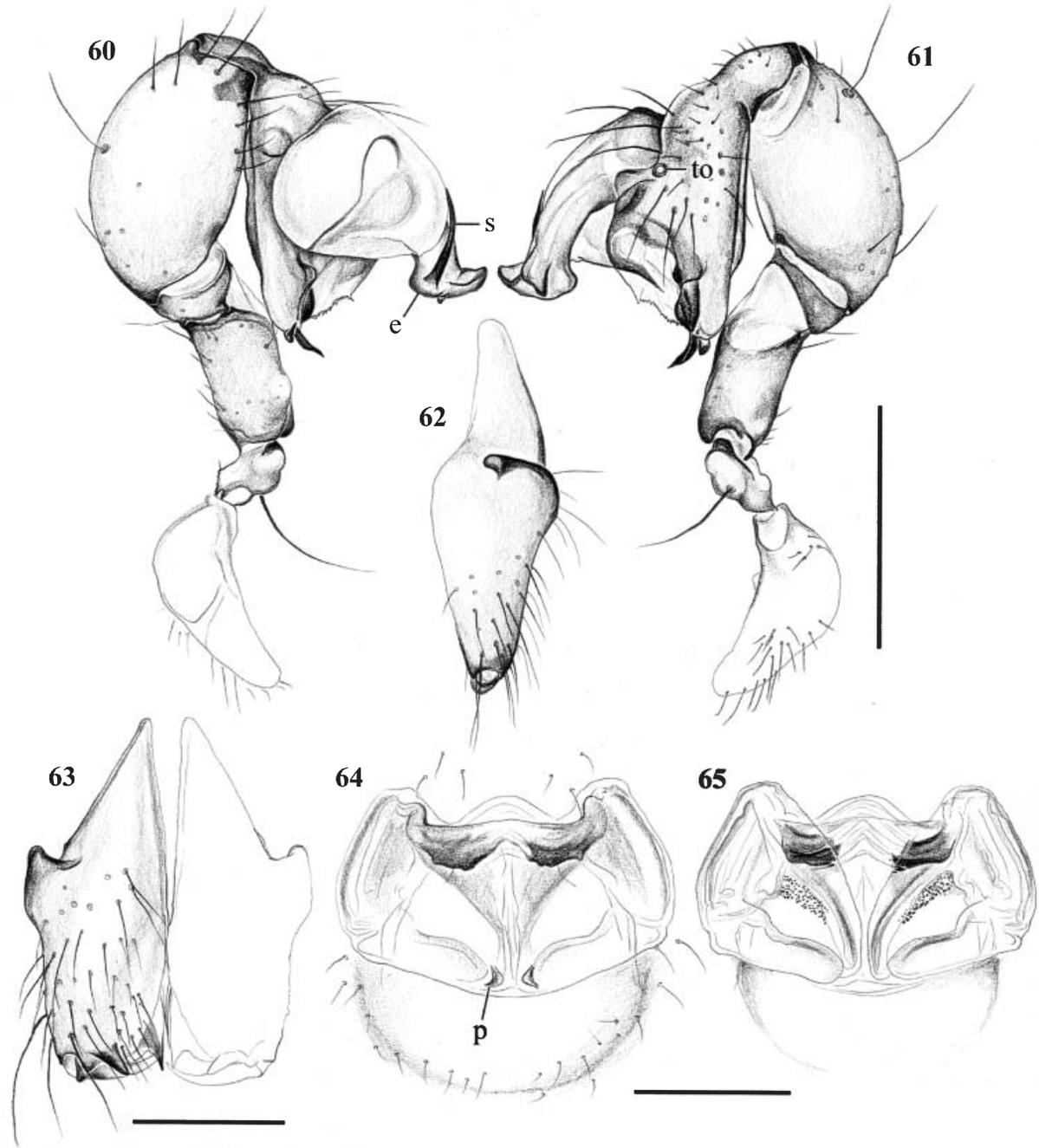
Female. In general similar to male, but ocular area and clypeus not brown. Tibia 1 (N = 11) 5.8–7.2 (\bar{x} = 6.4). Epigynum simple externally (Fig. 24), with pair of pockets ('p' in Fig. 64; distance between pockets 76 µm). Dorsal view as in Fig. 65.

Distribution. Known only from the Ranomafana area (Map 1).

Material examined. MADAGASCAR: *Fianarantsoa*: Ranomafana National Park: Talatakely: type above, together with 2♂ 8♀, same data. Ranomafana National Park at 21°S, 47°30'E, April 1992 (Kariko & Roth), 1♂ 2♀ in MCZ (33.989). 7 km W Ranomafana (~21°12'S, 47°27'E), 900 m a.s.l., March 8–13, 1990 (W. E. Steiner) 1♀ in USNM.



Figures 56–59. *Zatauvia zanahary*. Left male palp in prolateral (56) and retrolateral (57) views, and cleared epigynum in ventral (58) and dorsal (59) views. 'e': embolus; 'n': cymbium notch; 'p': pocket; 'pa': papilla on bulb; 'to': tarsal organ. Scale lines: 1 mm.



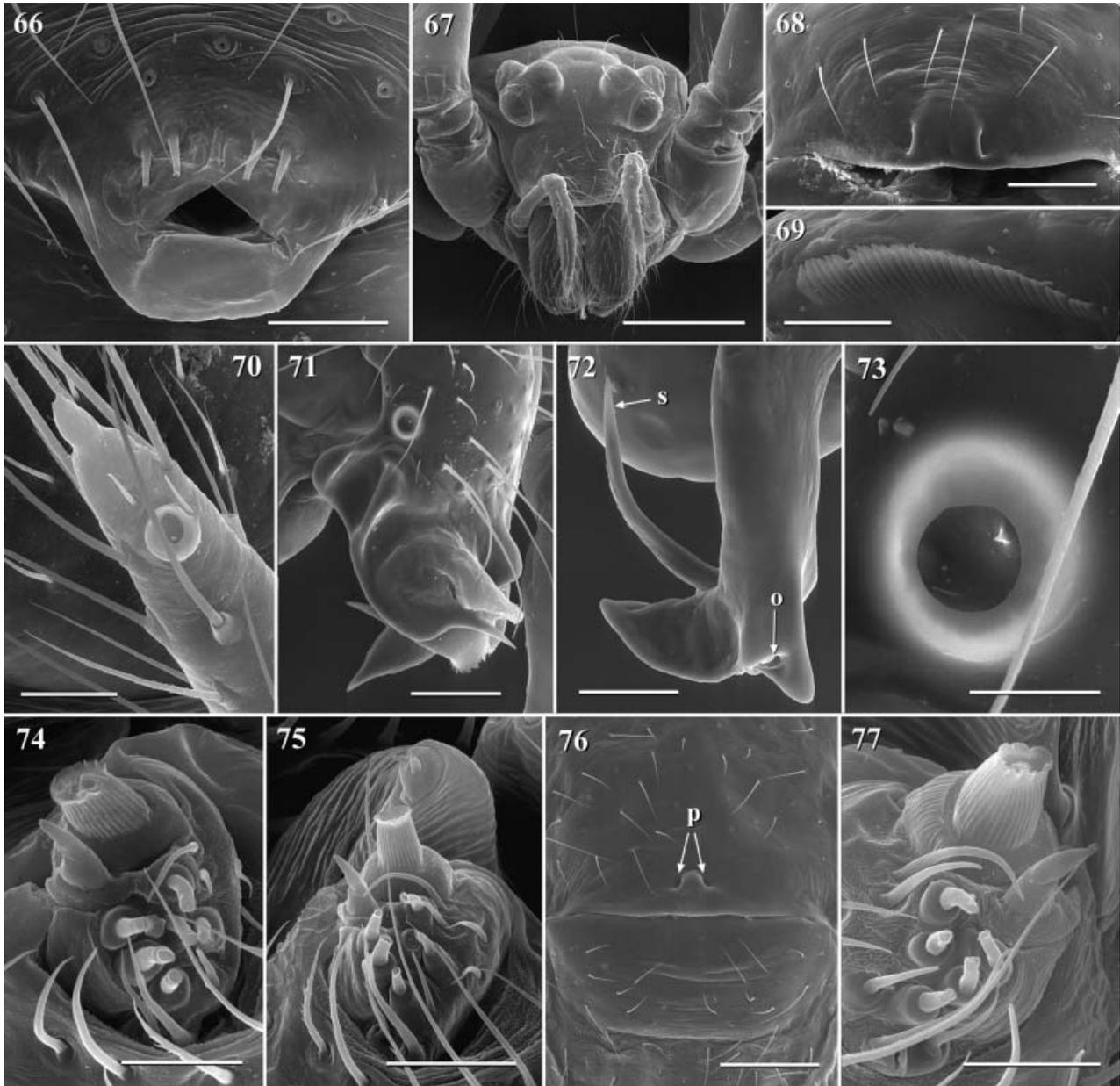
Figures 60–65. *Zatauvia voahangyae*. Left male palp in prolateral (60) and retrolateral (61) views, male chelicerae in lateral (62) frontal (63) views, and cleared epigynum in ventral (64) and dorsal (65) views. ‘e’: embolus; ‘p’: pocket; ‘s’: spine on embolus; ‘to’: tarsal organ. Scale lines: 0.5 mm (60–61), 0.2 mm (62–63), 0.3 mm (64–65).

ZATAVUA TALATAKELY, NEW SPECIES
(FIGS 17, 18, 78–80)

Type. Male holotype from Talatakely (21°15’S, 47°26’E), 915–1000 m a.s.l., Ranomafana National Park, Fianarantsoa, Madagascar; October 30 – November 20, 1998 (V. F. Lee & K. J. Ribardo); in CAS.

Etymology. Named for the type locality. The specific name is a noun in apposition.

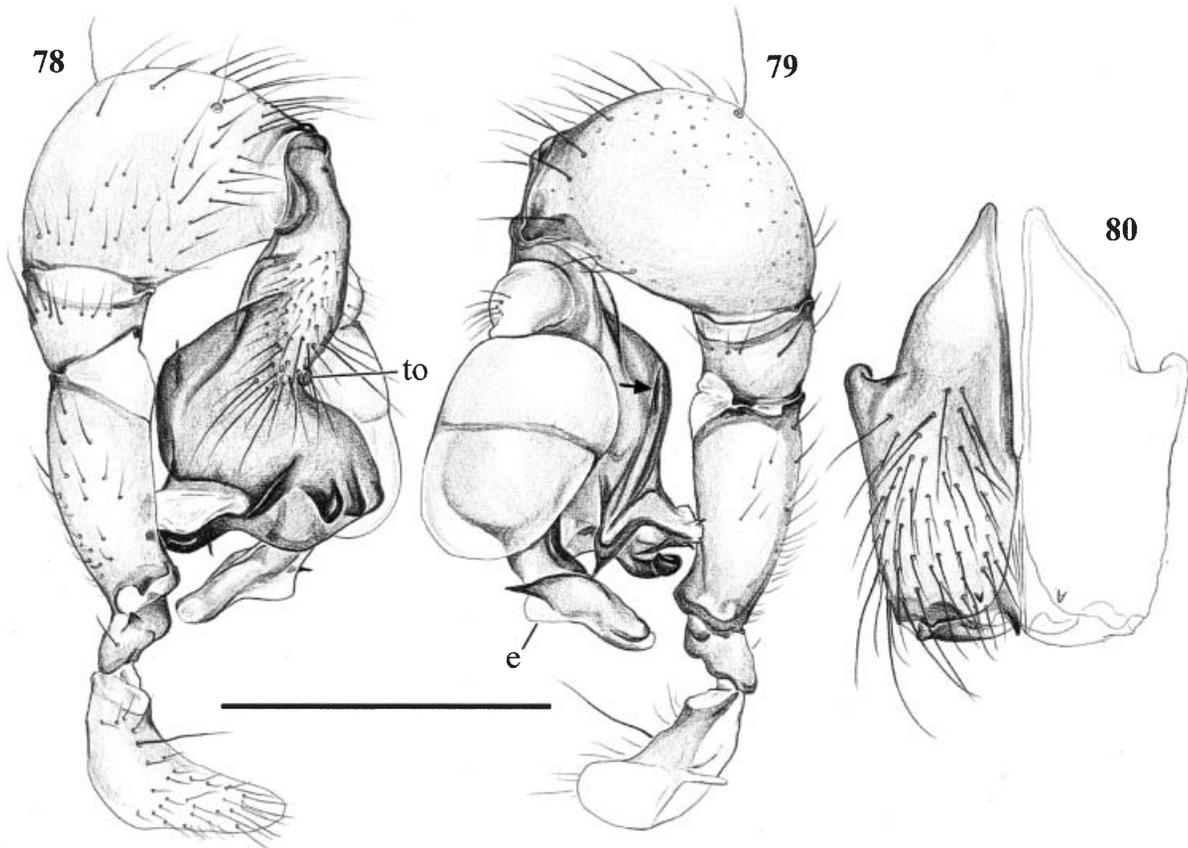
Diagnosis. Medium size species with cylindrical opisthosoma, distinguished from known congeners by the shape of the procurus (Figs 78 and 79: overall shape and several unnamed details).



Figures 66–77. *Zatauvia voahangyae* (66–75) and *Z. analalava* (76–77). 66, Male gonopore with epiandrous spigots. 67, Female prosoma, frontal view. 68, Epigynum with pockets. 69, Male pedipalpal coxa serrula. 70, Tip of female palp with tarsal organ. 71, Procurus, retrolatero-dorsal view. 72, Embolus with sclerotized spine ('s') and sperm duct opening ('o'). 73, Male palpal tarsal organ. 74, Female ALS. 75, Male ALS and PMS. 76, Epigynum with pockets ('p'). 77, Female ALS. Scale lines: 40 μm (66), 400 μm (67), 100 μm (68, 71), 30 μm (69–70, 75), 20 μm (73–74, 77), 200 μm (76).

Male (holotype). Total length 4.1, carapace width 1.6. Leg 1: 41.9 (10.8 + 0.8 + 10.0 + 18.0 + 2.3), tibia 2: 6.3, tibia 3: 4.2, tibia 4: 6.5; tibia 1 L/d: 63. Habitus as in Figures 17 and 18. Carapace ochre-yellow with dark brown median band, clypeus brown; sternum whitish. Legs ochre-yellow with slightly darker rings subdistally on femora (faint) and tibiae, patellae also darker. Opisthosoma ochre-grey, with slightly darker spots

shining through cuticle and dark brown plate above pedicel; ventrally pair of dark spots in front of genital area. Ocular area slightly elevated, not clearly separated from carapace; distance PME-PME 180 μm ; diameter PME 140 μm ; distance PME-ALE 60 μm . Thoracic furrow absent, only short line behind ocular area (this region widely depressed). Clypeus not modified. Sternum wider than long (0.96/0.64). Chelicerae



Figures 78–80. *Zatauvia talatakely*. Right male palp in retrolateral (78) and prolateral (79) views, and male chelicerae in frontal view (80). 'e': embolus; 'to': tarsal organ; arrow points to distinctive spine. Scale line: 1 mm (78, 79).

as in Fig. 80, with tiny apophyses near fangs, proximal apophyses in lateral view as in *Z. voahangyae* (cf. Fig. 62). Palps as in Figures 78 and 79; trochanter without apophysis, femur with small apophysis retrolaterally (proximally), procurus very complex and massive, with distinctive spine visible in prolateral view (arrow in Fig. 79) (cf. *Z. tamatave*). Embolus ('e' in Fig. 79) on one side only sclerotized, subterminal short branch with sclerotized spine. Legs without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 8%; tarsus 1 with >20 pseudosegments (only distally fairly distinct).

Variation. Tibia 1 in other male seen: 10.3; palps and chelicerae identical.

Female. Unknown.

Distribution. Known only from type locality (Map 1).

Material examined. MADAGASCAR: Fianarantsoa: Ranomafana National Park: Talatakely: type above. Talatakely at 21°14.9'S, 47°25.6'E, April 19–30, 1998 (C. E. Griswold, D. H. Kavanaugh, N. P. Penny, M. J. Raherilalao, J. S. Ranorianarisoa, J. Schweikert, D.

Ubick), 1♂ in CAS (originally together with *Smeringopus pallidus* in a vial labelled 'on buildings').

ZATAVUA ISALO, NEW SPECIES

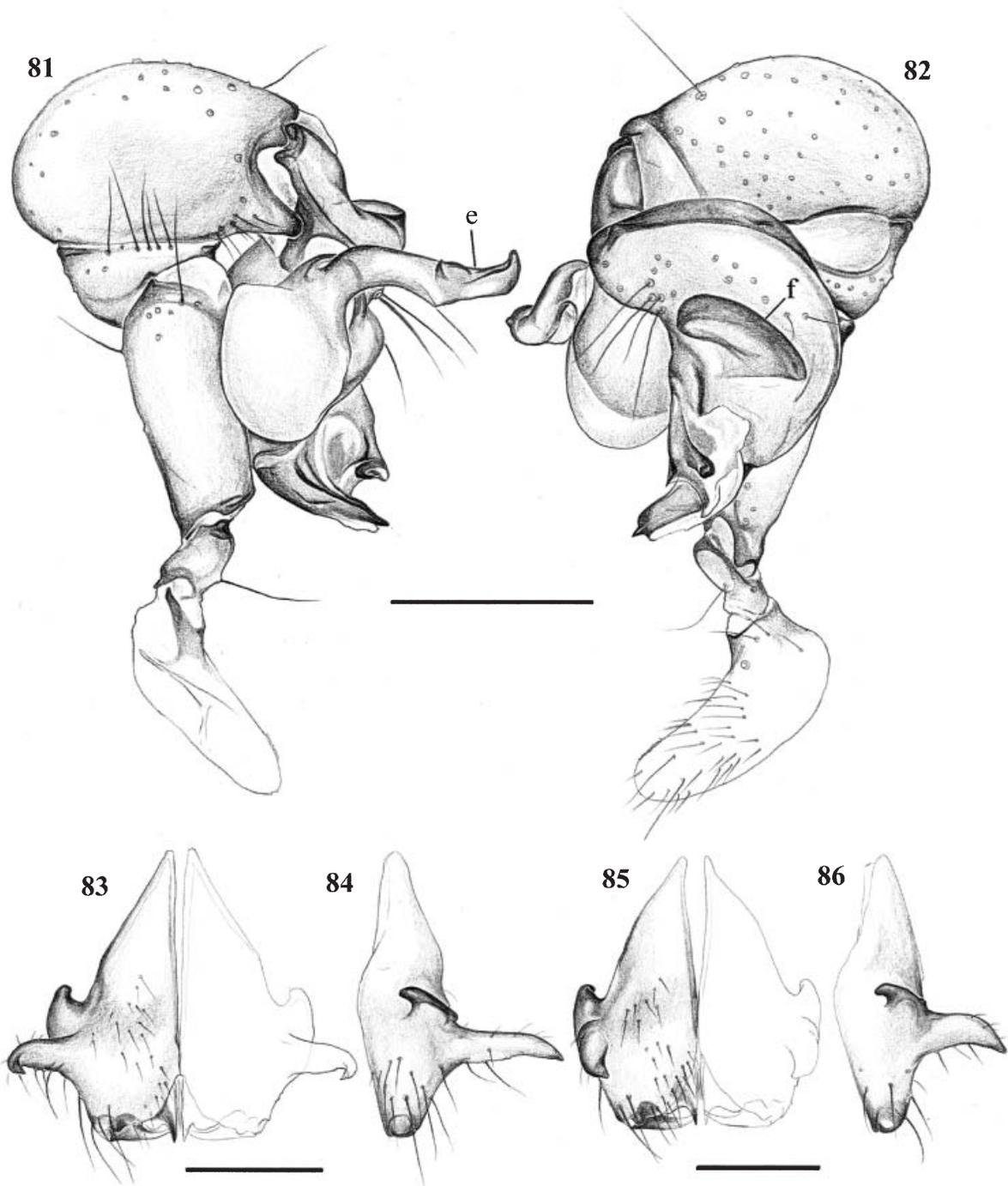
(FIGS 11, 12, 26, 81–84, 87, 88)

Type. Male holotype from Isalo National Park, Fianarantsoa, Madagascar; May 23–26, 1992 (V. Roth), in MCZ (34056).

Etymology. Named for the type locality. The specific name is a noun in apposition.

Diagnosis. Medium size species with globular opisthosoma; very closely related to *Z. madagascariensis* (Fage), with almost identical palps, but with male cheliceral apophyses and pockets on epigynum more widely spread (compare Fig. 83 with 85 and Fig. 87 with 89).

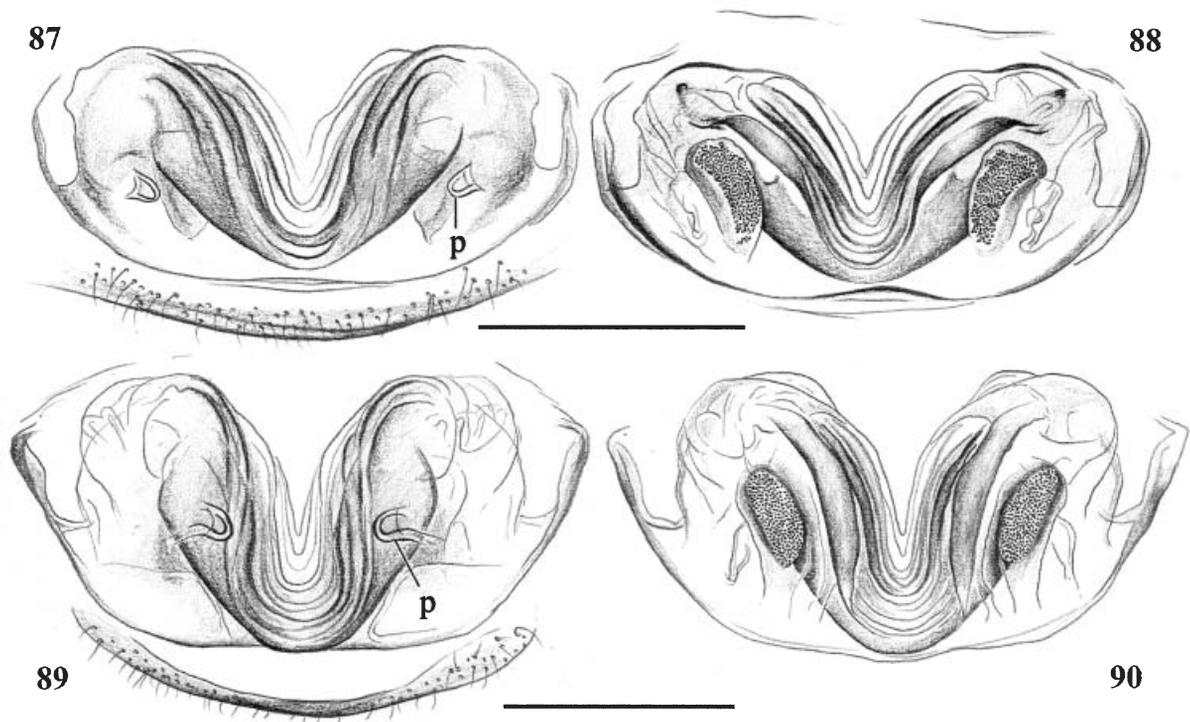
Male (holotype). Total length 2.7, carapace width 1.1. Leg 1 missing, tibia 2: 4.6, tibia 3: 2.9, tibia 4: 4.7; tibia 2 L/d: 46. Habitus as in Figures 11 and 12. Carapace pale ochre with distinctive light brown pattern, ster-



Figures 81–86. *Zatavua isalo* (81–84) and *Z. madagascariensis* (85, 86). Left male palp in prolateral (81) and retrolateral (82) views, and male chelicerae in frontal (83, 85) and lateral (84, 86) views. 'e': embolus; 'f': distinctive flap. Scale lines: 0.5 mm (81, 82), 0.3 mm (83–86).

num whitish. Legs ochre-yellow, with slightly darker rings on femora and tibiae (subdistally) and in patella area. Opisthosoma grey with black and white spots; ventrally grey, without marks. Ocular area elevated and clearly separated from carapace; distance PME-

PME 90 μ m; diameter PME 100 μ m; distance PME-ALE 30 μ m. Thoracic furrow distinct and relatively deep. Clypeus not modified. Sternum wider than long (0.76/0.56). Chelicerae as in Figures 83 and 84, without modified hairs on tips of apophyses (but with stri-



Figures 87–90. *Zatauvia isalo* (87–88) and *Z. madagascariensis* (89, 90). Cleared epigyna in ventral (87, 89) and dorsal (88, 90) views. 'p': pockets. Scale lines: 0.5 mm.

ated cuticle); distance between tips of apophyses 0.70. Palps as in Figures 81 and 82; trochanter and femur without apophyses, procurus complex, with thin flap retrolaterally ('f' in Fig. 82). Embolus ('e' in Fig. 81) with complex tip, only partly sclerotized, with subapical sclerotized spine. Legs without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 2 at 9%; tarsus 2 with about 20 pseudosegments (only distally about 10 fairly distinct).

Female. In general similar to male, but opisthosoma without black spots. Tibia 1: 5.3. Epigynum as in Figures 26 and 87; distance between pockets 0.57. Dorsal view as in Figure 88.

Distribution. Known only from type locality (Map 1).

Material examined. MADAGASCAR: Fianarantsoa: Isalo National Park: type above, together with 1♀, same data.

ZATAVUA MADAGASCARIENSIS (FAGE, 1945)

N. COMB. (FIGS 25, 85, 86, 89, 90)

Spermophora madagascariensis Fage, 1945: 303, fig. 1(a)–(d).

Types. One male, 3 females and 1 juvenile syntypes from grotte d'Andoharano (about 22°50'S, 43°40'E),

Manombo valley, Toliara, Madagascar; collection date unknown (M. R. Decary), in MNHN (MP AR 10389).

Diagnosis. Very closely related to *Z. isalo*, with almost identical palps (cf. Figs 81 and 82), but with male cheliceral apophyses and pockets on epigynum less widely spread. This species might be a senior synonym of *Z. fagei* (Millot), which was collected by the same collector but not within the cave of Andoharano but apparently outside ('région de la grotte d'Andoharano', Millot, 1946).

Male (syntype). Total length 2.8, carapace width 1.4. Legs 1 and 2 missing (leg 1 according to original description 2.8 cm [mm was a lapsus!]), tibia 3: 3.3, tibia 4: 5.0. Habitus as in *Z. isalo* (cf. Figs 11 and 12). Carapace pale ochre-yellow with pair of slightly darker marks parallel to lateral margins; sternum whitish with heart-shaped ochre yellow mark; legs pale ochre-yellow, with slightly darker rings on femora and tibiae (subdistally) and in patella area; opisthosoma monochromous grey. Ocular area elevated and clearly separated from carapace; distance PME-PME 100 µm; diameter PME 100 µm; distance PME-ALE 30 µm. Thoracic furrow distinct but shallow. Sternum wider than long (0.88/0.72). Clypeus unmodified. Chelicerae as in Figures 85 and 86, without modified hairs

on tips of apophyses; distance between tips of apophyses 0.45. Palps as in *Z. isalo*, but flat cuticular flap retrolaterally on procurus ('f' in Fig. 82) narrower in present species. Legs without spines, without curved hairs, few vertical hairs (most hairs missing, however).

Female. In general similar to male. Tibia 1 in a syn-type: 7.3. Epigynum as in Figures 25 and 89; distance between pockets 0.34. Dorsal view as in Fig. 90.

Distribution. Known only from type locality (Map 1).

Material examined. MADAGASCAR: *Toliara*: Manombo valley: types above.

ZATAVUA MAHAFALY, NEW SPECIES

(FIGS 5, 6, 27, 91–95)

Type. Male holotype from near Eloetse, by Lac Tsimanampetsoa (24°10'S, 43°45'E), Mahafaly, Toliara, Madagascar; September 15–16, 1992 (V. & B. Roth), in back of shelter cave, shaded to dark; in CAS.

Etymology. Named for the type locality. The specific name is a noun in apposition.

Diagnosis. Large species with globular opisthosoma, easily distinguished from known congeners by the widely spread male cheliceral apophyses (Fig. 93), the globular male palpal tibia (Figs 91 and 92), the massive curved procurus (Fig. 92), and the wide epigynum (Fig. 27).

Male (holotype). Total length 4.8, carapace width 2.1. Leg 1: 50.2 (13.5 + 0.8 + 14.0 + 20.2 + 1.7), tibia 2: 9.5, tibia 3: 6.5, tibia 4: 8.5; tibia 1 L/d: 78. Habitus as in Figures 5 and 6. Carapace pale ochre with light brown mark posteriorly; sternum pale ochre with dark margin. Legs ochre to light brown, patella area darker. Opisthosoma pale ochre. Ocular area slightly elevated, not clearly separated from carapace; distance PME-PME 150 µm; diameter PME 110 µm; distance PME-ALE 40 µm. Thoracic furrow absent, only shallow indentation behind ocular area. Clypeus not modified. Sternum wider than long (1.3/1.0). Chelicerae as in Figure 93, proximal apophyses directed backwards as in *Z. voahangyae* (cf. Fig. 62), distal apophyses widely spread, with sclerotized teeth at tip, without modified hairs; distance between outer tips of apophyses 1.95. Palps as in Figures 91 and 92, trochanter with small sclerotized hump ventrally, femur with distinct hump proximo-ventrally, tibia almost globular, procurus massive with complex tip. Embolus ('e' in Fig. 91) partly sclerotized, with subdistal conical projection but without spine. Legs without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 5%; tarsus 1 with >10 very indistinct pseudosegments.

Female. In general similar to male, but sternum with light brown marks. Tibia 1: 11.5, tibia 2: 7.3, tibia 3: 5.5, tibia 4: 7.3. Epigynum as in Figures 27 and 94; at lateral extremes with sclerotized ridges ('r' in Fig. 94; distance between ridges 1.62). Dorsal view as in Fig. 95.

Distribution. Known only from type locality (Map 1).

Material examined. MADAGASCAR: *Toliara*: Mahafaly: type above, together with 1♀, same data.

ZATAVUA KELY, NEW SPECIES

(FIGS 28, 96–101)

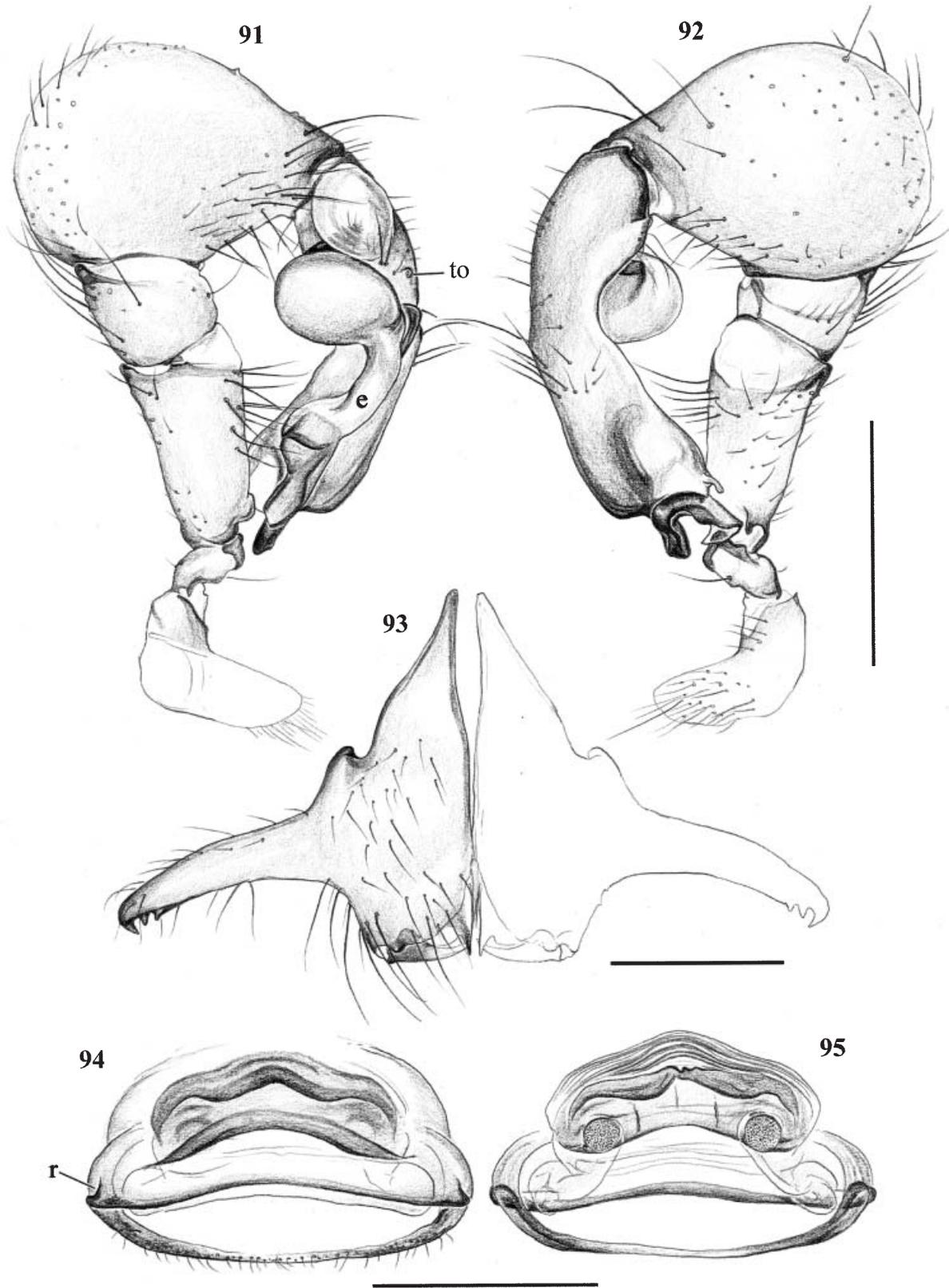
Type. Male holotype from English Camp (12°54'34"S, 49°06'36"E), Antsiranana, Madagascar; August 20–26, 1992 (V. & B. Roth); in CAS.

Etymology. 'Kely' is Malagasy for small and refers to the size of this species. The word is here used as noun in apposition.

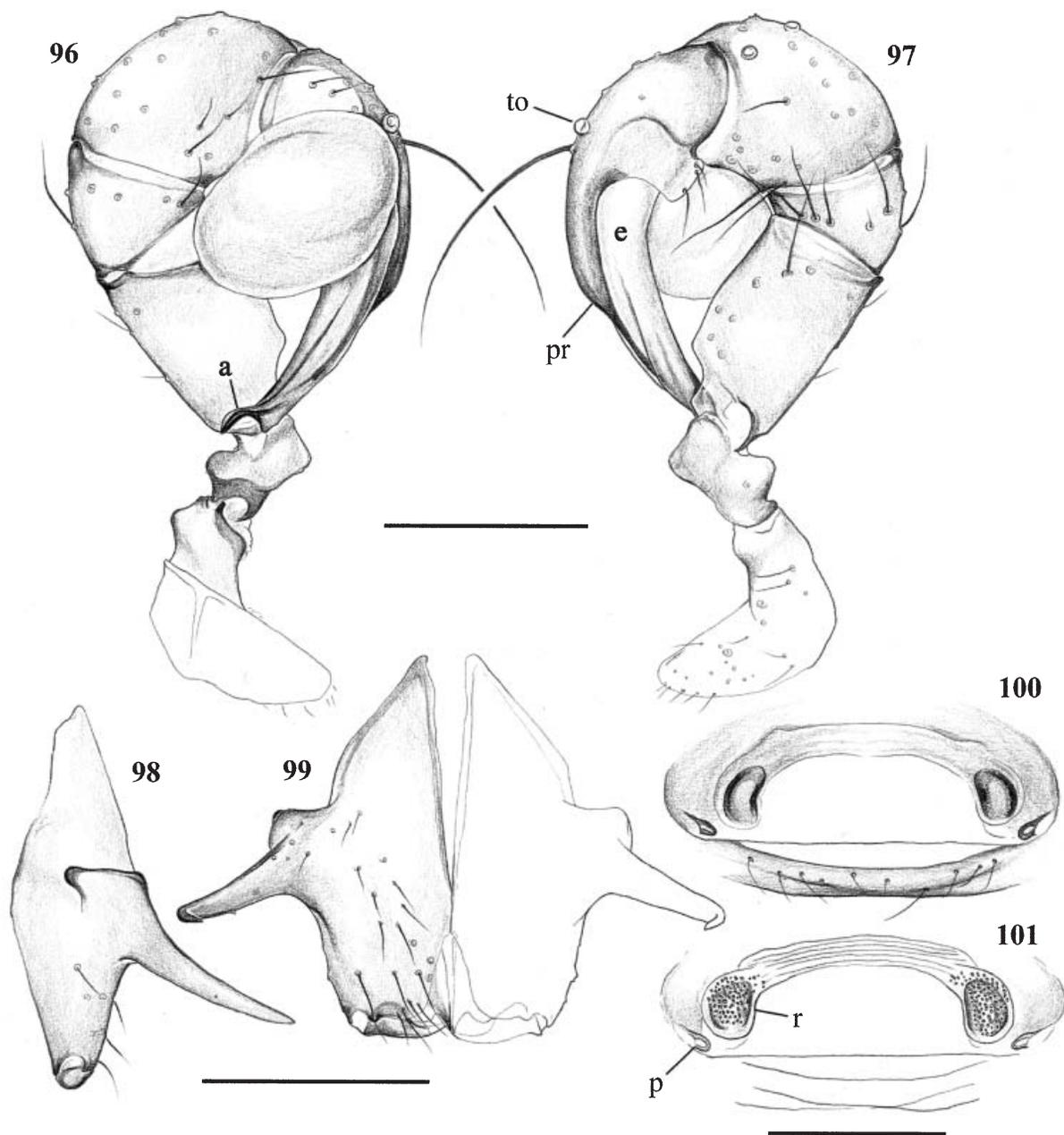
Diagnosis. Small species with globular opisthosoma, easily distinguished from known congeners by the widely spread male cheliceral apophyses (Fig. 99; *Z. mahafaly* has similar chelicerae but is much larger), the simple spine-like procurus ('pr' in Fig. 97), and the epigynum with lateral sclerotized structures ('r' in Fig. 101; receptacles?) shining through cuticle (Fig. 28).

Male (holotype). Total length 1.3, carapace width 0.6. Leg 1: 7.7 (2.0 + 0.2 + 2.2 + 2.6 + 0.7), tibia 2: 1.2, tibia 3: 0.8, tibia 4: 1.5; tibia 1 L/d: 37. Habitus similar to *Z. isalo* (cf. Figs 11 and 12). Prosoma and legs ochre-yellow. Opisthosoma ochre-grey, with slightly darker spots shining through cuticle. Ocular area slightly elevated, not clearly separated from carapace; distance PME-PME 50 µm; diameter PME 50 µm; distance PME-ALE 20 µm. Thoracic furrow present, but shallow and indistinct. Clypeus not modified. Sternum wider than long (0.44/0.32). Chelicerae as in Figures 98 and 99, distal apophyses widely spread, without modified hairs but striated cuticle at tips of apophyses; distance between tips of apophyses 0.45. Palps as in Figures 96 and 97; trochanter with small conical projection ventrally, procurus very simple, ending in sclerotized spine that is hidden in fold of embolus ('e' in Fig. 97). Embolus mostly sclerotized, with curved terminal apophysis ('a' in Fig. 96); sperm duct apparently opens at basis of apophysis. Legs without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 not seen; tarsus 1 with >10 pseudosegments (only distally fairly distinct).

Female. In general similar to male. Tibia 1: 1.8 in both females seen. Epigynum as in Fig. 28, protruding;



Figures 91–95. *Zatavia mahafaly*. Left male palp in prolateral (91) and retrolateral (92) views, male chelicerae in frontal view (93), and cleared epigynum in ventral (94) and dorsal (95) views. ‘e’: embolus; ‘r’: sclerotized ridge; ‘to’: tarsal organ. Scale lines: 1 mm (91, 92, 94, 95), 0.5 mm (93).



Figures 96–101. *Zatavua kely*. Left male palp in prolateral (96) and retrolateral (97) views, male chelicerae in lateral (98) and frontal (99) views, and cleared epigynum in ventral (100) and dorsal (101) views. 'a': apophysis on embolus; 'e': embolus; 'p': pocket; 'pr': procurus; 'r': putative receptacle; 'to': tarsal organ. Scale lines: 0.2 mm.

with pair of lateral pockets ('p' in Fig. 101) and oval structures that shine through cuticle (Figs 28 and 100). Distance between pockets 0.35.

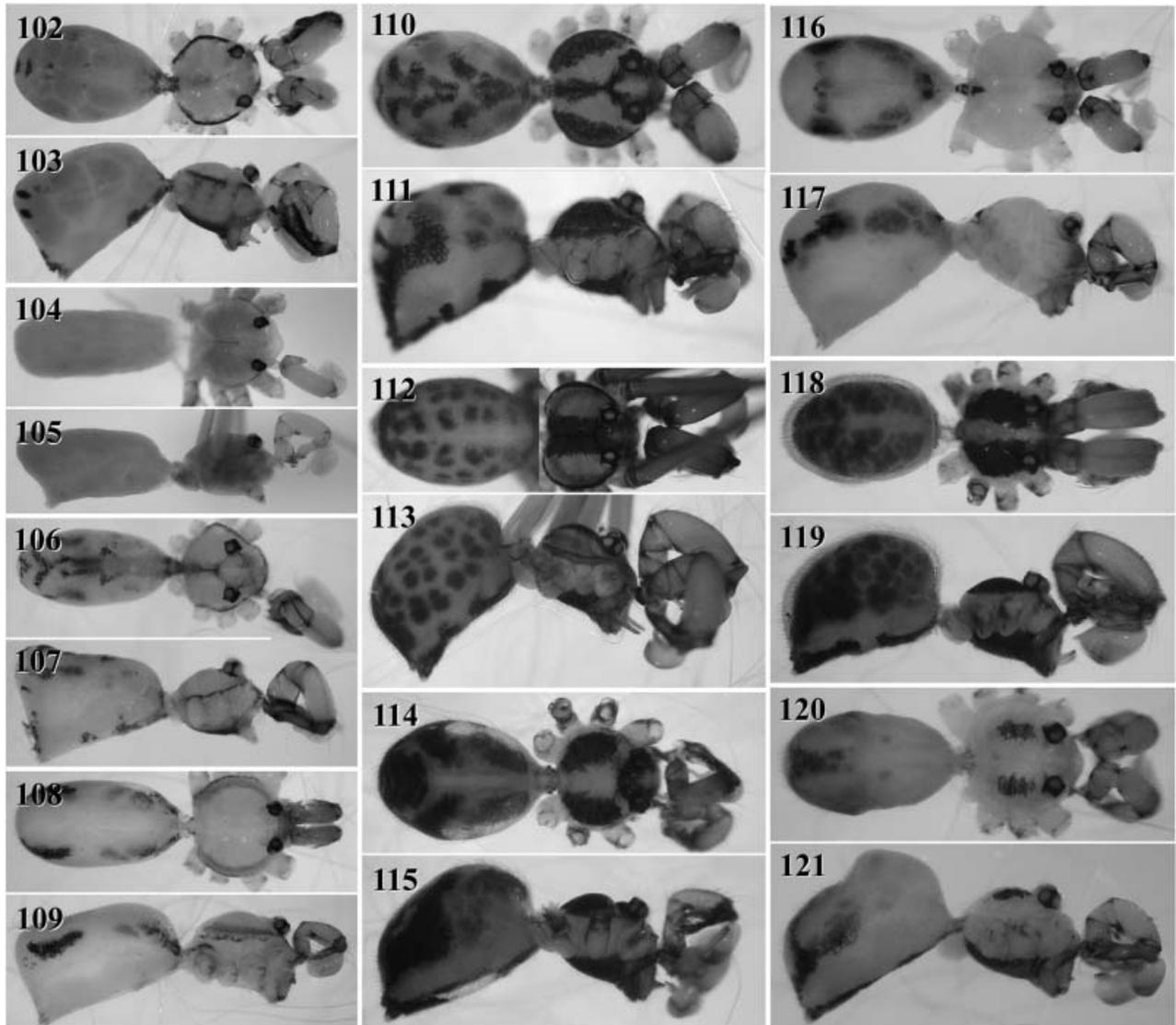
Distribution. Known only from type locality (Map 1).

Material examined. MADAGASCAR: Antsiranana: English Camp: type above, together with 2♀ and some juveniles, same data.

PARAMICROMERYS MILLOT, 1946

Paramicromerys Millot, 1946: 145; type species by original designation: *Micromerys madagascariensis* Simon, 1893.

Diagnosis. Long-legged, six-eyed pholcids of medium size (total length ~1.5–4 mm), with oval or slightly elongate opisthosoma. Distinguished from *Zatavua* by

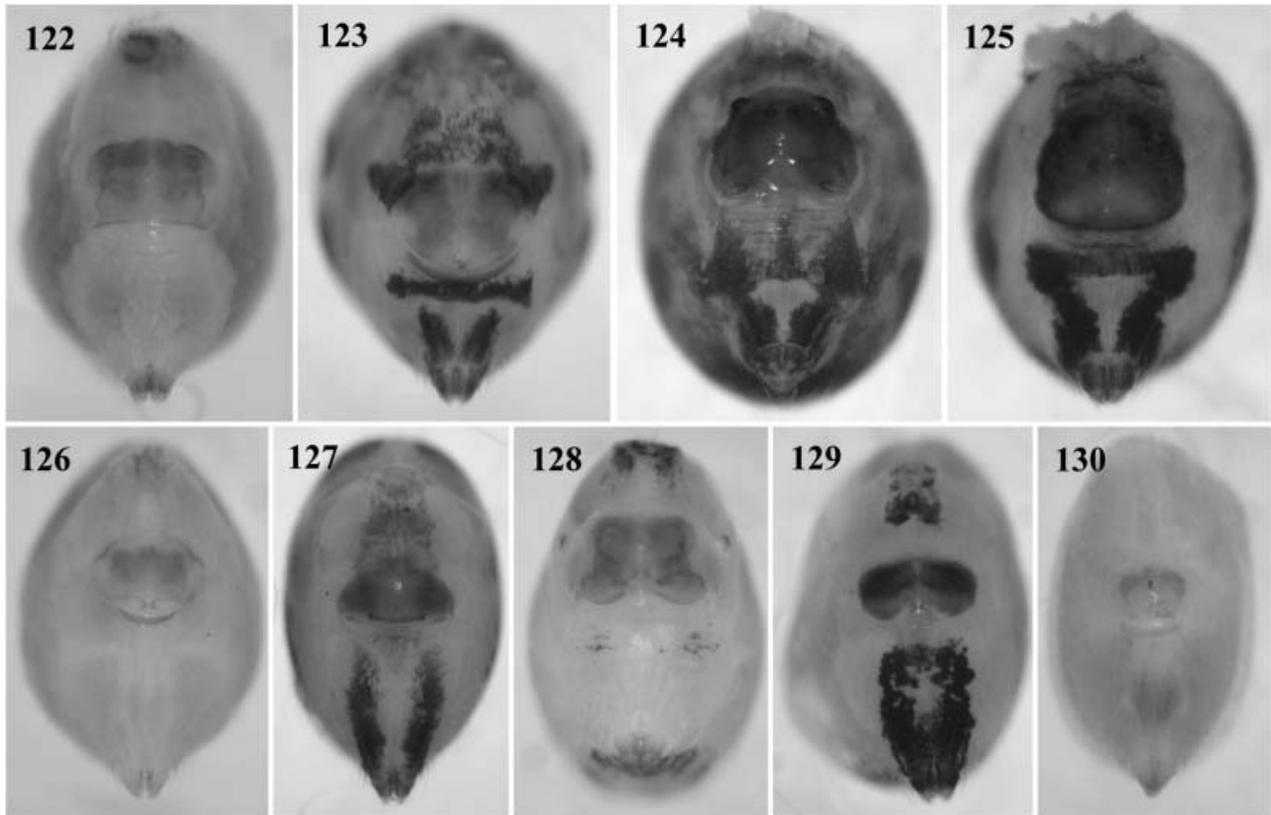


Figures 102–121. *Paramicromerys* habitus, males in dorsal and lateral views. 102–103, *P. betsileo*. 104–105, *P. mahira*. 106–107, *P. rothorum*. 108–109, *P. rabearivelo*. 110–111, *P. coddingtoni*. 112–113, *P. nampoinai*. 114–115, *P. scharffi*. 116–117, *P. ralamboi*. 118–119, *P. manantenina*. 120–121, *P. marojejy*.

lateral cheliceral apophyses not pointing backwards (Figs 136, 179, 193 and 201), absence of notch on cymbium, wide distance between eye triads (PME-PME > 230% of PME diameter, vs. <180% in *Zatavua*) and by reduction of spigots on ALS to basic set of two (Figs 148, 149, 160 and 188). Distinguished from other related genera by shift of tibia-tarsus joints, resulting in dorsal position of prolateral joint and ventral position of retrolateral joint (Figs 135, 155, 169, 178, 192, 199 and 205).

Description. Total length in males about 1.5–3.5 mm. Carapace oval or roundish, thoracic groove present but often very shallow and restricted to frontal half,

often with dark pattern that may be distinctive for species. Six eyes in two triads, on moderately elevated ocular area. Distance PME-ALE small (~30–50% of PME diameter), distance PME-PME large (~230–500% of PME diameter); no trace of AME. Clypeus never modified. Male chelicerae with pair of simple lateral apophyses and frontal apophyses in variable position and shape; the latter in some species with modified hairs imbedded in tips (*P. nampoinai*, *manantenina*; Figs 189, 190 and 195). Male palps small to very large in relation to overall size (compare Figs 109 and 113); coxa without apophysis, in some species with ventral hump; trochanter complex, with several sclerotized apophyses; femur very short, in



Figures 122–130. *Paramicromerys*, female opisthosomata, ventral views with epigynum. 122, *P. betsileo*. 123, *P. coddingtoni*. 124, *P. nampoinai*. 125, *P. manantenina*. 126, *P. ralamboi*. 127, *P. scharffi*. 128, *P. rothorum*. 129, *P. marojejy*. 130, *P. rabearivelo*.

some species with dorso-distal apophysis (arrows in Figs 178, 192 and 199); patella triangular in lateral view; tibia cylindrical, not highly expanded, with two trichobothria; tibia-cymbium joints distinctively shifted, resulting in dorsal position of prolateral joint and ventral position of retrolateral joint (Figs 135, 155, 169, 178, 192, 199 and 205); procurus usually complex, with cup-shaped tarsal organ (e.g. Figs 145, 150 and 165), in proximal position (e.g. Figs 135 and 174), with hinged process prolatero-ventrally ('hp' in Figs 154, 168 and 209); bulb consisting of proximal globular part and membranous embolus that is sometimes provided with distal transparent spine. Legs usually long (leg 1 about 10–13 × body length), medium-thin (tibia 1 L/d ~50–90), leg 1 always longest, legs 2 and 4 about same length, leg 3 shortest. Legs sometimes with macrosetae ventrally on femora (only femora 1, rarely also 2), with few vertical hairs, without curved hairs; retrolateral trichobothrium of tibia 1 at 7–12%. Prolateral trichobothrium missing on tibiae 1, present in all others. Tarsus 1 with over 20 pseudosegments, but only ~10–20 distal pseudosegments easily visible in dissecting microscope. Opisthosoma either oval or slightly elongate, rarely with

slight posterior elongation over spinnerets (Figs 105 and 107). Male gonopore with four epiandrous spigots in all species examined (*P. betsileo*, *coddingtoni*, *manantenina*; Figs 146, 162 and 186); ALS with only basic set of two spigots (examined: *P. betsileo*, *coddingtoni*, *ralamboi*, *manantenina*, *nampoinai*, *scharffi*, *rothorum*, *marojejy*, *rabearivelo*; Figs 148, 149, 160 and 188); other spinnerets typical for family (Fig. 147; cf. Huber, 2000).

Sexual dimorphism slight. Colour pattern often more variable in females than in males. Female legs never with spines. Epigynum shape very variable (Figs 122–130), often with pair of pockets.

Monophyly. The synapomorphy supporting this genus is the shift of the tibia-cymbium joints (see Description above).

Generic relationships. As discussed above, the sister group of *Paramicromerys* is not resolved in any of the 12 most parsimonious cladograms obtained. Instead, *Paramicromerys* is part of a polytomy that always includes East African '*Spermophora*', along with either *Spermophorides* or *Metagonia* and *Micromerys*

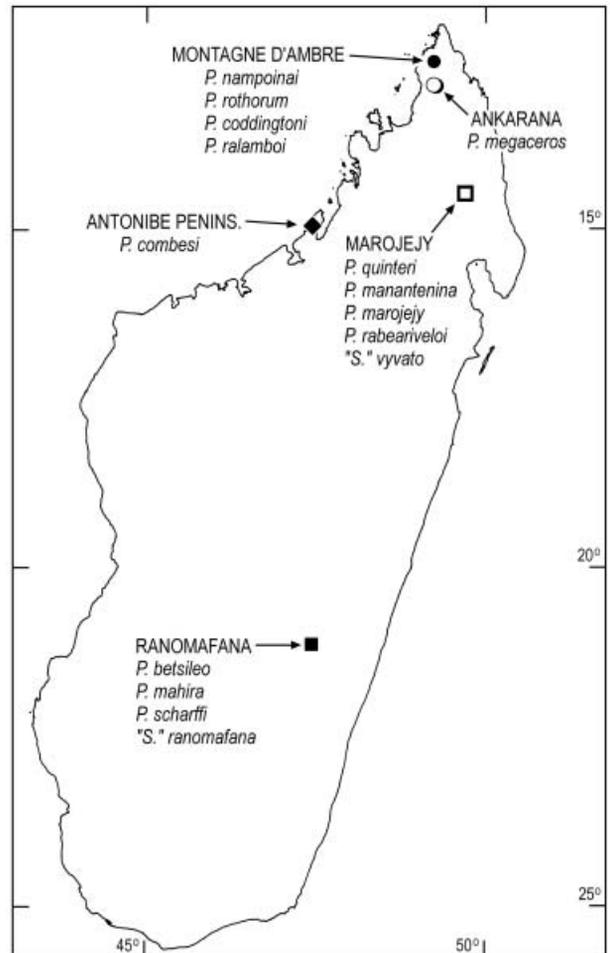
(Appendix 5). All these genera share a hinged process on the procurus that is here interpreted as homologous, and the reduction of the spigots on the ALS to the basic set of two.

Specific relationships. A close relationship between *P. nampoinai* and *manantenina* is supported by several synapomorphies: modified hairs on the tips of the cheliceral apophyses, short side branch on embolus, sclerotized cone-shaped structure proximally on procurus (Figs 178 and 192) that carries the tarsal organ (Fig. 187). Both species share with *P. scharffi* a proximo-dorsal apophysis on the male palpal femur (arrows in Figs 178, 192 and 199). A second species-group is characterized by a transparent spine distally on the embolus [*P. coddingtoni* and the putatively close relatives *combesi* (Millot), *ralamboi*, *quinteri*, *mahira*], but this might be a plesiomorphy. Both species groups share the spines ventrally on the frontal male femora [unknown in *P. quinteri*, *mahira*, and *combesi* (Millot)]. The type species *P. madagascariensis* (Simon) and *P. betsileo* have almost identical palps (compare Figs 131 and 135) and are therefore considered closely related. The other species included (*P. rothorum*, *marojejy*, *rabeariveloi*) all share the shift of the tibia-cymbium joints, but their exact position is unclear. Finally, *P. megaceros* (Millot) is tentatively assigned to *Paramicromerys* because it shares the wide distance between the eye triads and the simple lateral cheliceral apophyses, but it may be misplaced.

Natural history. No species has ever been studied in any detail, and little can be inferred from notes on the collection labels. In contrast to *Zatavua*, only one known species is cavernicole [the tentatively assigned *P. megaceros* (Millot)]. *Paramicromerys betsileo* has been collected abundantly on low foliage and saplings, by fogging of dead leaves on fallen trees, on roadside vegetation, and by beating low vegetation (often together with '*Spermophora*' *ranomafana* n. sp.).

Distribution. Known from Madagascar only. Most records are from just three localities (Map 2), but the high diversity at each of these localities suggests that the genus has a much wider distribution. No species has been collected at two localities more than a few kilometres apart. This is especially striking in the north, where two locations less than 200 km apart (Montagne d'Ambre and Marojejy Reserve) yielded four and five species, respectively (one species from Marojejy is not described herein), with no overlap.

Composition. The genus includes a total of 14 described species. Of these, two were described by Millot (1946), and are not treated below (*P. combesi*, *megaceros*). The remaining 12 species [11 new species and *P. madagascariensis* (Simon)], are described



Map 2. Known distribution of *Paramicromerys* and of Malagasy '*Spermophora*' species.

below. The collections studied contain three additional new species that are not described due to their poor state of preservation. Considering the facts that (1) most or all species seem to have small distributional ranges (see above) and that (2) all areas that were subjected to intense collecting yielded between four and five species, it seems reasonable to expect several dozen additional species not yet discovered.

PARAMICROMERYS MADAGASCARIENSIS (SIMON, 1893)
(FIGS 131, 132)

Micromerys madagascariensis Simon, 1893: 472–474, fig. 462. Timm, 1976: 72, figs 13, 14.

Paramicromerys madagascariensis: Millot, 1946: 146–147, fig. 21(a)–(d).

Type. Male holotype from unspecified locality in Madagascar; collector and collection date unknown, in MNHN (9277; AR 10501).

Diagnosis. Very closely related to *P. betsileo*, with almost identical palps (compare Figs 131 and 135), but with male cheliceral apophyses much closer together (compare Figs 132 and 133).

Male (holotype). Total length ~1.6 (deformed), carapace width ~0.7. Femur 1: 5.6, other segments and legs missing. Habitus and prosoma shape apparently as in *P. betsileo* (cf. Figs 102 and 103). Carapace ochre with black margin; sternum ochre; opisthosoma grey with dark spots dorsally. Ocular area deformed. Chelicerae as in Fig. 132, without modified hairs on tips of apophyses; distance between tips of apophyses 55 µm. Palps as in Fig. 131, differing from *P. betsileo* primarily by the shapes of the trochanter apophyses (arrows in Fig. 131).

Female. Unknown.

Distribution. Unknown.

Material examined. MADAGASCAR: type above.

PARAMICROMERYS BETSILEO, NEW SPECIES

(FIGS 102, 103, 122, 133–153)

Type. Male holotype from Vohiparara (21°14'S, 47°24'E), 900 m a.s.l., Ranomafana National Park, Fianarantsoa, Madagascar; December 5–7, 1993 (N. Scharff, S. Larcher, C. E. Griswold, R. Andriamasimanana); in CAS.

Etymology. Named for the Betsileo, one of the major tribes in Madagascar. The species name is a noun in apposition.

Diagnosis. Closely related to the type species *P. madagascariensis*, with almost identical palps, distinguished by the more widely spread male cheliceral apophyses (compare Figs 132 and 133). The MCZ has another close relative from the 'eastern highlands', differing primarily by details of the dorso-distal element of the procurus ('d' in Fig. 134; MCZ 34057).

Male (holotype). Total length 1.8, carapace width 0.76. Leg 1: 21.9 (5.5 + 0.3 + 5.3 + 8.3 + 2.5), tibia 2: 3.1, tibia 3: 2.2, tibia 4: 2.8; tibia 1 L/d: 83. Habitus as in Figures 102 and 103. Carapace ochre-yellow with blackish margin; sternum blackish except laterally. Legs ochre-yellow with dark rings on femora and tibiae (subdistally). Opisthosoma ochre-grey, with blackish spots posteriorly and light grey spots shining through cuticle. Ocular area distinctly separated from carapace, with each triad on additional elevation; distance PME-PME 260 µm; diameter PME 80 µm; distance PME-ALE 30 µm. Thoracic furrow indistinct, only frontally slightly indented dark line. Sternum wider than long (0.56/0.46). Chelicerae as in Figures 133, 136 and 141, tips of apophyses without

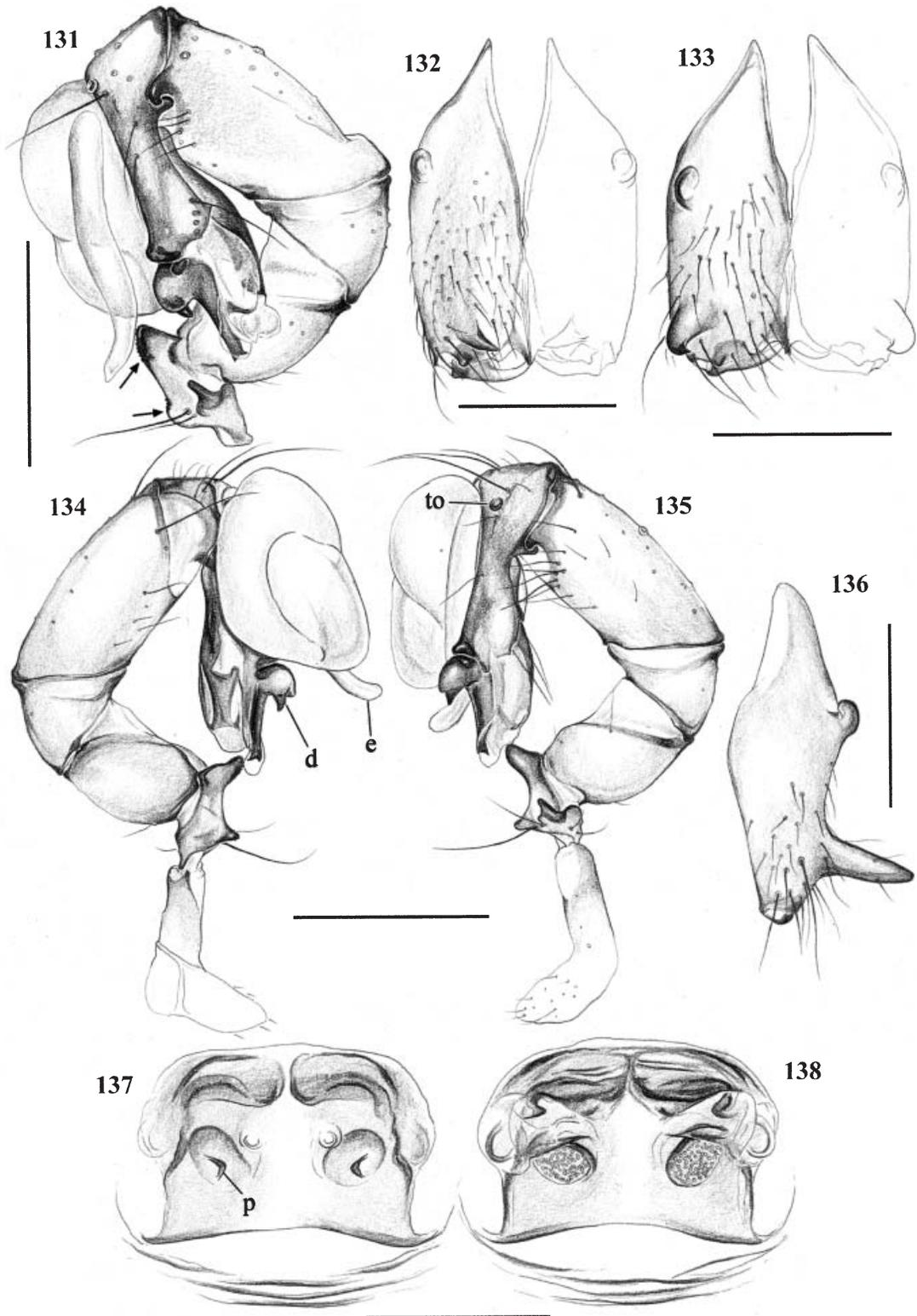
modified hairs (Fig. 140), distance between tips of apophyses 215 µm. Palps as in Figures 134 and 135, trochanter with three apophyses, one prolateral, one ventral pointing in retrolateral direction, and one retrolateral ('p', 'v', and 'r' in Fig. 142); procurus with distinctive dorsodistal element ('d' in Fig. 134). Embolus simple membranous tube ('e' in Fig. 134). Legs without spines, without curved hairs, few vertical hairs (most hairs missing in holotype, but present in other specimens); retrolateral trichobothrium of tibia 1 at 10%; tarsus 1 with >20 pseudosegments (distally about 20 very distinct). Epiandrous spigots and ALS spigots as in Figures 146 and 148.

Variation. Tibia 1 in 20 other males 4.8–5.8 (\bar{x} = 5.34). Some males have more dark spots dorsally on the opisthosoma.

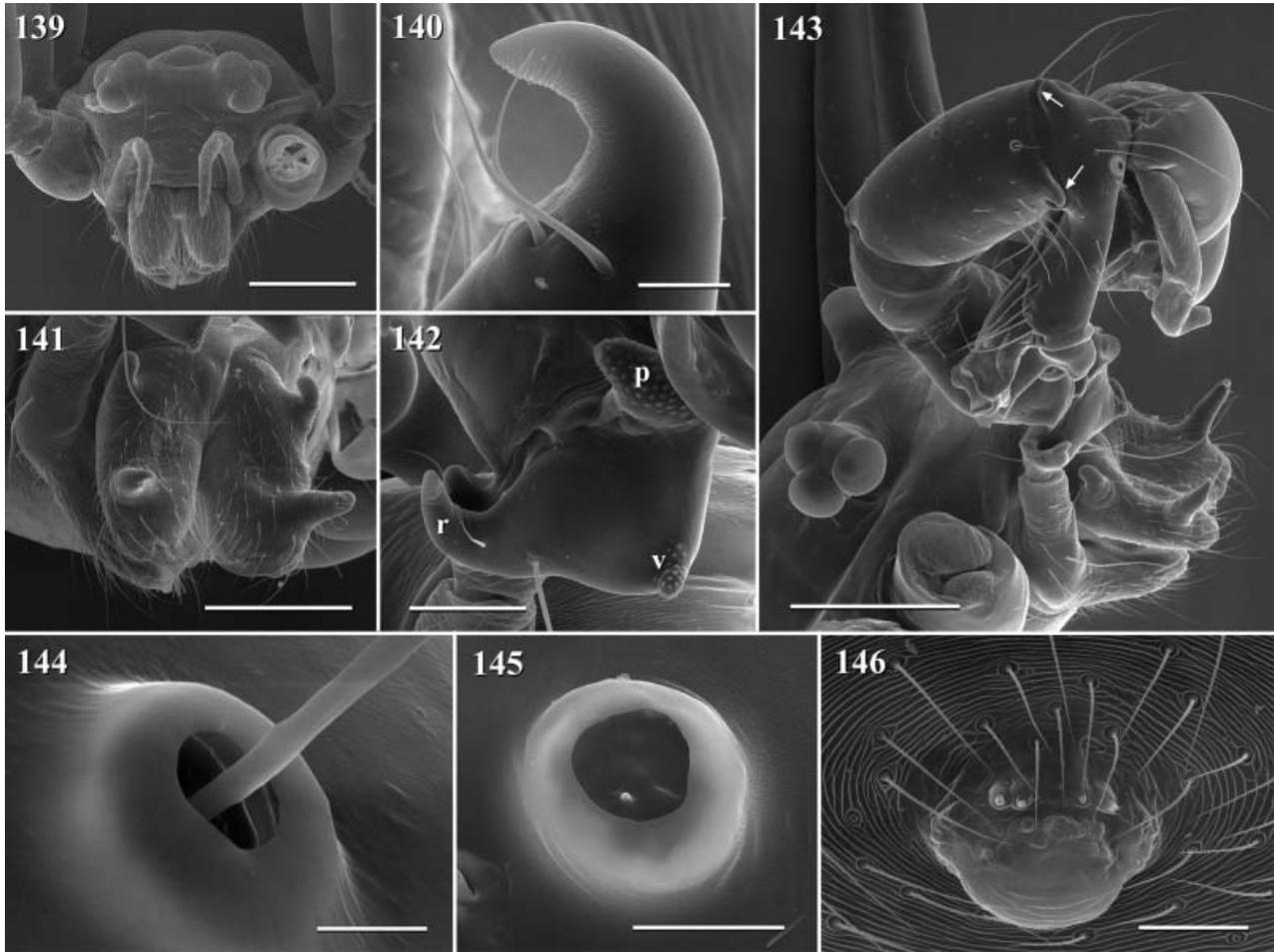
Female. In general similar to male, but femora proximally with dorso-frontal blackish pigment; distal palpal segments black; with significantly more variation in pattern on opisthosoma. Some females with several black spots parallel to marginal lines on carapace. Tibia 1 in 27 females: 3.6–4.8 (\bar{x} = 4.06). Epigynum as in Figures 122, 137 and 153, with pair of transparent prominences and pockets about 215 µm apart (Figs 137 and 153). Dorsal view as in Figure 138. Spinnerets and ALS spigots as in Figures 147 and 149.

Distribution. Known only from the Ranomafana National Park area (Map 2).

Material examined. MADAGASCAR: *Fianarantsoa*: Ranomafana N. P. Vohiparara: type above together with 2♂ 6♀, same collection data. Vohiparara: Piste Touristique (21°13.6'S, 47°24.0'E), c. 1000 m a.s.l., April 12–23, 1998 (C. E. Griswold, D. H. Kavanaugh, N. P. Penny, M. J. Raheirilalao, J. S. Ranorianarisoa, J. Schweikert, D. Ubick), 7♂ 11♀ in CAS. Vohiparara village (21°12.8'S, 47°23.0'E), April 10–11, 1998 (same collectors), 3♀ in CAS. *Ranomafana N. P.*, roadside vegetation near park entrance, c. 21°14.3'S, 47°26.0'E, c. 800 m a.s.l., April 22, 1998 (same collectors), 3♂ 3♀ in CAS. *Ranomafana N. P. Talatakely* (21°14.9'S, 47°25.6'E), April 5–30, 1998 (same collectors) 4♂ 1♀ in CAS. Talatakely at 21°15'S, 47°26'E, 915–1000 m a.s.l., October 30–November 20, 1998 (V. F. Lee & K. J. Ribardo), 1♀ in CAS. Talatakely at 21°15'S, 47°25'E, 900 m a.s.l., December 5–7, 1993 (N. Scharff, S. Larcher, C. E. Griswold, R. Andriamasimanana), 2♂ 4♀ in CAS. Vatoharanana (21°16.7'S, 47°26.1'E), primary forest, c. 1200 m a.s.l., April 15, 1998 (C. E. Griswold, D. H. Kavanaugh, N. P. Penny, M. J. Raheirilalao, J. S. Ranorianarisoa, J. Schweikert, D. Ubick) 1♂ 1♀ in CAS. *Ranomafana N. P.* at 21°12'S, 47°27'E, forest, from foliage, April 1992 (V. & B. Roth, S. Kariko), 1♂ in CAS. 7 km W Ranomafana at 21°16'S, 47°25'E, 900 m a.s.l., on low foliage and saplings, montane



Figures 131–138. *Paramicromerys madagascariensis* (131–132) and *P. betsileo* (133–138). 131, Left male palp, retrolateral view; arrows point to distinctive apophyses on trochanter. 132–133, Male chelicerae, frontal views. 134–135, Left male palp, pro- and retrolateral views. 136, Male chelicerae, lateral view. 137–138, Cleared epigynum, ventral (137) and dorsal (138) views. 'd': distinctive element of procurus; 'e': embolus; 'p': pocket; 'to': tarsal organ. Scale lines: 0.4 mm (131, 134–135), 0.2 mm (132, 133, 136), 0.3 mm (137, 138).



Figures 139–146. *Paramicromerys betsileo*. 139, Female prosoma, frontal view. 140, Tip of male chelical apophysis. 141, Male chelicerae. 142, Male palpal trochanter, ventral view, showing the prolateral ('p'), ventral ('v'), and retrolateral ('r') apophyses. 143, Male prosoma with palp, showing the shift of the tibia-cymbium joints (arrows). 144, Male palpal trichobothrium base. 145, Male palpal tarsal organ. 146, Male gonopore with epiandrous spigots. Scale lines: 300 μm (139, 143), 10 μm (140), 200 μm (141), 80 μm (142), 6 μm (144), 20 μm (145), 50 μm (146).

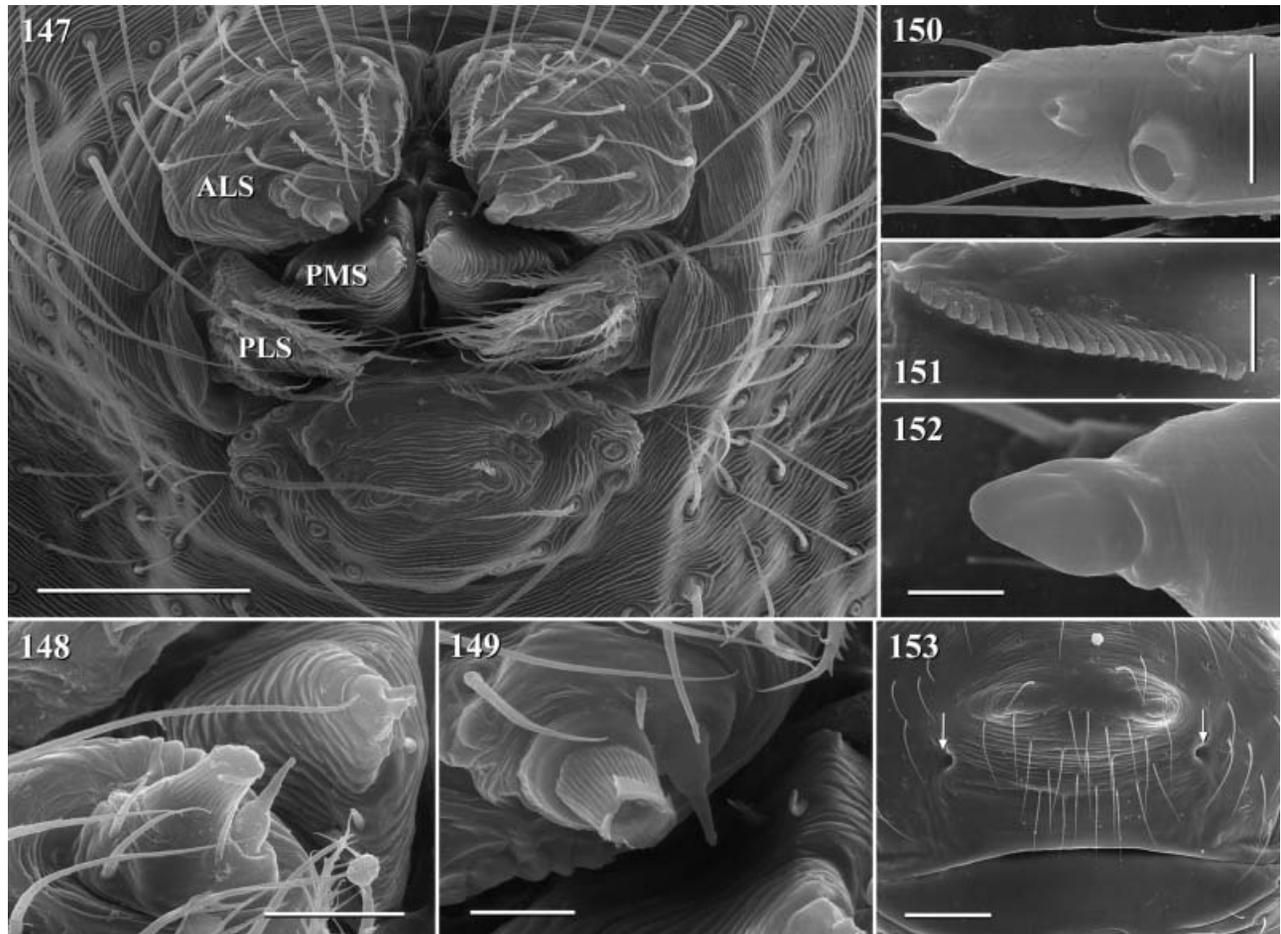
rainforest, September 5, 1993 (W. Steiner), 3♀ in USNM. 7 km W Ranomafana at 21°12'S, 47°27'E, 900 m a.s.l., March 1–13, 1990 (W. E. Steiner), 3♂ in USNM. 7 km W Ranomafana at 21°12'S, 47°27'E, 1100 m a.s.l., November 1–7, 1998 (W. E. Steiner), 2♂ 1♀ in USNM; same locality, Pyrethrin fogging of dead leaves on fallen tree, montane rainforest, October 8–21, 1988 (W. E. Steiner) 1♂ in USNM; same locality at 1000 m a.s.l., Pyrethrin fogging of treefall and vine tangle, montane rainforest, March 1–7, 1990 (W. E. Steiner), 1♂ in USNM. Valohoaka camp 8 km SW Ranomafana (21°19'S, 47°24'E), 1040 m a.s.l., beating low vegetation and dead leaf masses, montane rainforest, September 9, 1993 (W. Steiner), 1♂ 5♀ in USNM. Ranomafana N. P. at 21°S, 47°30'E, April–May 1992 (S. Kariko, V. & B. Roth), 3♂2♀ in MCZ (33990, 33951, part of 33989).

***PARAMICROMERYS CODDINGTONI*, NEW SPECIES**
(FIGS 110, 111, 123, 154–167)

Type. Male holotype from Montagne d'Ambre, 2.79 air km NE of park entrance (12°32'S, 49°10'E), ~1000 m a.s.l., forest, Antsiranana, Madagascar; November 21–30, 1993 (J. Coddington, C. E. Griswold, N. Scharff, S. Larcher, R. Andriamasimanana); in CAS.

Etymology. Named for the first collector, Jonathan Coddington from the National Museum of Natural History, Washington, D. C.

Diagnosis. Dark patterned species with oval opisthosoma (Fig. 110), with similar palps as *P. ralamboi*, but very different colour pattern; distinguished from this



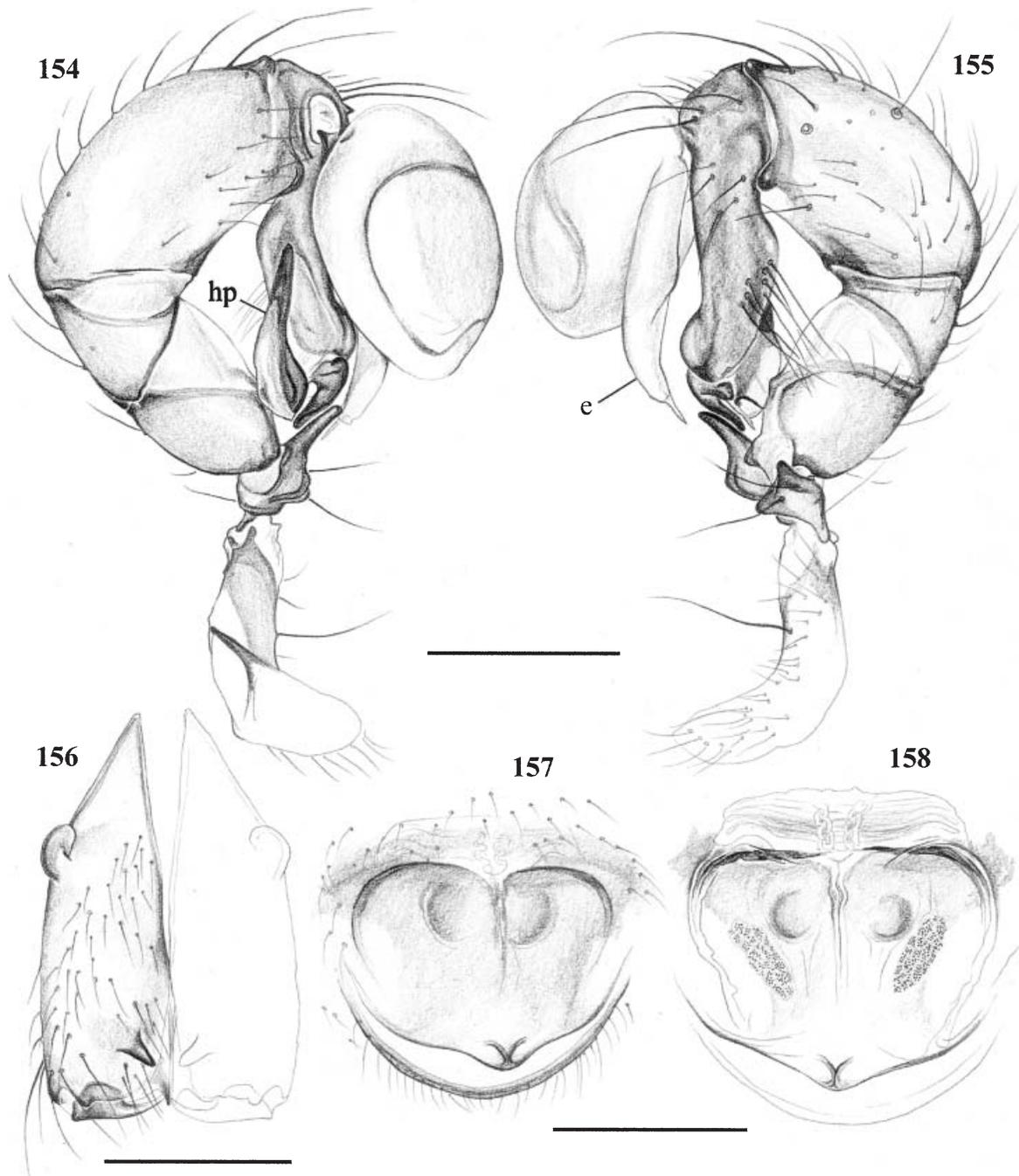
Figures 147–153. *Paramicromerys betsileo*. 147, Female spinnerets. 148, Male ALS and PMS. 149, Female ALS. 150, Tip of female palp with tarsal organ. 151, Male pedipalpal coxa serrula. 152, Reduced claw at tip of female palp. 153, Epigynum, showing pockets (arrows) and protrusions. Scale lines: 70 μm (147), 20 μm (148, 150, 151), 10 μm (149), 6 μm (152), 100 μm (153).

and other known congeners also by the shape of procurus (Fig. 155: distal elements) and epigynum (Fig. 157).

Male (holotype). Total length 1.6, carapace width 0.7. Leg 1: 15.6 (3.9 + 0.3 + 4.0 + 5.6 + 1.8), tibia 2: 2.3, tibia 3: 1.7, tibia 4: 2.3; tibia 1 L/d: 67. Habitus as in Figures 110 and 111. Carapace ochre with dark brown pattern, sternum brown, lighter frontally medially. Legs ochre-yellow, with dark rings subdistally on femora and tibiae. Opisthosoma grey with large spots shining through cuticle and dark pattern on surface; ventrally posteriorly as in female (cf. Fig. 123), frontally central dark spot and transversal band, genital area large spot. Ocular area distinctly separated from carapace, triads on additional elevations; distance PME-PME 220 μm ; diameter PME 70 μm ; distance PME-ALE 30 μm . Thoracic furrow deep and distinct. Sternum wider than long (0.56/0.40). Chelicerae as in

Figure 156, without modified hairs on tips of apophyses (Fig. 159); distance between tips of apophyses 30 μm . Palps as in Figures 154 and 155, trochanter with two prolateral apophyses (large one pointing in retrolateral direction), and two small retrolateral apophyses (Fig. 163); procurus as in Figures 154, 155 and 164, with small sclerotized cone proximally, distinct hinged process and additional distal structure that also appears hinged (arrow in Fig. 164); embolus simple ('e' in Fig. 155), with transparent distal spine. Legs with about 20 spines distally on femora 1 ventrally in single row, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 11%; tarsus 1 with numerous pseudosegments, but only distally about 10 fairly distinct (Fig. 166).

Variation. Tibia 1 in 10 other males: 3.6–4.2 (\bar{x} = 3.88). Dark rings on legs sometimes missing or very indistinct.

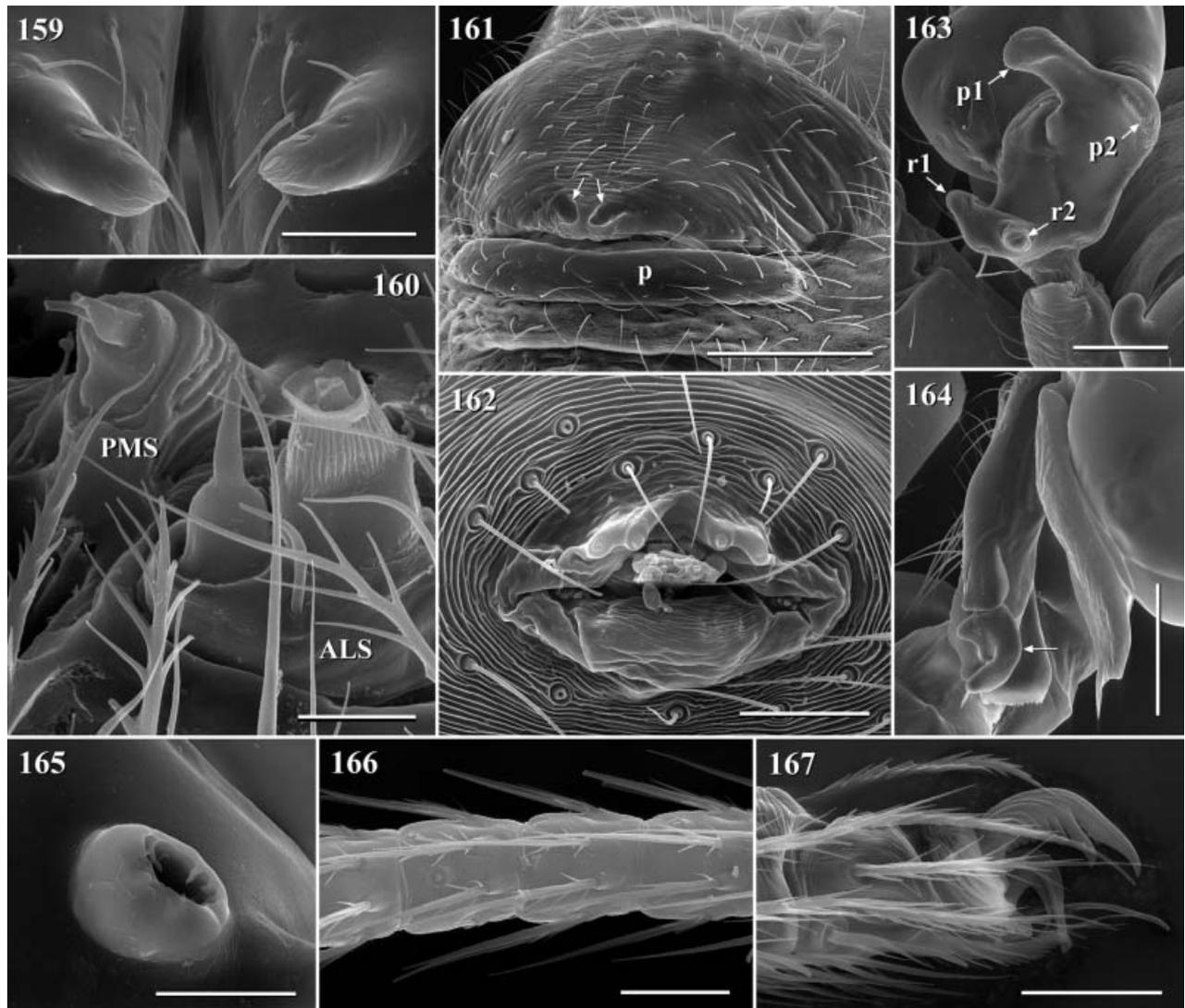


Figures 154–158. *Paramicromerys coddingtoni*. Left male palp in prolateral (154) and retrolateral (155) views, male chelicerae in frontal view (156), and cleared epigynum in ventral (157) and dorsal (158) views. ‘e’: embolus; ‘hp’: hinged process. Scale lines: 0.3 mm (154, 155, 157, 158), 0.2 mm (156).

Female. In general similar to male, but legs without spines; tibia 1 in 14 females: 2.8–3.2 (\bar{x} = 3.03). Epigynum large brown plate (Fig. 123), with pockets almost touching medially (Figs 157 and 161); with narrow posterior plate (‘p’ in Fig. 161). Dorsal view as in Figure 158. ALS and PMS as in Figure 160.

Distribution. Known only from type locality (Map 2).

Material examined. MADAGASCAR: Antsiranana: Montagne d’Ambre: type above, together with 10♂ 16♀, same collection data, in CAS; and 1♂ in separate vial, same collection data, in CAS.



Figures 159–167. *Paramicromerys coddingtoni*. 159, Male cheliceral apophyses. 160, Female ALS and PMS. 161, Epigynum with pockets (arrows) and posterior plate ('p'). 162, Male gonopore with (damaged) epiandrous spigots. 163, Male palpal trochanter, ventral view, showing two prolateral ('p1', 'p2') and two retrolateral ('r1', 'r2') apophyses. 164, Procurus and embolus, retrolatero-dorsal view (arrow points to distal hinged structure of procurus). 165, Male palpal tarsal organ. 166, Male tarsus 1, showing pseudosegmentation. 167, Tip of female third leg, showing tarsal claws. Scale lines: 30 μm (159, 166), 20 μm (160, 165, 167), 200 μm (161, 164), 40 μm (162), 100 μm (163).

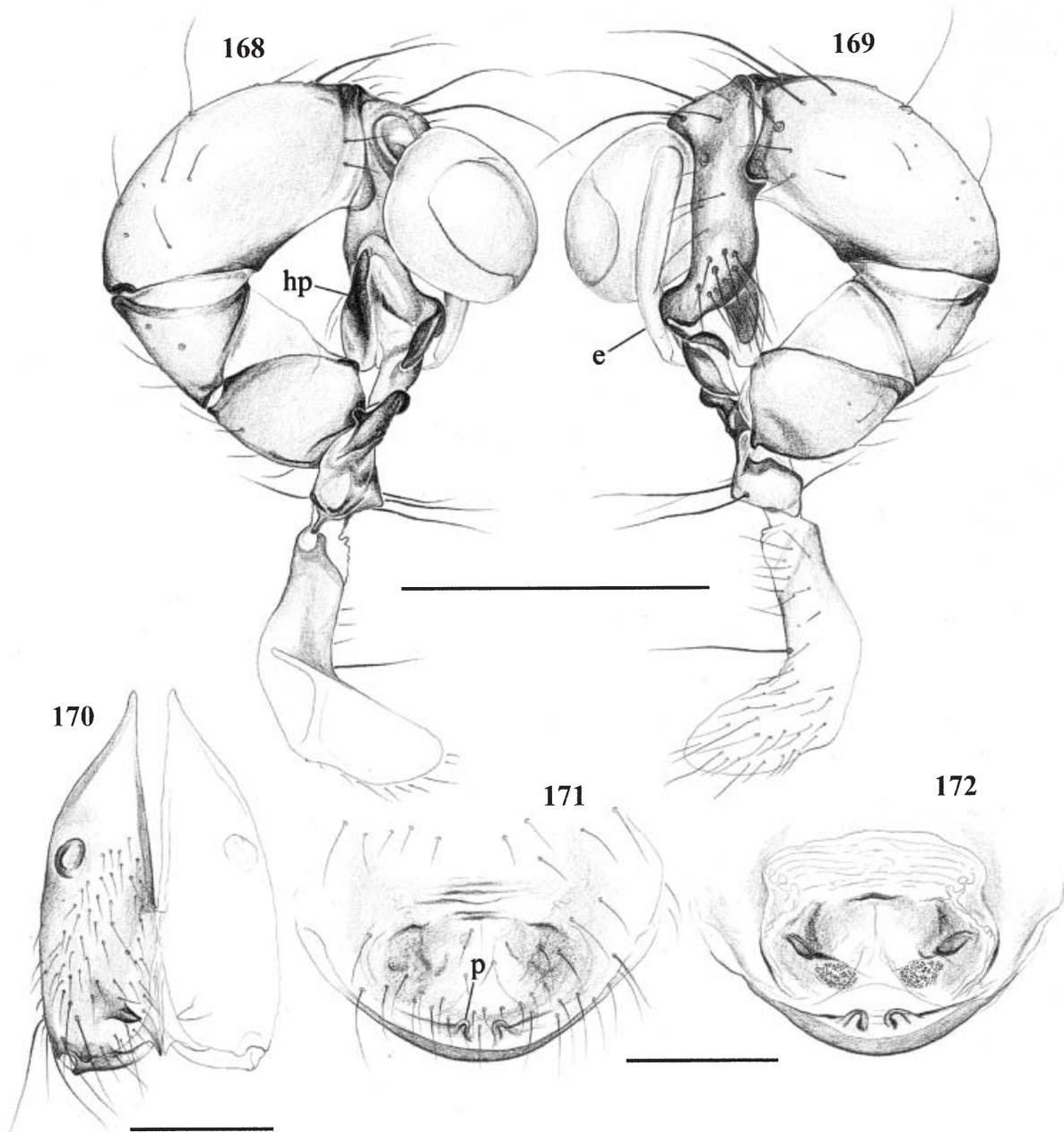
***PARAMICROMERYS RALAMBOI*, NEW SPECIES**
(FIGS 116, 117, 126, 168–172)

Type. Male holotype from Montagne d'Ambre, 2.79 air km NE of park entrance (12°32'S, 49°10'E), ~1000 m a.s.l., forest, Antsiranana, Madagascar; November 21–30, 1993 (J. Coddington, C. E. Griswold, N. Scharff, S. Larcher, R. Andriamasimanana); in CAS.

Etymology. Named for Emile Ralambo (1879–1963), outstanding Malagasy artist, representative of the national romanticism.

Diagnosis. Light species with oval opisthosoma, with similar palps as *P. coddingtoni*, but very different colour pattern (compare Figs 110 and 116); distinguished from this and other known congeners also by the shape of procurus (distal elements) and epigynum (Figs 169 and 171).

Male (holotype). Total length 2.1, carapace width 0.9. Leg 1: 23.2 (5.7 + 0.4 + 5.5 + 9.0 + 2.6), tibia 2: 3.5, tibia 3: 2.4, tibia 4: 3.5; tibia 1 L/d: 69. Habitus as in Figures 116 and 117. Carapace, sternum and legs pale ochre-yellow, only ocular area and clypeus light brown.



Figures 168–172. *Paramicromerys ralamboi*. Left male palp in prolateral (168) and retrolateral (169) views, male chelicerae in frontal view (170), and cleared epigynum in ventral (171) and dorsal (172) views. ‘e’: embolus; ‘hp’: hinged process; ‘p’: pocket. Scale lines: 0.5 mm (168, 169), 0.2 mm (170–172).

Opisthosoma ochre-grey with black spots posteriorly (type with smaller spots than photographed male); ventrally no pigments. Ocular area distinctly separated from carapace, triads on low elevations; distance PME-PME 220 μ m; diameter PME 80 μ m; distance PME-ALE 40 μ m. Thoracic furrow distinct but shallow. Sternum wider than long (0.68/0.52). Chelicerae

as in Figure 170, distance between tips of apophyses 50 μ m. Palps as in Figures 168 and 169, trochanter with small retrolateral and large prolateral apophyses; procurus with distinct hinged process (‘hp’ in Fig. 168); embolus simple (‘e’ in Fig. 169), with transparent distal spine. Legs with about 12 spines distally on femora 1 ventrally in single row, without curved

hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 12%; tarsus 1 with >30 pseudosegments, distally quite distinct.

Variation. Tibia 1 in 4 other males: 5.2–5.7.

Female. In general similar to male. Some females with black palps. Two females with wide black median band on carapace. Some females with dark rings subdistally on tibiae. Tibia 1 in 4 females: 3.8–4.5. Epigynum with median conical protrusion, pair of pockets ('p' in Fig. 171) about 50 µm apart, narrow posterior plate (Figs 126 and 171). Dorsal view as in Figure 172.

Distribution. Known only from type locality (Map 2).

Material examined. MADAGASCAR: *Antsiranana*: Montagne d'Ambre: type above, together with 5♂ 5♀, same collection data, in CAS.

PARAMICROMERYS QUINTERI, NEW SPECIES

(FIGS 173, 174)

Type. Male holotype from Marojejy, 10.5 km NW Manantenina (14°26.4'S, 49°44.5'E), Antsiranana, Madagascar; November 6–12, 1996 (E. L. Quinter), 1625 m a.s.l., along tributary at head Andranomifototra River, beating vegetation; in AMNH.

Etymology. Named for the collector, Eric Quinter from the American Museum of Natural History, New York.

Diagnosis. Light species with cylindrical opisthosoma, distinguished from similar species (*P. mahira*, *rabearivelo*, *coddingtoni*, *ralamboi*) by the shape of the distal elements of the procurus (Figs 173 and 174).

Male (holotype). Total length 2.2, carapace width 0.8. Leg 1 missing; tibia 2: 3.6, tibia 3: 2.3, tibia 4: 3.4. Habitus very similar to *P. mahira* (cf. Figs 104 and 105). Prosoma and legs ochre-yellow. Opisthosoma ochre-grey. Ocular area barely elevated, triads on low elevations; distance PME-PME 300 µm; diameter PME 60 µm; distance PME-ALE 30 µm. Thoracic furrow present only frontally, very shallow. Sternum wider than long (0.68/0.60). Chelicerae as in *P. coddingtoni* (cf. Fig. 156), distance between tips of apophyses about 35 µm. Palps as in Figures 173 and 174; trochanter with retrolateral ridge and large prolateral apophysis; femur with small apophysis proximo-dorsally; procurus with hinged process ('hp' in Fig. 173); embolus with distinctive bend (arrow in Fig. 174), with transparent distal spine. Legs without spines (but first legs missing!), without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 2 at 11%; tarsus 2 with >20 pseudosegments, distally quite distinct.

Female. Unknown.

Distribution. Known only from type locality (Map 2).

Material examined. MADAGASCAR: *Antsiranana*: Marojejy: type above.

PARAMICROMERYS MAHIRA, NEW SPECIES

(FIGS 104, 105, 175, 176)

Type. Male holotype from Ranomafana National Park, Mahira, summit (about 21°S, 47.5°E), Fianarantsoa, Madagascar; April 11, 1992 ('Albert for Kariko/Roth'), in MCZ (33971).

Etymology. Named for the type locality. The specific name is a noun in apposition.

Diagnosis. Light species with cylindrical opisthosoma, distinguished from similar species (*P. quinteri*, *rabearivelo*, *coddingtoni*, *ralamboi*) by the shape of the distal elements of the procurus (Figs 175 and 176).

Male (holotype). Total length 2.4, carapace width 0.8. Leg 1 missing; tibia 2: 4.0, tibia 3: 2.6, tibia 4: 3.6. Habitus as in Figures 104 and 105. Prosoma and legs ochre-yellow. Opisthosoma ochre-grey. Ocular area barely elevated, triads on low elevations; distance PME-PME 320 µm; diameter PME 80 µm; distance PME-ALE 40 µm. Thoracic furrow present only frontally, very shallow. Sternum wider than long (0.64/0.48). Chelicerae as in *P. ralamboi* (cf. Fig. 170; lost by author). Palps as in Figures 175 and 176, coxa with indistinct hump ventrally, trochanter with apophyses retrolaterally, ventrally (small) and prolaterally (large); procurus with distinct hinged process ('hp' in Fig. 175); embolus simple, with transparent distal spine. Legs without spines (but first legs missing!), without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 2 at 11%; tarsus 2 with >15 pseudosegments, only distally fairly distinct.

Female. Unknown.

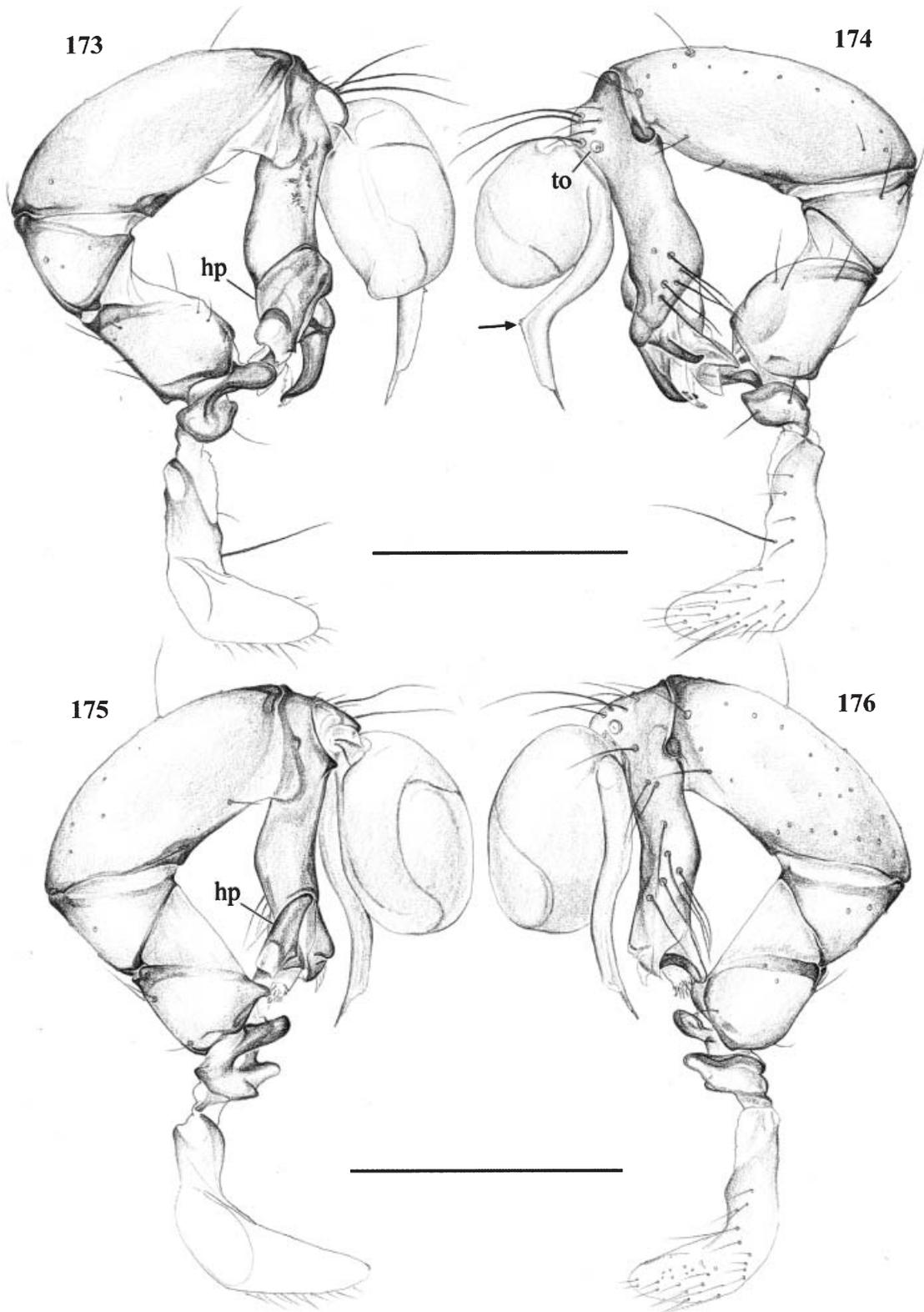
Distribution. Known only from type locality (Map 2).

Material examined. MADAGASCAR: *Fianarantsoa*: Ranomafana N. P.: type above.

PARAMICROMERYS MANANTENINA, NEW SPECIES

(FIGS 118, 119, 125, 177–190)

Type. Male holotype from Marojejy Reserve, 8.4 km NNW Manantenina (14°26'S, 49°45'E), 700 m a.s.l., Antsiranana, Madagascar; November 10–16, 1993 (C. E. Griswold, J. Coddington, N. Scharff, S. Larcher, R. Andriamasimanana); in CAS.



Figures 173–176. *Paramicromerys quinteri* (173–174) and *P. mahira* (175–176). Left male pedipalps in prolateral (173, 175) and retrolateral (174, 176) views. ‘hp’: hinged process; ‘to’: tarsal organ; arrow points to distinctive bend in embolus. Scale lines: 0.5 mm.

Etymology. Named for the type locality. The specific name is a noun in apposition.

Diagnosis. Dark species with large pedipalps, distinguished from the closest known relative (*P. nam-poinai*) by the pattern on the carapace (compare Figs 112 and 118), the male cheliceral armature (compare Figs 179 and 180 with Figs 193, 194), the much larger hinged process on the procurus and the presence of a papilla on the bulb ('pa' in Fig. 177). Also distinguished by the shape of the epigynum (compare Figs 124 and 125).

Male (holotype). Total length 2.8, carapace width 1.25. Leg 1: 34.6 (8.0 + 0.5 + 8.4 + 14.0 + 3.7), tibia 2: 5.0, tibia 3: 3.4, tibia 4 missing; tibia 1 L/d: 70. Habitus as in Figures 118 and 119. Carapace light ochre with dark brown pattern as in Figure 118, sternum brown with central circular light spot. Legs ochre to light brown, coxa, trochanter and femur with blackish pigment. Opisthosoma grey, with blackish spots superficially (posteriorly) and many dark spots shining through cuticle; ventrally posteriorly like female (cf. Fig. 125), with black longitudinal stripe connecting to black trapezoidal spot at genital area. Ocular area elevated, triads on additional elevations; distance PME-PME 460 µm; diameter PME 140 µm; distance PME-ALE 50 µm. Thoracic furrow distinct, relatively deep. Sternum wider than long (0.88/0.72). Chelicerae as in Figures 179 and 180, distal apophyses connected to chelicerae by membranous cuticle; with one tiny globular hair imbedded in tip of each distal apophysis (Figs 189 and 190). Palps as in Figures 177 and 178; coxa with small hump ventrally, trochanter very complex ('t' in Fig. 183) with three prolateral apophyses (largest one pointing in retrolateral direction), and bifid retrolateral apophysis; femur with proximo-dorsal apophysis (arrow in Fig. 178) and retrolateral ridge; palpal tarsal organ situated on sclerotized cone (Figs 178 and 187), procurus with large hinged process ('hp' in Figs 177 and 184) and complex tip (Fig. 185); bulb with distinctive papilla ('pa' in Fig. 177), embolus with short side branch, without distal spine ('e' in Fig. 183). Legs with spines in single rows ventrally distally on femora 1 (about 13) and 2 (about 4), without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 9%; tarsus 1 with >40 pseudosegments, fairly distinct distally. Epandrous spigots as in Fig. 186. ALS and PMS as in Fig. 188.

Variation. Tibia 1 in 4 other males: 7.0–8.0. Other males with up to 17 spines on femora 1; superficial pattern on opisthosoma very variable in intensity. Tibia 2/4 in other male: 4.4/4.3.

Female. In general similar to male. Tibia 1 in 3 females: 5.8–6.8. Epigynum large but simple brown

plate (Figs 125 and 181), apparently without pockets. Dorsal view as in Fig. 182.

Distribution. Known only from type locality (Map 2).

Material examined. MADAGASCAR: Antsiranana: Marojejy Res.: type above, together with 5♂ 5♀, same collection data, in CAS.

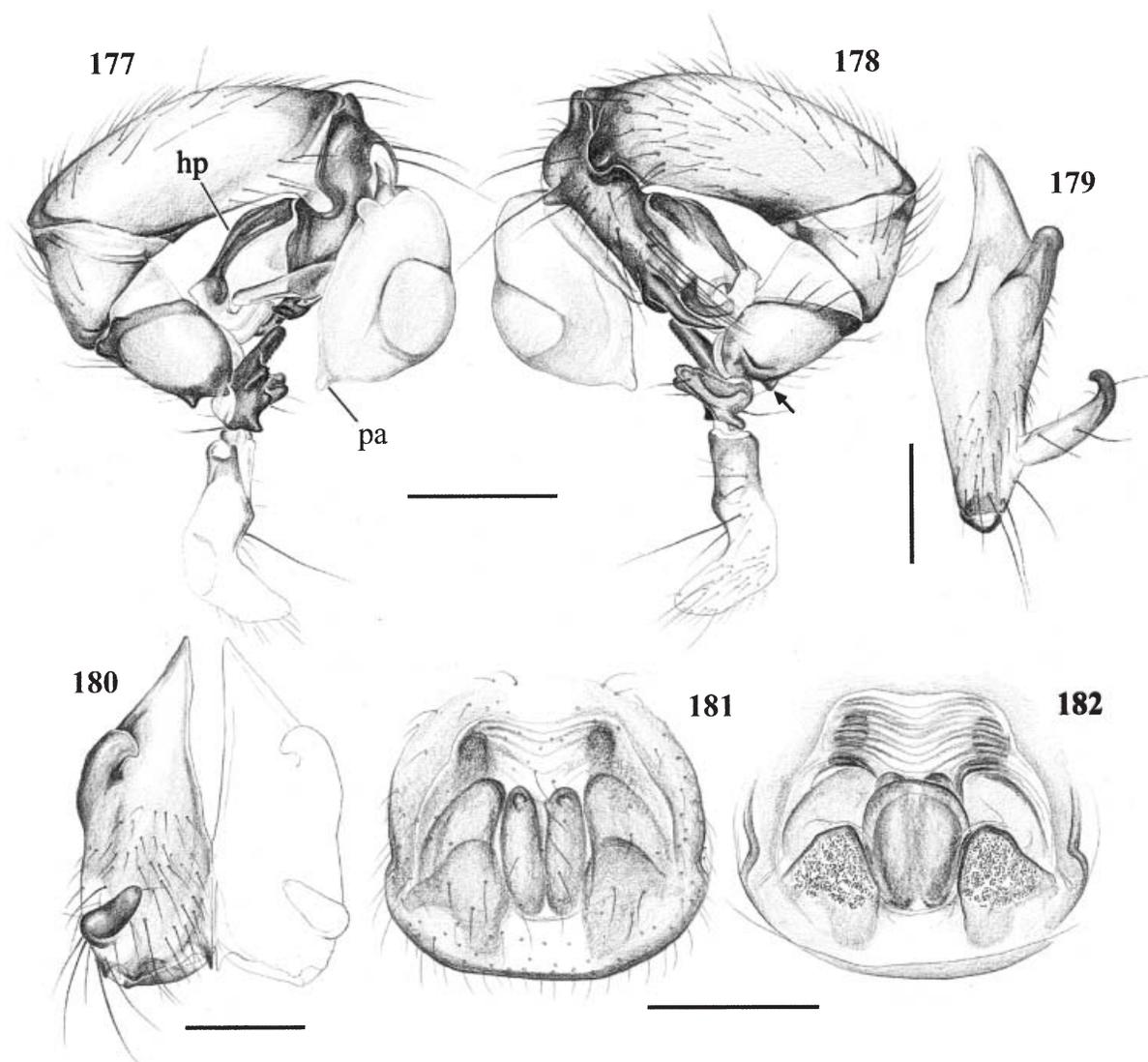
PARAMICROMERYS NAMPOINAI, NEW SPECIES
(FIGS 112, 113, 124, 191–197)

Type. Male holotype from Montagne d'Ambre, 2.79 air km NE of park entrance (12°32'S, 49°10'E), ~1000 m a.s.l., forest, Antsiranana, Madagascar; November 21–30, 1993 (J. Coddington, C. E. Griswold, N. Scharff, S. Larcher, R. Andriamasimanana); in CAS.

Etymology. Named for Malagasy King Andrianampoinimerina (also Nampoina; died in 1810), a remarkable organizer and administrator who developed a complex social system and administrative structure without benefit of written records and therefore of bureaucracy.

Diagnosis. Dark species with large pedipalps, distinguished from the closest known relative (*P. manantenina*) by the pattern on the carapace (compare Figs 112 and 118), the male cheliceral armature (compare Figs 179 and 180 with Figs 193 and 194), the much smaller hinged process on the procurus and the absence of a papilla on the bulb (compare Figs 177 and 191). Also distinguished by the epigynum with frontal apophyses (compare Figs 124 and 125).

Male (holotype). Total length 2.8, carapace width 1.25. Leg 1: 27.1 (6.5 + 0.5 + 6.5 + 10.2 + 3.4), tibia 2: 4.0, tibia 3: 3.2, tibia 4: 4.3; tibia 1 L/d: 50. Habitus as in Figures 112 and 113. Carapace ochre with dark brown pattern as in Figure 112, sternum brown with lighter stripe medially. Legs ochre with dark ring distally on femora. Opisthosoma grey, with blackish spots superficially (posteriorly) and many dark spots shining through cuticle. Ocular area elevated, triads on additional elevations; distance PME-PME 320 µm; diameter PME 140 µm; distance PME-ALE 50 µm. Thoracic furrow distinct, relatively deep. Sternum wider than long (0.88/0.64). Chelicerae as in Figures 193 and 194, with two tiny globular hairs imbedded in tip of each distal apophysis (Fig. 195); distance between tips of apophyses 515 µm. Palps as in Figures 191 and 192; coxa with small apophysis ventrally, trochanter with two prolateral apophyses, one ventral and one retrolateral apophysis; femur with proximo-dorsal apophysis (arrow in Fig. 192) and retrolateral ridge; procurus with sclerotized cone proximally (probably carrying the tarsal organ as in *P. manantenina*), with small hinged process ('hp' in Fig. 191); bulb without papilla, embolus ('e' in



Figures 177–182. *Paramicromerys manantenina*. Left male palp in prolateral (177) and retrolateral (178) views, male chelicerae in lateral (179) and frontal (180) views, and cleared epigynum in ventral (181) and dorsal (182) views. 'hp': hinged process; 'pa': papilla on bulb; arrow points to proximo-dorsal femur apophysis. Scale lines: 0.5 mm (177, 178), 0.2 mm (179, 180), 0.4 mm (181, 182).

Fig. 191) with short side branch, without distal spine. Legs with spines in single rows ventrally distally on femora 1 (about 5), without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 11%; tarsus 1 with >30 pseudosegments, fairly distinct distally.

Variation. Tibia 1 in 2 other males: 6.3, 6.4. Other males with up to 9 spines on femora 1; one male also with about four spines on femora 2.

Female. In general similar to male. Tibia 1 in 4 females: 5.1–5.8. Epigynum with pair of distinctive apophyses frontally (Fig. 124, 'a' in Fig. 196) and light

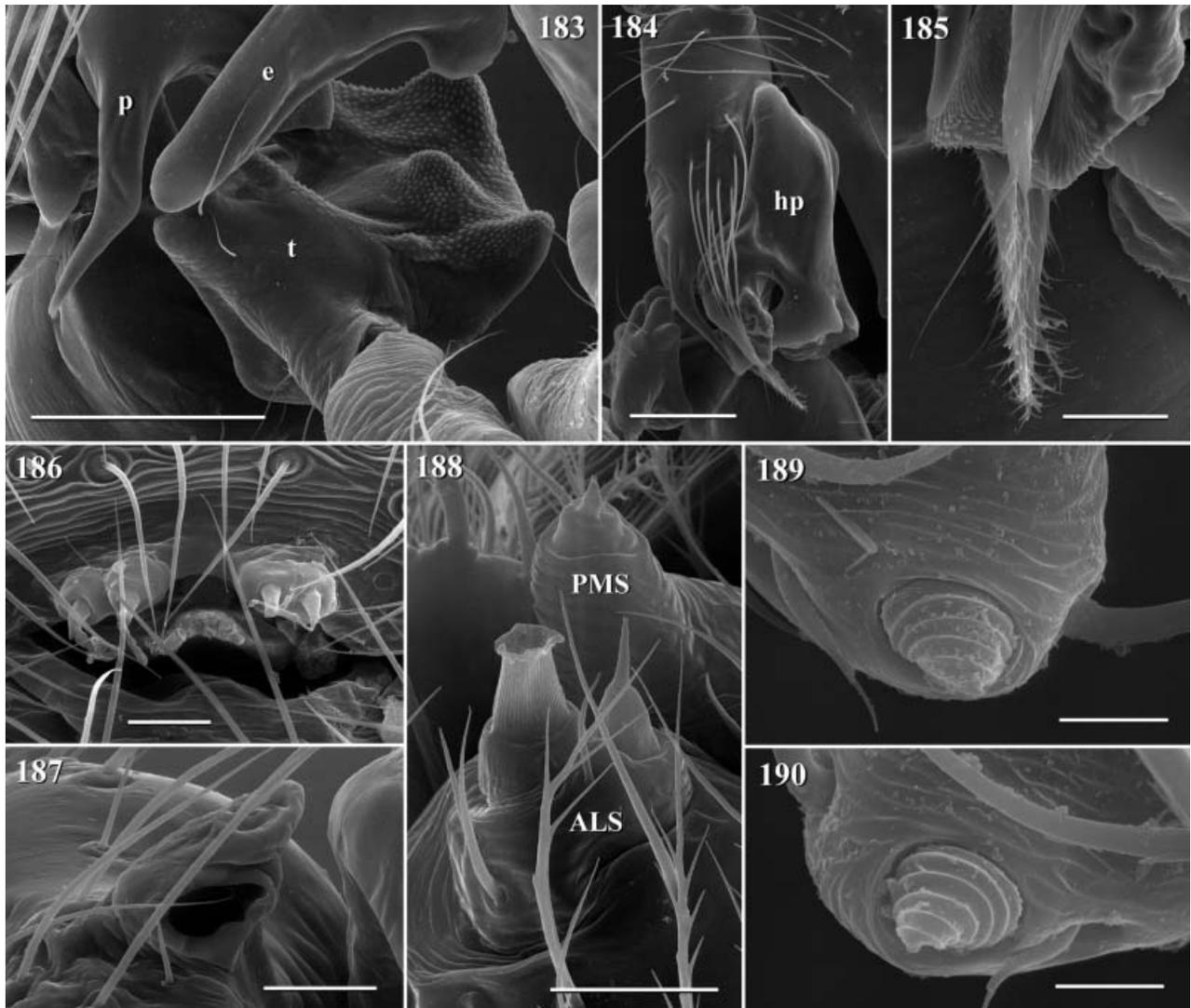
prominence medially, with pair of pockets ('p' in Fig. 197) about 500 µm apart. Dorsal view as in Fig. 197.

Distribution. Known only from type locality (Map 2).

Material examined. MADAGASCAR: *Antsiranana*: Montagne d'Ambre: type above, together with 2♂ 7♀, same collection data, in CAS.

***PARAMICROMERYS SCHARFFI*, NEW SPECIES**
(FIGS 114, 115, 127, 198–203)

Type. Male holotype from Talatakely (21°15'S, 47°25'E), 900 m a.s.l., Ranomafana National Park,



Figures 183–190. *Paramicromerys manantenina*. 183, Male palpal trochanter ('t') and tips of procurcus ('p') and embolus ('e'). 184, Procurcus with hinged process ('hp'). 185, Structure on tip of procurcus. 186, Male gonopore with epiandrous spigots. 187, Conical elevation on male palpal cymbium with tarsal organ. 188, Male ALS and PMS. 189–190, Modified hairs imbedded in tips of male cheliceral apophyses. Scale lines: 200 μm (183, 184), 50 μm (185), 20 μm (186), 40 μm (187), 30 μm (188), 5 μm (189, 190).

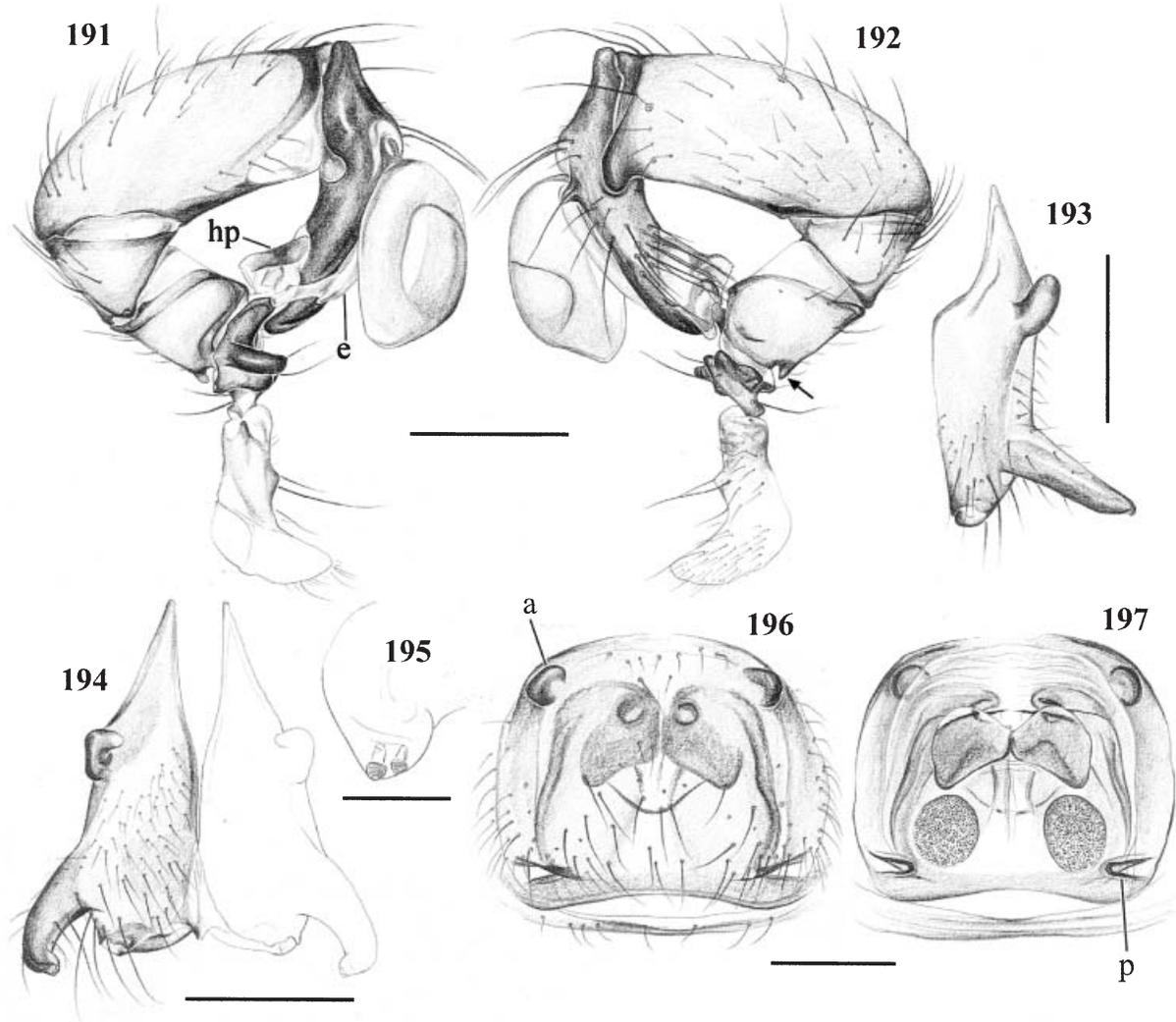
Fianarantsoa, Madagascar; December 5–7, 1993 (N. Scharff, S. Larcher, C. E. Griswold, R. Andriamasi-manana); in CAS.

Etymology. Named for the first collector, Nikolaj Scharff from the Zoological Museum, Copenhagen.

Diagnosis. Relatively large dark species, distinguished from known congeners by the shapes of procurcus and male chelicerae (Figs 198–201), and by the shape of the epigynum (Fig. 127).

Male (holotype). Total length 3.2, carapace width 1.4. Leg 1: 39.1 (9.2 + 0.4 + 9.3 + 15.2 + 5.0), tibia 2: 5.8,

tibia 3: 4.2, tibia 4: 5.8; tibia 1 L/d: 72. Habitus as in Figures 114 and 115. Carapace ochre with dark brown pattern, ocular area brown; sternum dark brown with light longitudinal stripe frontally. Legs ochre to light brown, trochanter and femora proximally with blackish marks. Opisthosoma grey with dark brown superficial pattern, ventrally with black stripes like female (cf. Fig. 127) but merging and continuing towards brown genital area. Ocular area elevated, triads on additional elevations; distance PME-PME 320 μm ; diameter PME 120 μm ; distance PME-ALE 40 μm . Thoracic furrow distinct and relatively deep. Sternum wider than long (0.88/0.80). Chelicerae as in Figs 200



Figures 191–197. *Paramicromerys nampoinai*. Left male palp in prolateral (191) and retrolateral (192) views, male chelicerae in lateral (193) and frontal (194) views, tip of male cheliceral apophysis with two modified hairs (195), and cleared epigynum in ventral (196) and dorsal (197) views. 'a': apophysis; 'e': embolus; 'hp': hinged process; 'p': pocket; arrow points to proximo-dorsal apophysis on femur. Scale lines: 0.5 mm (191, 192), 0.3 mm (193, 194), 50 μ m (195), 0.3 mm (196, 197).

and 201, distance between tips of apophyses 335 μ m. Palps as in Figures 198 and 199, trochanter with ventral and branched retrolateral apophysis; procurus with hinged process ('hp' in Fig. 198); embolus simple membranous tube ('e' in Fig. 199), without distal spine. Legs with spines ventrally on femora 1 (single row distally), without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 7%; tarsus 1 with numerous pseudosegments (probably >40), but difficult to count.

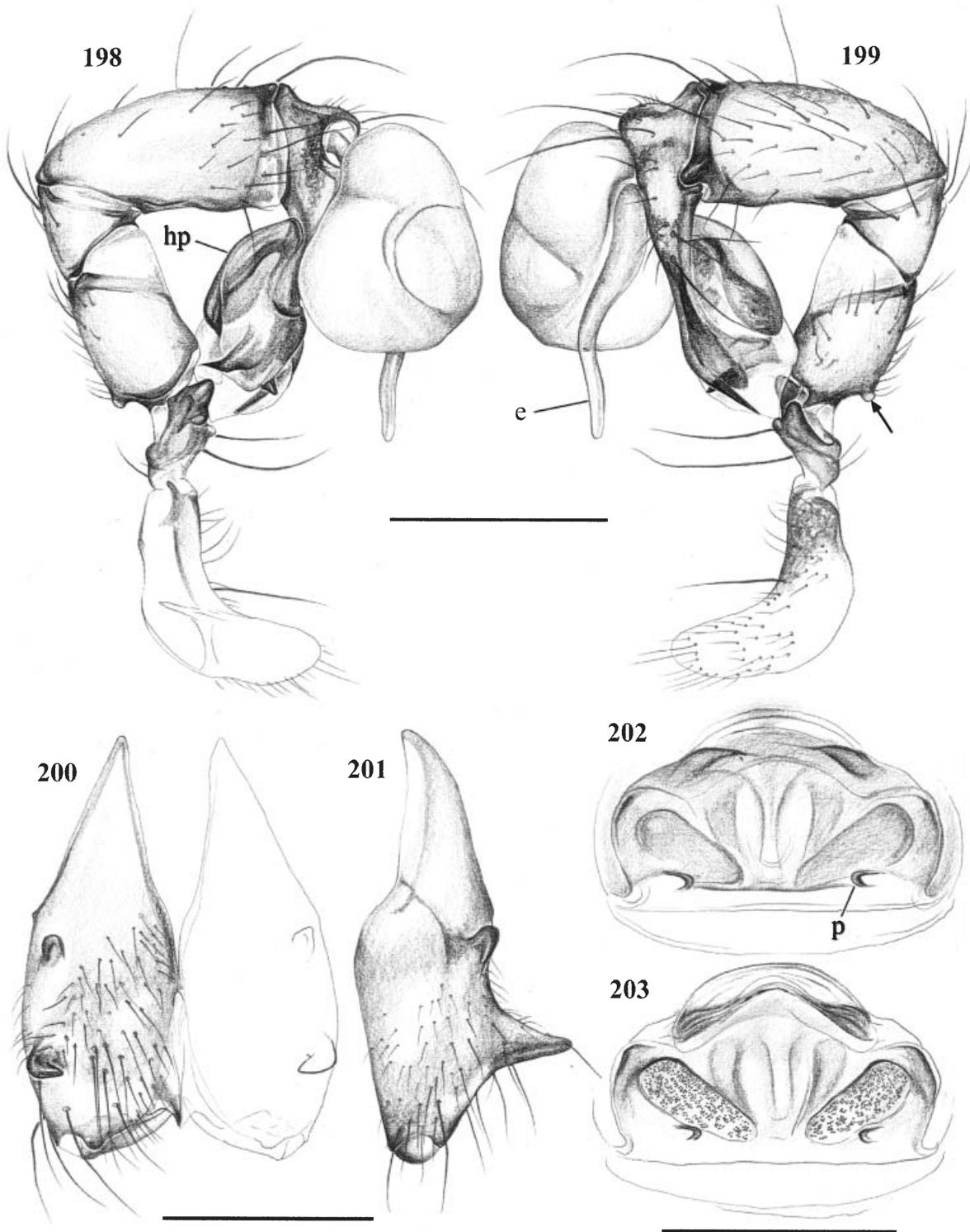
Variation. Tibia 1 in 7 other males 7.8–10.4 (the males from Mahira are larger than those from Talatakely and Vatoharanana: 10.1–10.4 vs. 7.8–8.9). Some males

with about 5 spines on femora 1; some males also with dark spots shining through cuticle on opisthosoma.

Female. In general similar to male. Tibia 1 in 11 females: 7.0–8.3 (\bar{x} = 7.77). Epigynum as in Figures 127 and 202, with pair of pockets ('p' in Fig. 202) about 365 μ m apart. Dorsal view as in Figure 203.

Distribution. Known only from the Ranomafana National Park area (Map 2).

Material examined. MADAGASCAR: *Fianarantsoa*: Ranomafana N. P.: Talatakely: type above together with 4♀, same collection data, in CAS. Talatakely at



Figures 198–203. *Paramicromerys scharffi*. Left male palp in prolateral (198) and retrolateral (199) views, male chelicerae in frontal (200) and lateral (201) views, and cleared epigynum in ventral (202) and dorsal (203) views. ‘e’: embolus; ‘hp’: hinged process; ‘p’: pocket; arrow points to proximo-dorsal apophysis on femur. Scale lines: 0.5 mm (198, 199, 202, 203), 0.3 mm (200, 201).

21°14.9'S, 47°25.6'E, April 5–30, 1998 (C. E. Griswold, D. H. Kavanaugh, N. P. Penny, M. J. Raheirilalao, J. S. Ranorianarisoa, J. Schweikert, D. Ubick), 2♂ in CAS. Vatoharanana (21°16.7'S, 47°26.1'E), primary forest, c. 1200 m a.s.l., April 29, 1998 (same collectors) 2♂ 2♀ in CAS; same collection data, under overhang along trail, 1♀ in CAS. Vohiparara: Piste Touristique (21°13.6'S, 47°24.0'E), c. 1000 m a.s.l., April 12, 14, 1998 (same collectors), 5♂ 8♀ in CAS. 7 km W Ranomafana at 21°12'S, 47°27'E, 1100 m a.s.l., October 8–21, 1988 (W. E. Steiner), 2♀ in USNM; same collection data, flight intercept yellow pan trap in Malaise trap, island in stream, montane rainforest, 1♂ in USNM. Ranomafana N. P., Mahira, summit, April 11, 1992 ('Albert for Kariko/Roth'), 2♂ 2♀ in MCZ (33971); same locality, April 8, 1992 (V. Roth), on trail, mossy forest, 1♀ in MCZ (33958). Ranomafana N. P., Mahira, trail, April 10, 1992 ('Georges for Kariko/Roth'), 1♂ 1♀ in MCZ (33972, 33985).

PARAMICROMERYS ROTHORUM, NEW SPECIES

(FIGS 106, 107, 128, 204–208)

Type. Male holotype from Montagne d'Ambre (12°30'57"S, 49°11'04"E), Antsiranana, Madagascar; August 12, 1992 (V. & B. Roth); in CAS.

Etymology. Named for the collectors, Vincent and Barbara Roth.

Diagnosis. Small species with posteriorly elevated opisthosoma; distinguished from similar congeners by the male palp (shapes of trochanter apophyses and procurus; Figs 204 and 205), and the shape of the epigynum (Fig. 128).

Male (holotype). Total length 1.7, carapace width 0.72. Leg 1 missing; tibia 2: 3.3, tibia 3: 2.1, tibia 4 missing. Habitus as in Figures 106 and 107. Carapace pale ochre with brown pattern as in Figure 106; sternum brown, laterally light ochre. Legs ochre-yellow with dark rings subdistally on femora and tibiae and subproximally on metatarsi. Opisthosoma grey with dark brown pattern; ventrally pair of spots between genital area and spinnerets. Ocular area distinctly separated from carapace, with triads on additional elevations; distance PME-PME 280 µm; diameter PME 80 µm; distance PME-ALE 30 µm. Thoracic furrow distinct (especially frontally), but not deep. Sternum wider than long (0.52/0.44). Chelicerae as in Fig. 206; distance between tips of apophyses 55 µm. Palps as in Figs 204 and 205, trochanter with large prolateral apophysis ('t' in Fig. 204) and pair of smaller retrolateral apophyses; procurus complex, with at least one apparently hinged process; embolus simple ('e' in Fig. 205), without distal spine. Legs without spines, without curved hairs, few vertical hairs

(most hairs missing in holotype, but present in other specimens).

Variation. Leg 1 in other male examined: 22.0 (5.2 + 0.3 + 5.3 + 9.0 + 2.2); tibia 2: 3.2, tibia 3: 2.1, tibia 4: 2.9; tibia 1 L/d: 88; retrolateral trichobothrium of tibia 1 at 10%; tarsus 1 with >30 pseudosegments, distally fairly distinct.

Female. In general similar to male, but distal palpal segment black, with some slightly darker spots on carapace parallel to lateral black line; all femora dorsally proximally blackish. Tibia 1 in 3 females: 3.6–3.8. Epigynum as in Figures 128 and 207, with pair of pockets ('p' in Fig. 207) close together (distance about 50 µm); dorsal view as in Figure 208.

Distribution. Known only from type locality (Map 2).

Material examined. MADAGASCAR: *Antsiranana*: Montagne d'Ambre: type above, together with 1♀, same data, in CAS; same collection data, 1♂ 2♀ in CAS.

PARAMICROMERYS MAROJEJY, NEW SPECIES

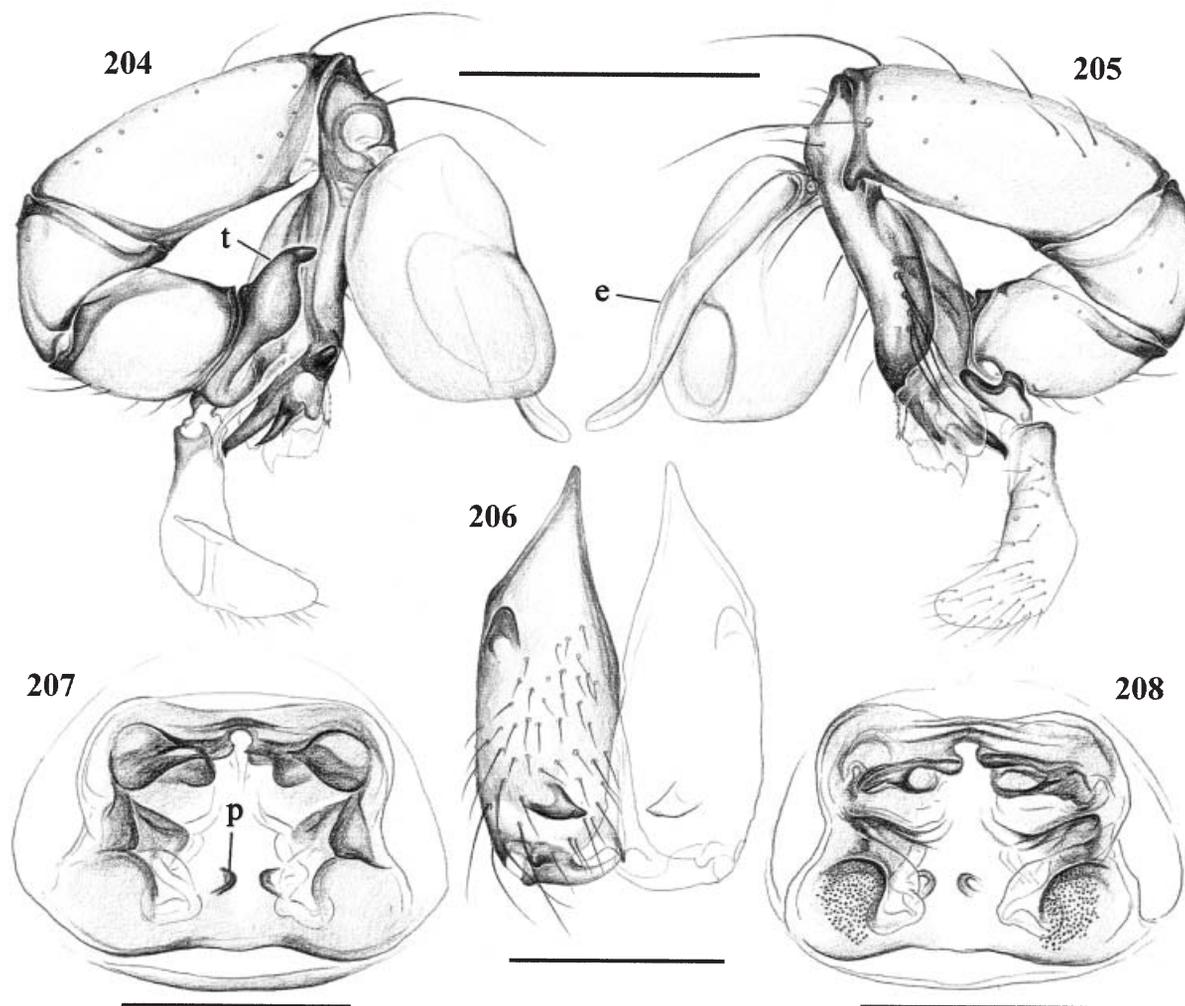
(FIGS 120, 121, 129, 209–212)

Type. Male holotype from Marojejy Reserve, 8.4 km NNW Manantenina (14°26'S, 49°45'E), 700 m a.s.l., Antsiranana, Madagascar; November 10–16, 1993 (C. E. Griswold, J. Coddington, N. Scharff, S. Larcher, R. Andriamasimanana); in CAS.

Etymology. Named for the type locality. The specific name is a noun in apposition.

Diagnosis. Light species with oval opisthosoma, easily distinguished from known congeners by the retrolateral apophysis on the male palpal femur (arrow Fig. 210) and by the shapes of procurus and epigynum (Figs 129 and 209–211).

Male (holotype). Total length 2.0, carapace width 0.8. Leg 1: 21.1 (5.2 + 0.3 + 5.1 + 8.2 + 2.3), tibia 2: 2.9, tibia 3: 2.0, tibia 4: 2.8; tibia 1 L/d: 71. Habitus as in Figures 120 and 121. Carapace pale ochre-yellow, with pair of brown spots; sternum brown laterally, ochre to light brown medially. Legs ochre to light brown. Opisthosoma ochre-grey with dark pattern as in Figures 120 and 121; ventrally posteriorly like female (cf. Fig. 129), frontally dark spot with light central part. Ocular area barely elevated, only triads on low elevations; distance PME-PME 240 µm; diameter PME 80 µm; distance PME-ALE 30 µm. Thoracic furrow indistinct and shallow frontally, absent posteriorly. Sternum wider than long (0.56/0.48). Chelicerae as in *P. ralamboi* (cf. Fig. 170), distance between tips of apophyses 50 µm. Palps as in Figures 209 and 210, trochanter with retrolateral sclerotized ridge, ventral



Figures 204–208. *Paramicromerys rothorum*. Left male palp in prolateral (204) and retrolateral (205) views, male chelicerae in frontal (206) view, and cleared epigynum in ventral (207) and dorsal (208) views. ‘e’: embolus; ‘p’: pocket; ‘t’: trochanter apophysis. Scale lines: 0.5 mm (204, 205), 0.2 mm (206), 0.3 mm (207, 208).

small apophysis and bifid prolateral apophysis; femur with distinctive retrolateral apophysis (arrow in Fig. 210); procurus with distinct hinged process (‘hp’ in Fig. 209); embolus simple (‘e’ in Fig. 210), with strong distal spine (flattened). Legs without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 8%; tarsus 1 with >20 pseudosegments, only a few distally fairly distinct.

Variation. Tibia 1 in 11 other males: 4.8–5.5 (\bar{x} = 5.03).

Female. In general similar to male. Tibia 1 in 18 females: 3.2–4.0 (\bar{x} = 3.51). Epigynum relatively small (Fig. 129), simple plate with pockets (‘p’ in Fig. 211) about 35 μ m apart. Dorsal view as in Fig. 212.

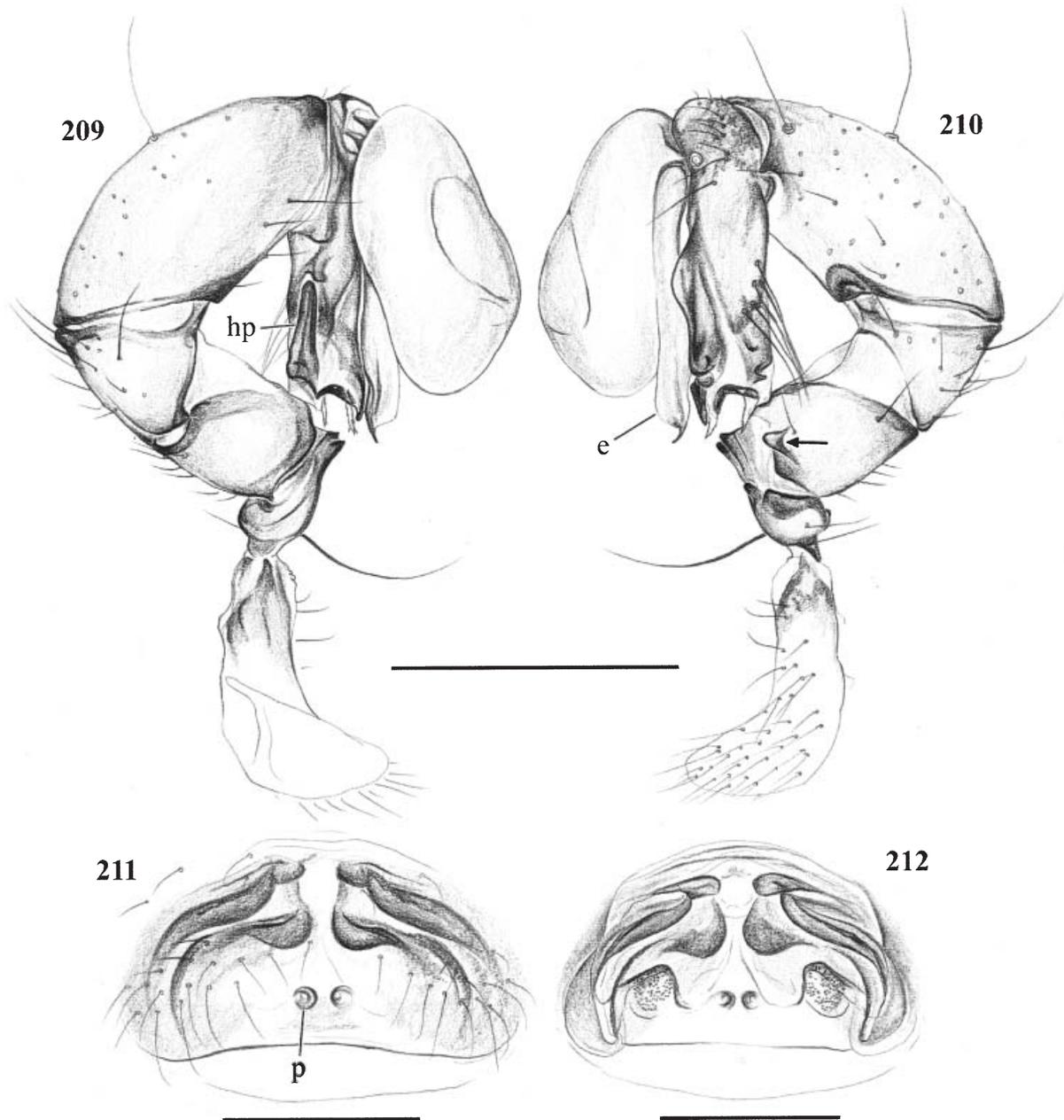
Distribution. Known only from type locality (Map 2).

Material examined. MADAGASCAR: *Antsiranana*: Marojejy Res.: type above, together with 5♂ 8♀, same collection data, in CAS; and 7♂ 18♀, same collection data, in CAS.

***PARAMICROMERYS RABEARIVELOI*, NEW SPECIES**
(FIGS 108, 109, 130, 213–217)

Type. Male holotype from Marojejy Reserve, 8.4 km NNW Manantenina (14°26’S, 49°45’E), 700 m a.s.l., Antsiranana, Madagascar; November 10–16, 1993 (C. E. Griswold, J. Coddington, N. Scharff, S. Larcher, R. Andriamasimanana); in CAS.

Etymology. Named for Jean-Joseph Rabearivelo (1901–37), gifted Malagasy poet whose struggle



Figures 209–212. *Paramicromerys marojejy*. Left male palp in prolateral (209) and retrolateral (210) views, and cleared epigynum in ventral (211) and dorsal (212) views. 'e': embolus; 'hp': hinged process; 'p': pocket; arrow points to distinctive femur apophysis. Scale lines: 0.4 mm (209, 210), 0.2 mm (211, 212).

against a severe colonial system cut short his work and, eventually, his life.

Diagnosis. Light species with cylindrical opisthosoma, easily distinguished from known congeners by the proximal and median position of the male cheliceral apophyses (Fig. 215). '*Spermophora*' *vyvato* (which occurs at the same locality) has apophyses in a similar

position (compare Figs 215 and 240), but extremely different palps.

Male (holotype). Total length 2.1, carapace width 0.84. Leg 1: 24.9 (6.1 + 0.4 + 5.8 + 9.8 + 3.5), tibia 2: 3.5, tibia 3: 2.4, tibia 4: 3.5; tibia 1 L/d: 64. Habitus as in Figures 108 and 109. Carapace pale ochre-yellow, laterally with black line and light brown band; sternum

whitish. Legs ochre-yellow. Opisthosoma ochre-grey, with blackish spots as in Figures 108 and 109; ventrally only small spot in genital area. Ocular area barely elevated, only triads on low elevations; distance PME-PME 200 μm ; diameter PME 80 μm ; distance PME-ALE 30 μm . Thoracic furrow distinct but very shallow. Sternum wider than long (0.64/0.48). Chelicerae as in Figure 215. Palps as in Figures 213 and 214, trochanter with retrolateral and pointed prolateral apophyses; procurus apparently with ventral hinged process (difficult to see); embolus simple ('e' in Fig. 213), with distal transparent spine. Legs without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 7%; tarsus 1 with >40 pseudosegments, distinct distally.

Variation. Tibia 1 in 2 other males: 5.4, 6.4.

Female. In general similar to male. Tibia 1 in 4 females: 4.6–5.1. Epigynum very small, light brown, as in Figures 130 and 216. Dorsal view as in Figure 217.

Distribution. Known only from type locality (Map 2).

Material examined. MADAGASCAR: *Antsiranana*: Marojejy Res.: type above, together with 5♂ 7♀, same collection data, in CAS.

'SPERMOPHORA' INCERTAE SEDIS

Two new Malagasy species are tentatively assigned to *Spermophora*, even though this assignment is almost certainly wrong in at least the second species. Both lack the synapomorphies of *Zatavua* and *Paramicromerys*, and do not show any other special similarities that would justify a tentative assignment to any of the two genera. On the other hand, *Spermophora* in its present status is polyphyletic anyway, and it seems preferable to reconsider the following two species in future revisions rather than to create new but poorly supported genera for them.

'SPERMOPHORA' RANOMAFANA, NEW SPECIES

(FIGS 218–220, 224–237)

Type. Male holotype from Talatakely (21°15'S, 47°25'E), 900 m a.s.l., Ranomafana National Park, Fianarantsoa, Madagascar; December 5–7, 1993 (N. Scharff, S. Larcher, C. E. Griswold, R. Andriamasi-manana); in CAS.

Etymology. Named for the type locality. The specific name is a noun in apposition.

Diagnosis. Light species with very high opisthosoma (Fig. 219), distinguished from known congeners and other Malagasy pholcids by the shape of the sclero-

tized apophysis on the bulb ('a' in Fig. 224), the slender simple procurus, and the structure with pockets ('pp' in Figs 229, 235 and 237) on the female opisthosoma between epigynum and spinnerets.

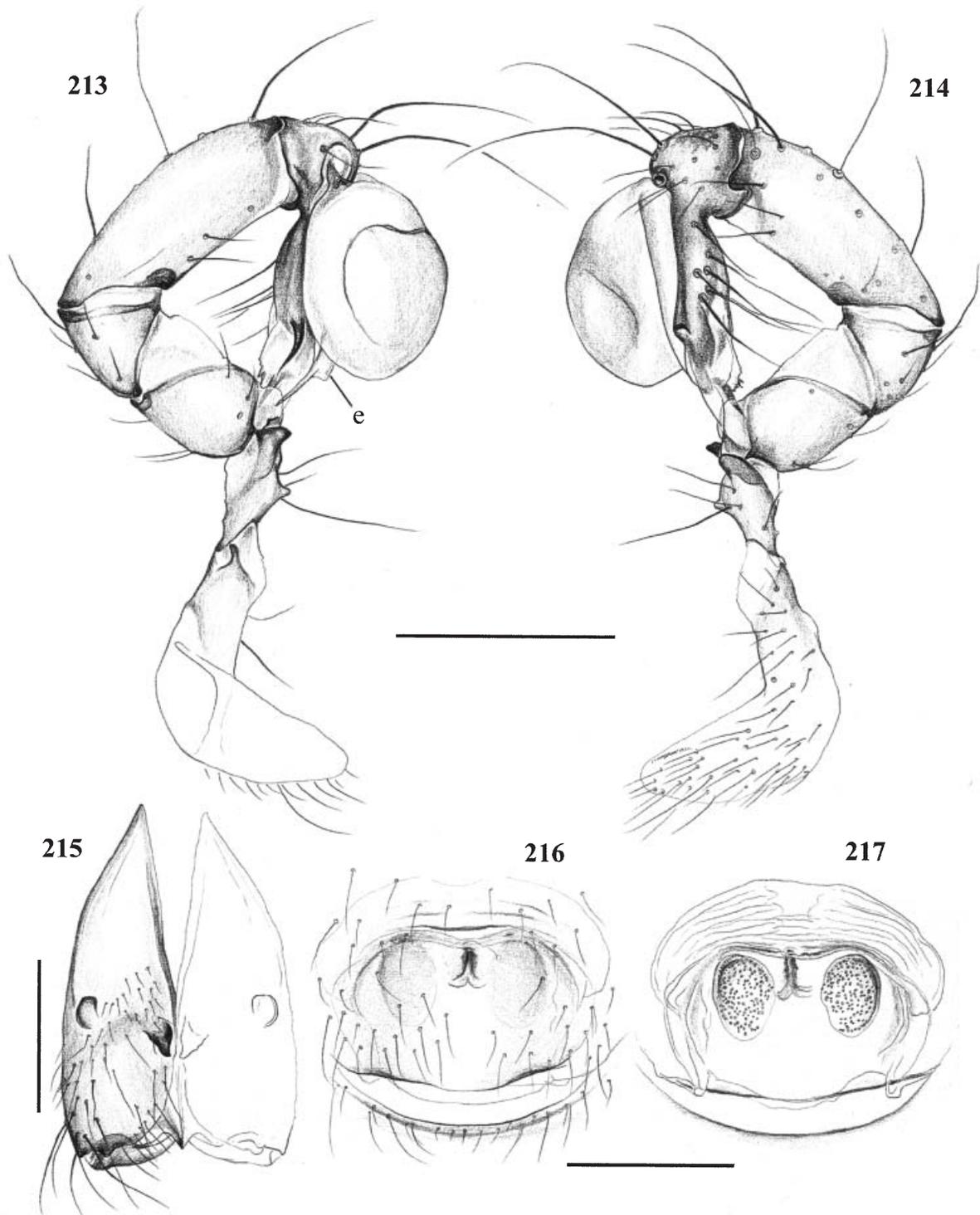
Male (holotype). Total length 1.9, carapace width 0.78. Leg 1: 18.8 (4.8 + 0.3 + 4.7 + 6.7 + 2.3), tibia 2: 2.7, tibia 3: 1.8, tibia 4: 2.5; tibia 1 L/d: 71. Habitus as in Figures 218 and 219. Carapace ochre-yellow with black marginal lines; sternum pale ochre-yellow. Legs ochre-yellow, without marks. Opisthosoma ochre-grey, with some large blackish spots; ventrally no marks. Ocular area barely elevated, triads on low elevations; distance PME-PME 220 μm ; diameter PME 60 μm ; distance PME-ALE 25 μm ; no trace of AME. Thoracic furrow present only frontally, low and indistinct. Clypeus unmodified. Sternum wider than long (0.52/0.48). Chelicerae as in Figures 226 and 227, distance between tips of apophyses 270 μm . Palps as in Figures 224 and 225, trochanter with retrolateral apophysis (longer in dorsal than in retrolateral view); procurus slender and simple, distally with small hinged process ('hp' in Figs 224 and 236). Embolus ('e' in Fig. 224) simple membranous tube, without distal spine; distinctive sclerotized apophysis distally on bulb. Legs without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 9%; tarsus 1 with >30 pseudosegments, distally fairly distinct. Epiandrous spigots as in Figure 231. ALS and PMS spigots as in Figure 233.

Variation. Tibia 1 in 46 other males 3.9–5.0 (\bar{x} = 4.46).

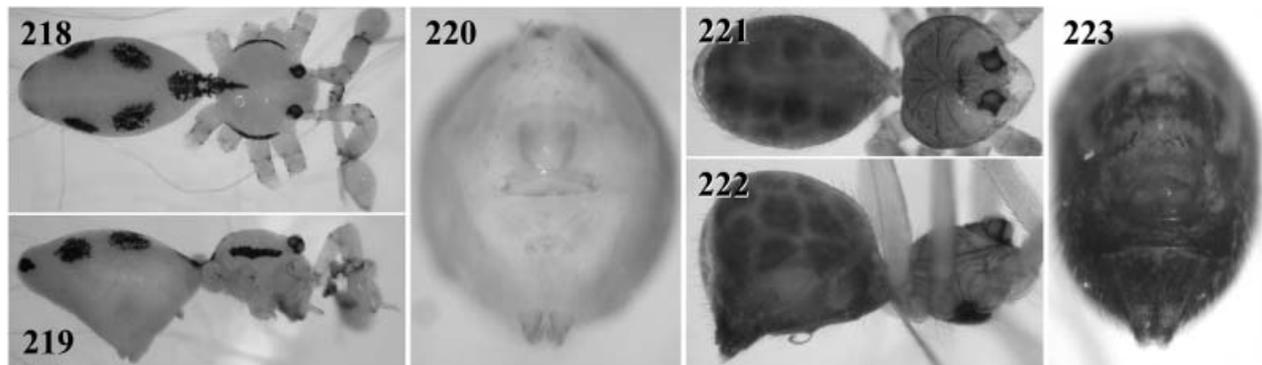
Female. In general similar to male, but most females with blackish pigment proximally on femora (dorso-frontally); some females black on clypeus, chelicerae and palps; with significantly more variation in pattern on opisthosoma. Tibia 1 in 44 females: 2.8–4.0 (\bar{x} = 3.45). Epigynum as in Figures 220 and 228, with pair of anterior pockets ('ap' in Figs 229 and 237) about 255 μm apart, and additional pair ('pp' in Figs 229, 235 and 237) between epigynum and spinnerets, about 120 μm apart. Dorsal view as in Figure 229.

Distribution. Known only from the Ranomafana National Park area (Map 2).

Material examined. MADAGASCAR: *Fianarantsoa*: Ranomafana N. P.: Talatakely: type above together with 11♂ 15♀, same collection data, in CAS; 2♀, same collection data, in CAS. Talatakely at 21°14.9'S, 47°25.6'E, April 5–30, 1998 (C. E. Griswold, D. H. Kavanaugh, N. P. Penny, M. J. Raherilalao, J. S. Ranorianarisoa, J. Schweikert, D. Ubick), 7♂ 10♀ in CAS; same collection data, at night, 2♂ 3♀ in CAS; Vohiparara: Piste Touristique (21°13.6'S, 47°24.0'E), c. 1000 m a.s.l., April 19–23, 1998 (C. E. Griswold, D.



Figures 213–217. *Paramicromerys rabearivelo*. Left male palp in prolateral (213) and retrolateral (214) views, male chelicerae in frontal view (215), and cleared epigynum in ventral (216) and dorsal (217) views. 'e': embolus. Scale lines: 0.3 mm (213, 214), 0.2 mm (215–217).



Figures 218–223. ‘*Spermophora*’ spp. habitus, males in dorsal and lateral views, and female opisthosomata, ventral views with epigynum. 218–220, ‘*S.*’ *ranomafana*. 221–223, ‘*S.*’ *vyvato*.

H. Kavanaugh, N. P. Penny, M. J. Raheirilalao, J. S. Ranorianarisoa, J. Schweikert, D. Ubick), 5♂ 8♀ in CAS. Vatoharanana (21°16.7'S, 47°26.1'E), primary forest, c. 1200 m a.s.l., April 15, 1998 (C. E. Griswold, D. H. Kavanaugh, N. P. Penny, M. J. Raheirilalao, J. S. Ranorianarisoa, J. Schweikert, D. Ubick) 6♂ 5♀ in CAS. Ranomafana N. P., roadside vegetation near park entrance, c. 21°14.3'S, 47°26.0'E, c. 800 m a.s.l., April 22, 1998 (same collectors), 1♂ 1♀ in CAS. Vohiparara at 21°14'S, 47°24'E, December 5–7, 1993 (N. Scharff, S. Larcher, C. E. Griswold, R. Andriamasimanana), 3♀ in CAS. 7 km W Ranomafana at 21°12'S, 47°27'E, 900 m a.s.l., March 1–13, 1990 (W. E. Steiner), 5♂ in USNM; same collection data, sweeping old paddy, 1♂ in USNM; same locality, January 20–February 28, 1990 (W. E. Steiner), flight intercept yellow pan trap in Malaise trap in small clearing, montane rainforest, 10♂ in USNM. 7 km W Ranomafana at 21°16'S, 47°25'E, 900 m a.s.l., on low foliage and saplings, montane rainforest, September 5, 1993 (W. Steiner), 4♂ 4♀ in USNM. 7 km W Ranomafana at 21°12'S, 47°27'E, 1100 m a.s.l., November 1–7, 1988 (W. E. Steiner), 1♂ 1♀ in USNM. Valohoaka camp 8 km SW Ranomafana (21°19'S, 47°24'E), 1040 m a.s.l., low foliage and saplings, night, montane rainforest, September 8, 1993 (W. Steiner), 1♂ in USNM.

‘SPERMOPHORA’ VYVATO, NEW SPECIES
(FIGS 221–223, 238–243)

Type. Male holotype from Marojejy Reserve, 8.4 km NNW Manantenina (14°26'S, 49°45'E), 700 m a.s.l., Antsiranana, Madagascar; November 10–16, 1993 (C. E. Griswold, J. Coddington, N. Scharff, S. Larcher, R. Andriamasimanana); in CAS.

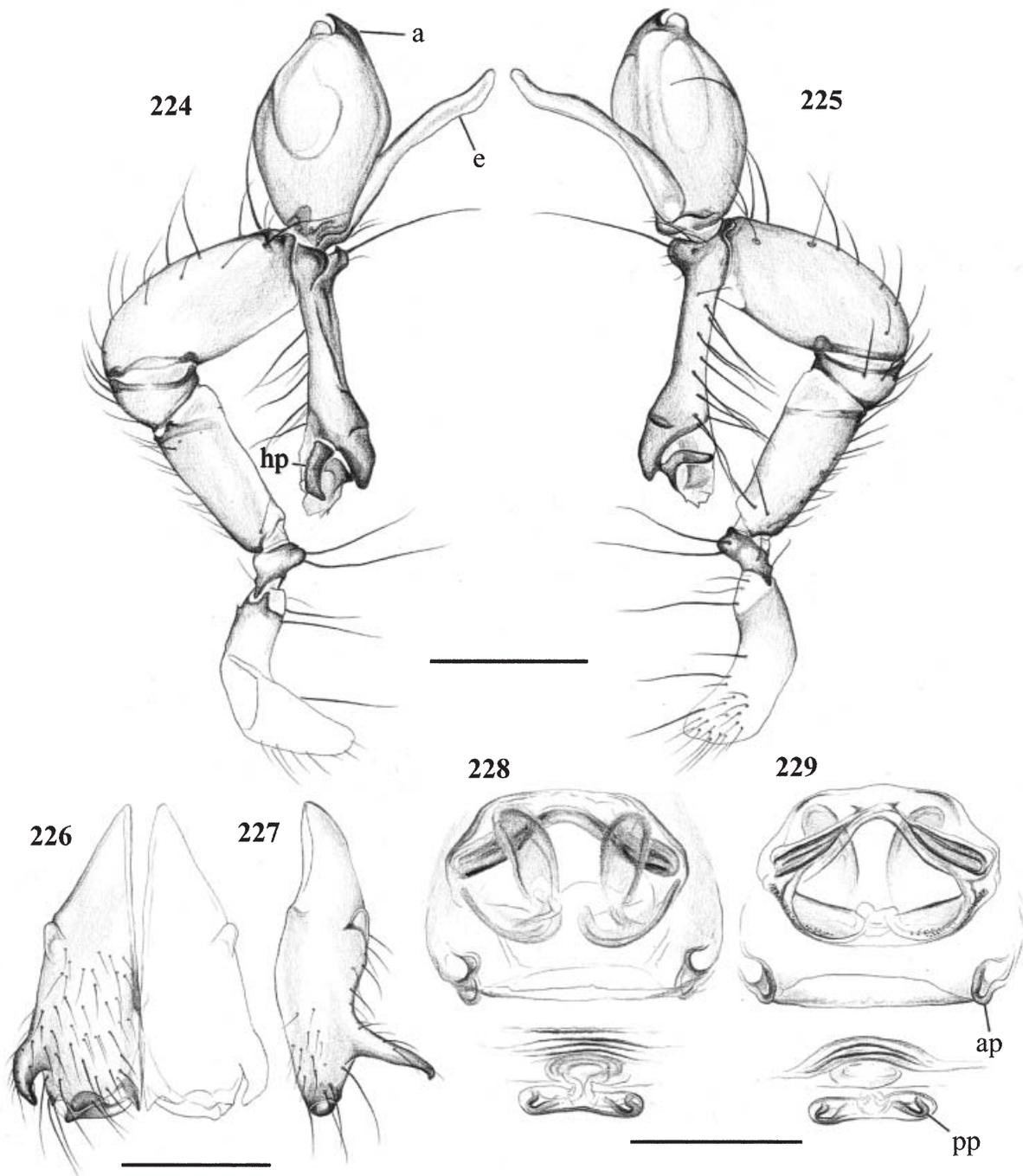
Etymology. The specific name is a noun in apposition, contracted from Vy, Vato, Sakélika, a group of Mala-

gasy intellectuals founded in 1913 to oppose French colonialism.

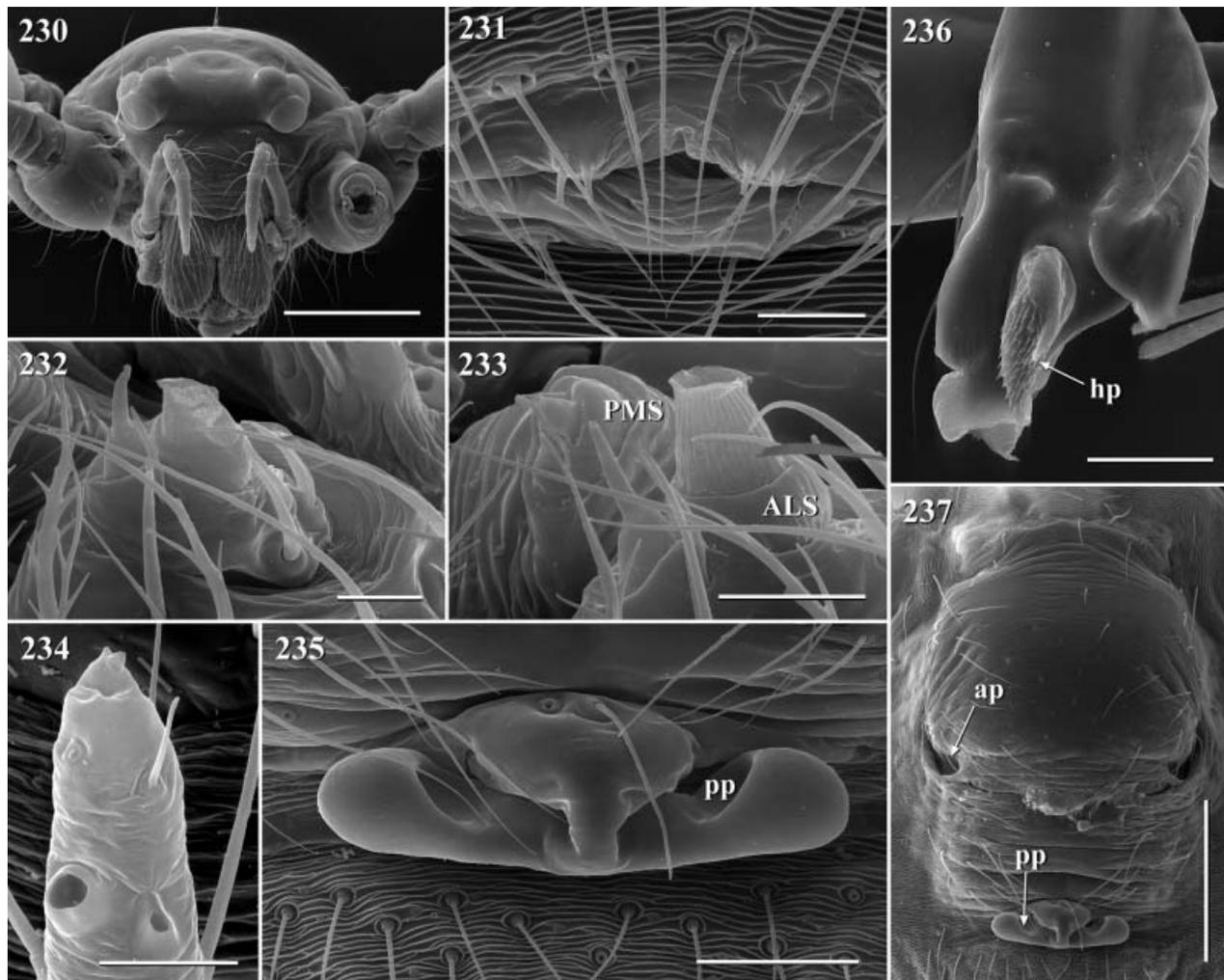
Diagnosis. Small species with globular opisthosoma, easily distinguished from known congeners and from other Malagasy pholcids by the unusual male palp (Figs 238 and 239) and the proximal and median position of the male cheliceral apophyses (Fig. 240). *Paramicromerys rabearivelo* has apophyses in a similar position, but extremely different palps.

Male (holotype). Total length 1.4, carapace width 0.68. Leg 1: 10.9 (2.9 + 0.3 + 2.9 + 3.5 + 1.3), tibia 2: 1.6, tibia 3: 1.3, tibia 4: 1.8; tibia 1 L/d: 52. Habitus as in Figures 221 and 222. Carapace ochre with brown pattern; sternum dark brown. Legs ochre, slightly darker subdistally on femora and tibiae. Opisthosoma greenish-grey, with large dark spots shining through cuticle (Fig. 222); ventrally brownish. Ocular area barely elevated, only triads on low elevations; distance PME-PME 110 µm; diameter PME 80 µm; distance PME-ALE 20 µm; no trace of AME. Thoracic furrow present only frontally, very shallow. Clypeus unmodified. Sternum wider than long (0.48/0.40). Chelicerae as in Figure 240, with one globular hair on the tip of each apophysis (Fig. 241); distance between tips of apophyses 22 µm. Palps as in Figures 238 and 239, trochanter with retrolateral apophysis; procurus with short basis and two, apparently hinged, distal structures ('p1' and 'p2' in Fig. 239); embolus ('e' in Fig. 239) simple, without distal spine. Legs without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium of tibia 1 at 18%; tarsus 1 with >15 pseudosegments, only distally fairly distinct.

Female. In general similar to male, but darker, with black spots close to lateral margins on carapace and on posterior side of ocular area; legs dark brown; opisthosoma with black pattern on surface. Tibia 1:



Figures 224–229. *Spermophora ranomafana*. Left male palp in prolateral (224) and retrolateral (225) views, male chelicerae in frontal (226) and lateral (227) views, and cleared epigynum in ventral (228) and dorsal (229) views. ‘a’: bulbal apophysis; ‘ap’: anterior pocket; ‘e’: embolus; ‘hp’: hinged process; ‘pp’: posterior pocket. Scale lines: 0.3 mm (224, 225), 0.2 mm (226–229).



Figures 230–237. *'Spermophora' ranomafana*. 230, Female prosoma, frontal view. 231, Male gonopore with epiandrous spigots. 232, Female ALS. 233, Male ALS and PMS. 234, Tip of female palp with tarsal organ. 235, Structure on female opisthosoma between epigynum and spinnerets, with pair of pockets. 236, Tip of procurus with hinged process ('hp'). 237, Epigynum with posterior structure. 'ap': anterior pocket; 'pp': posterior pocket. Scale lines: 300 μm (230), 20 μm (231, 234), 10 μm (232, 233), 50 μm (235), 60 μm (236), 200 μm (237).

2.2. Epigynum as in Figures 223 and 242, distance between pockets 24 μm . Dorsal view as in Figure 243.

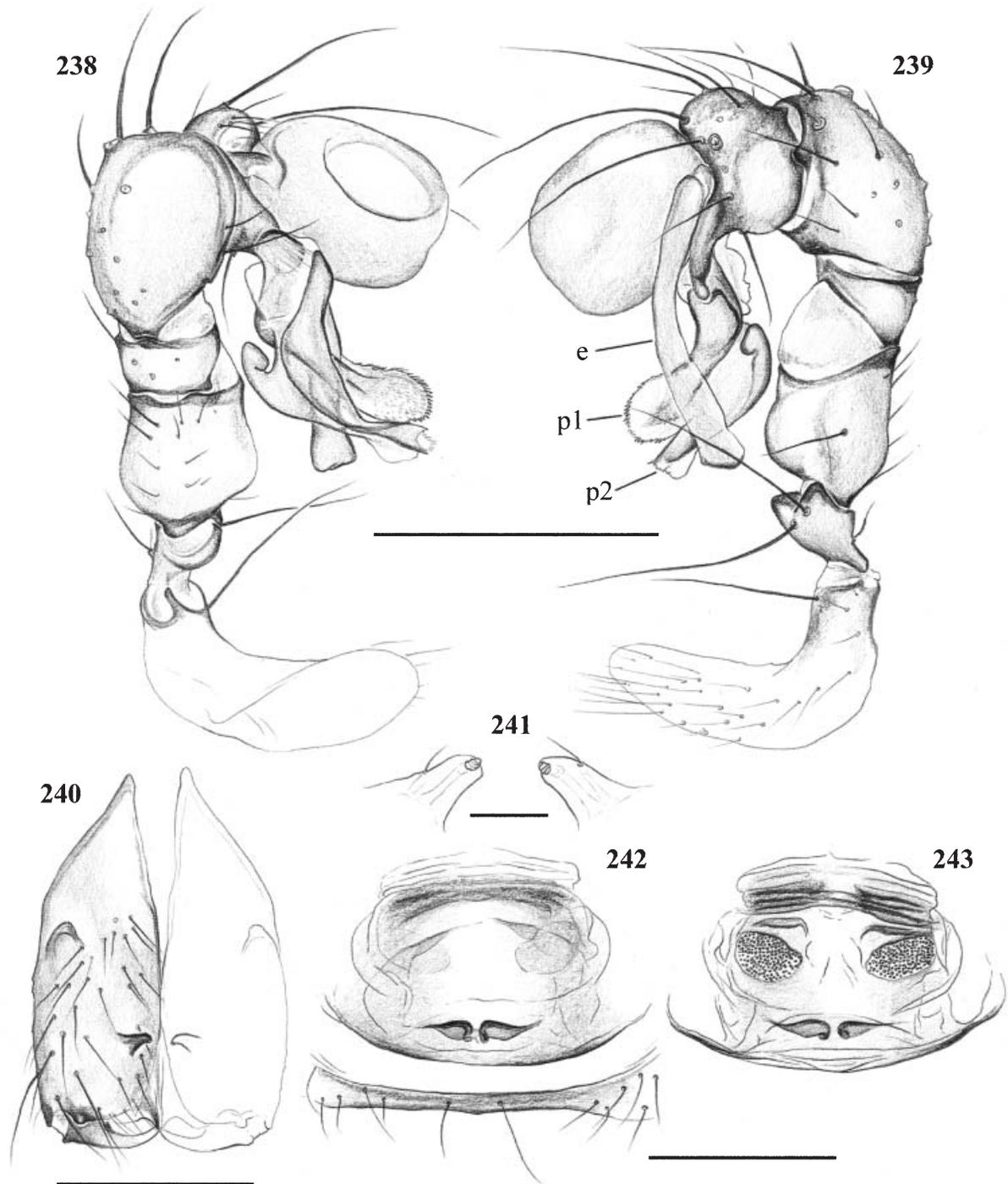
Distribution. Known only from type locality (Map 2).

Material examined. MADAGASCAR: *Antsiranana*: Marojejy Res.: type above, together with 1 ♀, same collection data, in CAS.

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Figures 238–243. *Spermophora vyvato*. Left male palp in prolateral (238) and retrolateral (239) views, male chelicerae in frontal (240) view, male cheliceral apophyses with single modified hair imbedded in each tip (241) and cleared epigynum in ventral (242) and dorsal (243) views. 'e': embolus; 'p1', 'p2': distal procurus elements. Scale lines: 0.3 mm (238, 239), 0.2 mm (240, 242, 243), 30 μ m (241).

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APPENDIX 1

TAXA USED IN THE CLADISTIC ANALYSIS

Filistatidae	
1. <i>Kukulcania hibernalis</i> (Hentz)	Costa Rica: San José Prov. (UCR)
Ochyroceratidae	
2. <i>Ochyrocera</i> sp.	Costa Rica: San José Prov. (AMNH)
Diguetidae	
3. <i>Diguetia signata</i> Gertsch	USA: Arizona (AMNH)
Plectreuridae	
4. <i>Plectreurys tristis</i> Simon	USA: Arizona (AMNH)
Pholcidae	Yemen: Ja'ar (AMNH)
5. <i>Ninetis subtilissima</i> Simon	USA: California (AMNH)
6. <i>Pholcophora americana</i> Banks	USA: Arkansas (AMNH)
7. <i>Psilochorus pullulus</i> (Hentz)	Guatemala: Department Sololá (UCR)
8. <i>Ixchela furcula</i> (F. O. Pickard-Cambridge)	Galápagos Islands (AMNH)
9. <i>Aymaria conica</i> (Banks)	Galápagos Islands (AMNH)
10. <i>Mesabolivar junin</i> Huber	Peru: Junin (AMNH)
11. <i>Coryssocnemis simla</i> Huber	Trinidad: Arima Valley (AMNH)
12. <i>Ciboneya nuriae</i> Huber & Pérez González	Cuba: Pinar del Rio (IES)
13. <i>Physocyclus globosus</i> (Taczanowski)	Costa Rica: San José (UCR)
14. <i>Artema atlanta</i> Walckenaer	USA: Arizona (AMNH)
15. <i>Smeringopus pallidus</i> (Blackwall)	Costa Rica: San José Prov. (AMNH)
16. <i>Crossopriza lyoni</i> (Blackwall)	India: West Bengal (AMNH)
17. <i>Holocnemus pluchei</i> (Scopoli)	Spain: Almeria (AMNH)
18. <i>Trichocyclus arabana</i> Huber	Australia: Western Australia (WAM)
19. <i>Zatavua isalo</i> , n. sp.	Madagascar: Fianarantsoa (MCZ)
20. <i>Zatavua madagascariensis</i> (Fage)	Madagascar: Toliara (MNHN)
21. <i>Zatavua zanahary</i> , n. sp.	Madagascar: Antsiranana (CAS)
22. <i>Zatavua voahangyae</i> , n. sp.	Madagascar: Fianarantsoa (CAS)
23. <i>Zatavua analalava</i> , n. sp.	Madagascar: Toamasina (MRAC)
24. <i>Zatavua vohiparara</i> , n. sp.	Madagascar: Fianarantsoa (CAS)
25. <i>Zatavua tamatave</i> , n. sp.	Madagascar: Toamasina (MRAC)
26. <i>Zatavua griswoldi</i> , n. sp.	Madagascar: Antsiranana (CAS)
27. <i>Belisana australis</i> Huber	Australia: Northern Territory (QMB)
28. <i>Belisana</i> sp. 1	Sumatra: Ketambe, Gn Leuser, no further data (CDL)
29. <i>Belisana</i> sp. 2	Sumatra: Ketambe, leg. Suharto, March 2–4, 1986 (CDL)
30. <i>Belisana</i> sp. 3	Thailand: Chiang Mai Prov., leg. Schwendinger, August 22–September 22, 1990 (MHNG)
31. <i>Spermophora senoculata</i> (Dugès)	USA: New York City (AMNH)
32. <i>Spermophora yao</i> Huber	Australia: Queensland (QMB)
33. <i>Spermophora peninsulæ</i> Lawrence	South Africa: Western Cape Prov. (CAS)
34. <i>Spermophora</i> sp. 1	Sumatra: Kerinci Nat. Park, leg. Djojosedharmo, July 21–30, 1988 (CDL)
35. <i>Spermophora</i> sp. 2	Lesser Sunda Isl.: Sumbawa, leg. Djojosedharmo, January 1–3, 1990 (CDL)
36. <i>Spermophora</i> sp. 3	South Africa: Western Cape Prov., leg. Dippenaar-S., February 1, 1989 (NCP)
37. ' <i>Spermophora</i> ' sp. 4	South Africa: Kwa Zulu-Natal, Bonamanzi, leg. Huber, April 1, 2001 (ZFMK)
38. ' <i>Spermophora</i> ' sp. 5	South Africa: Kwa Zulu-Natal, Cape Vidal, leg. Huber, April 3, 2001 (ZFMK)
39. ' <i>Spermophora</i> ' sp. 6	Tanzania: Iringa, Kihanga Strm. ('TA080'), ZMUC-SI Expedition, 1997 (ZMUC)
40. ' <i>Spermophora</i> ' sp. 7	Comoros: Grande Comore, leg. A. Lambillon, July 1968 (MRAC)
41. ' <i>Spermophora</i> ' sp. 8	Comoros: Mayotte, leg. R. Jocqué, July 19–August 2, 1998 (MRAC)
42. ' <i>Spermophora</i> ' sp. 9	Tanzania: Iringa, Kihanga Strm. ('TA076'), ZMUC-SI Exp., 1997 (USNM)

APPENDIX 1

Continued

43. <i>'Spermophora'</i> sp. 10	Tanzania: Tanga, Mazumbai, leg. Griswold, November 11–20, 1995 (CAS)
44. <i>'Spermophora'</i> <i>ranomafana</i> , n. sp.	Madagascar: Fianarantsoa (CAS)
45. <i>'Spermophora'</i> <i>vyvato</i> n. sp.	Madagascar: Antsiranana (CAS)
46. <i>Micromerys gracilis</i> Bradley	Australia: Northern Territory (QMB)
47. <i>Micromerys daviesae</i> Deeleman-Reinhold	Australia: Queensland (QMB)
48. <i>Metagonia argentinensis</i> Mello-Leitão	Brazil: Rio Grande do Sul (MCN)
49. <i>Metagonia rica</i> Gertsch	Costa Rica: San José Prov. (UCR)
50. <i>Metagonia delicata</i> (O. Pickard-Cambridge)	Nicaragua: Bluefields (UCR)
51. <i>Pholcus phalangioides</i> (Fuesslin)	USA: San Francisco (AMNH)
52. <i>Leptopholcus delicatulus</i> Franganillo	Cuba: Oriente (AMNH)
53. <i>Micropholcus fauroti</i> (Simon)	USA: Texas (AMNH)
54. <i>Spermophorides</i> sp. 1	Canary Islands: Lanzarote, leg. Wunderlich (ZFMK)
55. <i>Spermophorides</i> sp. 2	Mallorca, leg. Hillyard, December 21, 1980 (BMNH)
56. <i>Paramicromerys rothorum</i> , n. sp.	Madagascar: Antsiranana (CAS)
57. <i>Paramicromerys betsileo</i> , n. sp.	Madagascar: Fianarantsoa (CAS)
58. <i>Paramicromerys marojeji</i> , n. sp.	Madagascar: Antsiranana (CAS)
59. <i>Paramicromerys rabearivelo</i> , n. sp.	Madagascar: Antsiranana (CAS)
60. <i>Paramicromerys coddingtoni</i> , n.sp.	Madagascar: Antsiranana (CAS)
61. <i>Paramicromerys ralamboi</i> , n. sp.	Madagascar: Antsiranana (CAS)
62. <i>Paramicromerys scharffi</i> , n. sp.	Madagascar: Fianarantsoa (CAS)
63. <i>Paramicromerys nampoinai</i> , n. sp.	Madagascar: Antsiranana (CAS)
64. <i>Paramicromerys manantenina</i> , n. sp.	Madagascar: Antsiranana (CAS)

APPENDIX 2

CHARACTERS SCORED FOR THE CLADISTIC ANALYSIS

- Eye number*: (0) eight; (1) six. All Malagasy taxa treated in this paper have six eyes. It must be noted that the presumably ancestral state of eight eyes is regained twice in the cladogram shown in Appendix 4 (in the node leading to *Pholcus*, *Leptopholcus* and *Micropholcus*, and in *Micromerys*). Such a regain of a complex character is dubious and suggests a flaw in data choice.
- Distance between posterior median eyes (PME)*: (0) $>1.75 \times$ diameter of PME; (1) $<1.75 \times$ diameter of PME. Cladistic analysis suggests that grouping of all eyes close together is primitive (as in *Zatavua*), while a large distance between the triads is derived (as in *Paramicromerys* and many other pholcines).
- Distance between PME and anterior lateral eyes (ALE)*: (0) $<0.55 \times$ diameter of PME; (1) $>0.55 \times$ diameter of PME. State '1' is common in the New World clade. Within the pholcines included in the data matrix, only *'Spermophora'* sp. 9 has independently evolved state '1'.
- Sculpture of carapace*: (0) without median indentation; (1) with median groove; (2) with roughly circular indentation behind ocular area. The primitive condition is ambiguous. Therefore, it remains open whether the grooves in *Zatavua isalo* and *madagascariensis* (Fage) are primitive or derived within *Zatavua*.
- Conical median elevation on female carapace*: (0) absent; (1) present. This character is a synapomorphy of a species group within *Zatavua*; it has convergently evolved in *Physocyclus*.
- Clypeus height*: (0) shorter than chelicerae; (1) as long as or longer than chelicerae. State '1' is a synapomorphy of Pholcidae.
- Paired modification on male clypeus*: (0) absent; (1) present. State '1' is a synapomorphy of a spe-

- cies group within *Zatavua*; it has convergently evolved in *Metagonia*.
8. *Sternum width*: (0) wider than long; (1) longer than wide. All pholcids have a wide sternum. In the present matrix, state '1' unites *Diguetia* and *Plectreureys*.
 9. *Anterior humps on male sternum*: (0) absent; (1) present. In the present data set, humps are a synapomorphy of ninetines. However, they also occur in the New World clade.
 10. *Epiandrous spigots*: (0) absent; (1) present. Epiandrous spigots seem to be present in all pholcines except in *Spermophorides*.
 11. *Spigots on posterior lateral spinnerets (PLS)*: (0) present; (1) absent. State '1' is a synapomorphy of Pholcidae.
 12. *Spigots on anterior lateral spinnerets (ALS)*: (0) about seven spigots present; (1) only basic set of two spigots present. The presence of several spigots is ancestral (as retained in *Zatavua*). *Paramicromerys* and some related genera have reduced the spigots to the basic set of two, as has convergently occurred in several other taxa (Huber, 2000). It must be noted that the presumably ancestral state is regained in the cladogram shown in Appendix 4 (by *Metagonia*), suggesting a flaw in data choice (cf. character 1).
 13. *'Pseudoentelegyny'*: (0) absent; (1) present. State '1' (in which the spermatheca is provided with two ducts, in analogy to the insemination and fertilization ducts of entelegyne spiders; see Huber, 1997) occurs in *Metagonia* only (Huber, 2000).
 14. *Long folded scape on epigynum*: (0) absent; (1) present. This unique structure is a synapomorphy of some Eastern and Central African '*Spermophora*' species (for illustrations see, e.g. Berland, 1920: fig. 163; Tullgren, 1910: fig. 37k; Fage & Simon, 1936: fig. 11c). The scape of *Zatavua vohiparara* (Fig. 36) is not folded and not considered homologous.
 15. *Female internal genitalia*: (0) symmetric; (1) asymmetric. State '1' occurs in *Metagonia* only (Huber, 2000).
 16. *Posterior pocket or pockets on female opisthosoma*: (0) absent; (1) present between epigynum and spinnerets; (2) present on posterior plate. State '2' is presumably a synapomorphy of *Spermophorides* ('aa' in figs 7, 15, 23, 31 and 48 in Senglet, 1972); state '1' is a synapomorphy of 'true' *Spermophora* or of a subgroup of *Spermophora*. '*Spermophora ranomafana*' is the only known Malagasy taxon with posterior pockets (state '1'; Figs 228, 235 and 237), but these are here interpreted as convergent to the pockets in 'true' *Spermophora*. This character might more appropriately be coded as two binary characters but doing so does neither change the length nor the topology of the consensus cladogram.
 17. *Trochanter cuneal notch*: (0) absent; (1) present. This character unites Pholcidae with Diguettidae + Plectreureidae (Huber, 2000).
 18. *Relative length of male femur 1 and tibia 1*: (0) about same length; (1) femur 1 > 1.15 × tibia 1. In the present data set, state '1' unites *Diguetia* and *Plectreureys*.
 19. *Enlarged femora of walking legs*: (0) absent; (1) present. Present only in the New World clade (Huber, 2000).
 20. *Spines (macrotrichia) in single row ventrally on male femora*: (0) absent; (1) present. Spines characterize a species group within *Paramicromerys*, but have independently evolved several times (Huber, 2000). In the present data set, also the spines in an East African and a Comoran '*Spermophora*' species (spp. 8 and 10) are considered to have evolved independently.
 21. *Relative length of tibia 1 and tibia 4*: (0) about same length; (1) tibia 1 > 1.15 × tibia 4. Relatively long tibiae 4 (state '0') occur in ninetines, in *Micromerys*, and in *Ciboneya*. The ancestral state is presumably state '1'.
 22. *Number of trichobothria on tibiae*: (0) more than three; (1) three. The reduction to three trichobothria on legs 2–4 is a synapomorphy of Pholcidae. For legs 1 see next character.
 23. *Prolateral trichobothrium on tibia 1*: (0) present; (1) absent. The optimization of this character is ambiguous. The prolateral trichobothrium is absent in all pholcines except in *Micromerys*. Within the present data set it is further absent in ninetines, in *Crossopriza*, and in *Ciboneya*.
 24. *Position of retrolateral trichobothrium on tibia*: (0) distal (after 45% of tibia length); (1) proximal (before 45% of tibia length). In the present data set, state '0' is a synapomorphy of ninetines.
 25. *Leg length*: (0) short-legged: male tibia 1 up to 2.5 × carapace width; (1) long-legged: male tibia 1 longer than 2.5 × carapace width. In the present data set, short legs are a synapomorphy of ninetines, and have convergently evolved in *Belisana* sp. 3.
 26. *Tarsal pseudosegments*: (0) absent; (1) present. Pseudosegments are a synapomorphy of Pholcidae, and have secondarily been reduced in *Micromerys* (Huber, 2001).
 27. *Number of tarsal pseudosegments on male tarsi 1*: (0) up to 10; (1) more than 10. Only ninetines have fewer than 10 pseudosegments.
 28. *Regularity of pseudosegments*: (0) regular segmentation; (1) irregular, 'broken' cuticle. State '1' is considered a synapomorphy of holocnemines, but

- the regaining of regular segmentation in *Trichocyclus* is dubious.
29. *Sexual dimorphism of chelicerae*: (0) absent; (1) present. The presence of modifications on the male chelicerae is a synapomorphy of Pholcidae.
 30. *Macrosetae proximally on male chelicerae*: (0) absent; (1) present. State '1' is a synapomorphy of a group of central and eastern African '*Spermophora*' species, including in the present data set '*Spermophora*' spp. 6 and 9.
 31. *Stridulatory files laterally on male chelicerae*: (0) absent; (1) present. In the present data set, cheliceral stridulation is interpreted as having evolved four times convergently (*Plectreurys*, *ninetines*, *Holocnemus* + *Crossopriza*, *Physocyclus* + *Trichocyclus*). It is not known in pholcines with the exception of some *Metagonia* species (Huber, 2000).
 32. *Shape of cheliceral lamina*: (0) not pointed; (1) pointed. A strongly pointed lamina is a synapomorphy of holocnemines.
 33. *Proximolateral apophyses on the male chelicerae*: (0) absent; (1) present. These apophyses are present in all pholcines except in *Metagonia*. They have rarely evolved in other taxa (not in the present data set; see Huber, 2000).
 34. *Direction of proximolateral cheliceral apophyses*: (0) pointing upwards (1) pointing backwards. State '0' is usual in pholcines, only *Zatavua* has state '1' (e.g. Figs 62, 84, 86 and 98).
 35. *Globular or conical hairs on male chelicerae*: (0) absent; (1) spread over surface; (2) imbedded in apophysis. Globular or conical hairs that are spread over the surface have evolved at least twice (*Metagonia*, *Artema*). In at least four occasions, modified hairs evolved that are imbedded in the tip of an apophysis (*Smeringopus* and relatives, *Pholcus* and relatives, some East African and Comoran '*Spermophora*' species here represented by '*S.*' *vyvato* and '*S.*' spp. 6–10, and within *Paramicromerys*). Note that the modified hairs in '*Spermophora*' *vyvato* and in *Paramicromerys nampoinai* + *manantenina* are here interpreted to have evolved independently.
 36. *Pair of long modified hairs on tip of male cheliceral apophysis*: (0) absent; (1) present. These distinctive hairs are a synapomorphy of a group of mainly Southern African '*Spermophora*' species, here represented by '*Spermophora*' spp. 4 and 5.
 37. *Retrolateral apophysis in the 'knee' of the male palpal coxa*: (0) absent; (1) present. This apophysis is a synapomorphy of the New World clade (Huber, 2000).
 38. *Ventral apophysis distally on male palpal coxa*: (0) absent; (1) present. This apophysis is a synapomorphy of a group of Eastern African '*Spermophora*' species ('*Spermophora*' spp. 6, 9, 10 in the present data set).
 39. *Retrolateral apophysis on male palpal trochanter*: (0) absent; (1) present. This apophysis is present in most pholcines with the exception of *Zatavua* (also absent in *Metagonia a.*, *Paramicromerys marojeji*, and *Spermophora* sp. 2).
 40. *Proximodorsal apophysis on male palpal femur*: (0) absent or simple hump; (1) present, pointing ventrally; (2) present, pointing dorsally. State '1' is a synapomorphy of a group of species within *Paramicromerys*; state '2' is a synapomorphy of a group of species of South African *Spermophora* (represented herein by *S. peninsulae* and *S. sp. 3*).
 41. *Position of the dorsal male palpal trichobothrium*: (0) regular, i.e. not extremely distal; (1) extremely distal. Some East African '*Spermophora*' species (spp. 6, 9, 10) and '*S.*' *vyvato* are characterized by an extremely distal dorsal trichobothrium.
 42. *Shift of male palpal tibia-cymbium joints*: (0) absent; (1) prolateral joint shifted to ventral position, retrolateral joint shifted to dorsal position (2) prolateral joint shifted to dorsal position, retrolateral joint shifted to ventral position. State '1' is a synapomorphy of *Zatavua* (e.g. Figs 29, 33 and 47), state '2' is a synapomorphy of *Paramicromerys* (e.g. Figs 143, 155 and 192).
 43. *Retrolateral notch on cymbium*: (0) absent; (1) present. A notch retrolaterally on the cymbium (e.g. Figs 34, 48 and 57) is a synapomorphy of a species group within *Zatavua*.
 44. *Procurus (paracymbium)*: (0) absent; (1) present. The procurus is a synapomorphy of Pholcidae. One single species is known to lack a procurus (Huber, 2002).
 45. *Procurus attachment site on cymbium*: (0) straight or ventrally; (1) dorsally. State '1' is a synapomorphy of *Spermophorides* (see figs 3, 11 and 19, etc. in Senglet, 1972; fig. 229 in Wunderlich, 1992; figs 188, 228 and 243 in Wunderlich, 1987).
 46. *Hinged process on procurus*: (0) absent; (1) present. A hinged process on the procurus is here considered to have evolved twice: once in South African *Spermophora* (represented herein by *S. peninsulae* and *S. sp. 3*), and in a group of genera including *Paramicromerys*, *Metagonia*, *Micromerys*, *Spermophorides*, and East African and Central African '*Spermophora*'. Within the latter group it is reduced in '*Spermophora*' spp. 6, 9, 10.
 47. *Ventral pocket and dorsal apophysis on procurus*: (0) absent; (1) present. This putative functional unity (Huber & Eberhard, 1997) unites the genera *Trichocyclus*, *Physocyclus* and *Artema*.
 48. *'Brush' of pseudotrichia distally on procurus*: (0) absent; (1) present. Like the previous character,

- this character unites *Trichocyclus*, *Physocyclus* and *Artema*.
49. *Dorsal knob on procurus*: (0) absent; (1) present. This refers to a unique sclerotized structure dorsally on the procurus in Comoran representatives of a clade of largely East African '*Spermophora*' species (herein represented by '*Spermophora*' spp. 7 and 8).
50. *Palpal tarsal organ shape*: (0) flat/exposed; (1) cup-shaped/capsulate. Most pholcines have capsulate tarsal organs. The only known exceptions are '*Spermophora*' sp. 10 and *Belisana* spp. 2 and 3.
51. *Orifice of capsulate tarsal organ*: (0) wide: >35% of outer diameter; (1) narrow: <35% of outer diameter. Ninetines share a narrow orifice (and small size; see Huber, 2000). State '1' has convergently evolved in *Trichocyclus* and in *Spermophora* sp. 2.
52. *Palpal tarsal organ position*: (0) proximal; (1) distal. A distal tarsal organ (e.g. Figs 30, 33 and 44) is the synapomorphy of a clade within *Zatavua*.
53. '*Spermophora flap*': (0) absent; (1) present. This structure (a ventral unhinged process of the procurus; see Huber, 2001) characterizes true '*Spermophora*' or a subgroup thereof (*S. senoculata*, *yao*, *peninsulae*, and spp. 1–3 herein).

APPENDIX 3
DATA MATRIX USED FOR CLADISTIC ANALYSIS

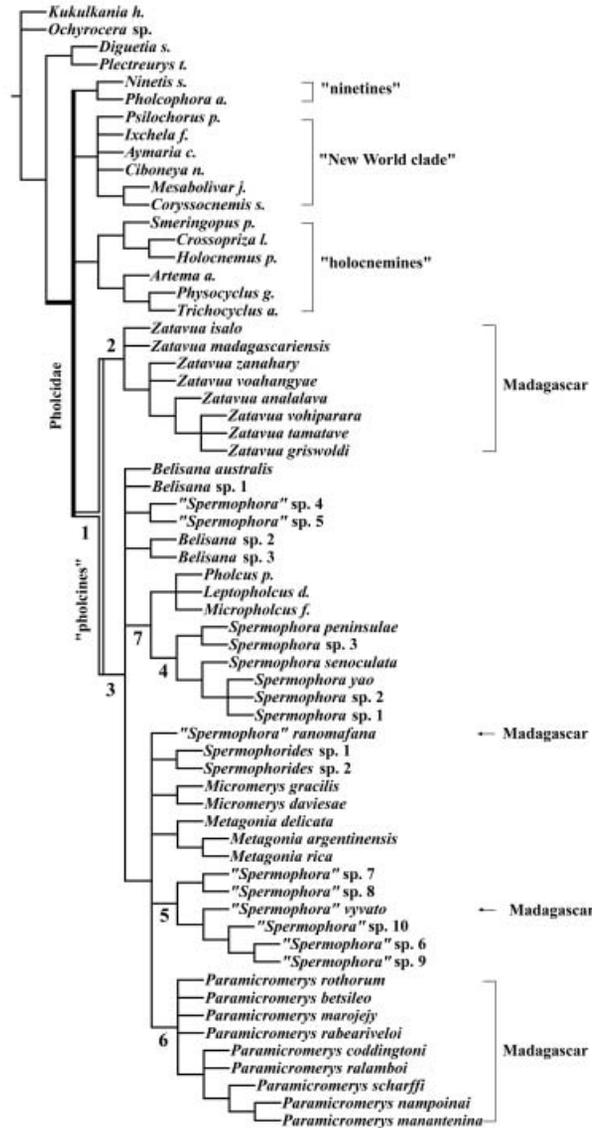
	10	20	30	40	50	
1. <i>Kukulcania h.</i>	0111?00001	00?0000000	10??10--00	0?0-000000	0000-----1	00-
2. <i>Ochyrocera</i> sp.	1??1000001	0000000000	10??10--00	0-0-000000	0000-----1	00-
3. <i>Diguetia s.</i>	1??0000100	00?0001100	00??00--00	000-000000	0000-----1	00-
4. <i>Plectreureys t.</i>	0010000100	10?0001100	00??00--00	100-000000	?000-----0	-0-
5. <i>Ninetis s.</i>	0100010011	1000001000	0110010010	100-000000	0001000001	100
6. <i>Pholcophora a.</i>	0101010011	1000001000	0110010010	100-000000	0001000001	100
7. <i>Psilochorus p.</i>	0101010000	1100001000	1101111010	000-001000	0001000000	-00
8. <i>Ixchela f.</i>	0111010000	1100001000	1101111010	000-001000	0001000000	-00
9. <i>Aymaria c.</i>	0112010000	11?0001000	1101111010	000-001000	0001000000	-00
10. <i>Mesabolivar j.</i>	0111010000	11?0001010	1101111010	000-001010	0001000000	-00
11. <i>Coryssocnemis s.</i>	0111010000	1100001010	1101111010	000-001000	0001000000	-00
12. <i>Ciboneya n.</i>	0101010000	1100001000	0111111010	000-001000	0201000000	-00
13. <i>Physocyclus g.</i>	0102110000	1000001000	1101111110	110-000000	0001001101	000
14. <i>Artema a.</i>	0102010001	1000001000	1101111110	0?0-100000	0001001101	000
15. <i>Smeringopus p.</i>	0102010001	1000001000	1101111110	010-200000	0001000001	000
16. <i>Crossopriza l.</i>	0102010001	1100001001	1111111110	110-200000	0001000001	000
17. <i>Holocnemus p.</i>	0102010001	1100001001	1101111110	110-200000	000100000?	000
18. <i>Trichocyclus a.</i>	0101010000	1000001000	1101111010	110-000000	0001001101	100
19. <i>Zatavua isalo</i>	110101000?	1000001?00	?1?1111010	0011000000	011100000?	?00
20. <i>Zatavua madagascariensis</i>	110101000?	1000001?00	?1??111010	0011000000	011100000?	?00
21. <i>Zatavua zanahary</i>	1100010001	1?00001000	1111111010	0011000000	011100000?	?10
22. <i>Zatavua voahangyae</i>	1100010001	1000001000	1111111010	0011000000	01?1000001	010
23. <i>Zatavua analalava</i>	110001100?	1000001000	1111111010	0011000000	011100000?	?10
24. <i>Zatavua vohiparara</i>	110011100?	1000001000	1111111010	0011000000	011100000?	?10
25. <i>Zatavua tamatave</i>	110011100?	1?00001000	1111111010	0011000000	011100000?	?10
26. <i>Zatavua griswoldi</i>	1100111001	1000001000	1111111010	0011000000	0111000001	010
27. <i>Belisana australis</i>	1100010001	1000001000	11?1111010	0010000011	0001000001	000
28. <i>Belisana</i> sp. 1	1000010001	1000001000	1111111010	0010000010	0001000001	00?
29. <i>Belisana</i> sp. 2	1100010001	1000001000	1111111010	0010000010	0001000000	-00
30. <i>Belisana</i> sp. 3	1100010001	1000001000	?111011010	0010000010	0001000000	-00
31. <i>Spermophora senoculata</i>	1000010001	1000011000	1111111010	0010200010	0001000001	001
32. <i>Spermophora yao</i>	1000010001	1000011000	11?1111010	0010000010	0001000001	001

APPENDIX 3
Continued

	10	20	30	40	50	
33. <i>Spermophora peninsulae</i>	1100010001	1000001000	1111111010	0010200012	0001010001	001
34. <i>Spermophora</i> sp. 1	1000010001	1000011000	1111111010	0010000010	0001000001	001
35. <i>Spermophora</i> sp. 2	1000010001	1000011000	1111111010	0010000000	0001000001	101
36. <i>Spermophora</i> sp. 3	1100010001	1000001000	1111111010	0010200012	0001010001	001
37. ' <i>Spermophora</i> ' sp. 4	0100010001	1000001000	1111111010	0010010010	0201000001	000
38. ' <i>Spermophora</i> ' sp. 5	1100010001	1000001000	1111111010	0010010010	0001000001	000
39. ' <i>Spermophora</i> ' sp. 6	1001010001	1101001000	1111111011	0010200110	10010?0001	000
40. ' <i>Spermophora</i> ' sp. 7	100101000?	1?00001000	1111111010	0010200010	000101001?	?0?
41. ' <i>Spermophora</i> ' sp. 8	1001?1000?	1?????1001	?111111010	0010200010	000101001?	?00
42. ' <i>Spermophora</i> ' sp. 9	1011010001	1101001000	1111111011	0010200110	1001000001	00?
43. ' <i>Spermophora</i> ' sp. 10	1001010001	1101001001	1111111010	0010200110	1001000000	-00
44. ' <i>Spermophora</i> ' <i>ranomafana</i>	1001010001	1100011000	1111111010	0010000010	0001010001	000
45. ' <i>Spermophora</i> ' <i>vyvato</i>	110101000?	1100001000	1111111010	0010200010	100101000?	?00
46. <i>Micromerys gracilis</i>	1000010001	1100001100	010110--10	0010000010	0001010001	000
47. <i>Micromerys daviesae</i>	1000010001	1100001000	010110--10	0010000010	0001010001	000
48. <i>Metagonia argentinensis</i>	1100011001	1010101000	11?1111010	000-100000	0001010001	000
49. <i>Metagonia rica</i>	1100011001	1010101000	1111111010	000-100010	0001010001	000
50. <i>Metagonia delicata</i>	1000010001	1110101000	1111111010	000-100010	0001010001	000
51. <i>Pholcus p.</i>	0000010001	1000001000	1111111?10	0010200010	0001000001	000
52. <i>Leptopholcus d.</i>	0000010001	1000001000	1111111010	0010200010	0001000001	000
53. <i>Micropholcus f.</i>	0000010001	1000001000	1111111010	0010200010	0001000001	000
54. <i>Spermophorides</i> sp. 1	1101010000	1100021000	1111111010	0010000010	0001110001	000
55. <i>Spermophorides</i> sp. 2	1101010000	1100021000	1111111010	0010000010	0001110001	000
56. <i>Paramicromerys rothorum</i>	100101000?	1100001000	1111111010	0010000010	020101000?	?00
57. <i>Paramicromerys betsileo</i>	1001010001	1100001000	1111111010	0010000010	0201010001	000
58. <i>Paramicromerys marojejy</i>	100101000?	1100001000	1111111010	0010000000	020101000?	?00
59. <i>Paramicromerys rabearivelo</i>	100101000?	1100001000	1111111010	0010000010	020101000?	?00
60. <i>Paramicromerys coddingtoni</i>	1001010001	1100001001	1111111010	0010000010	0201010001	000
61. <i>Paramicromerys ralamboi</i>	100101000?	1100001001	1111111010	0010000010	020101000?	?00
62. <i>Paramicromerys scharffi</i>	100101000?	1100001001	1111111010	0010000011	020101000?	?00
63. <i>Paramicromerys nampoinai</i>	100101000?	1100001001	1111111010	0010200111	020101000?	?00
64. <i>Paramicromerys manantenina</i>	1001010001	1100001001	?111111010	0010200011	0201010001	000

APPENDIX 4

Strict consensus of 15 most parsimonious cladograms obtained by NONA. Length = 123; CI = 47; RI = 82. Only nodes mentioned in the text are numbered: node 1: 'pholcines', the group to which all taxa treated herein belong; node 2: *Zatavua* n. gen.; node 3: sister group of *Zatavua*; node 4: 'real' *Spermophora*, represented by Asian, Australian and African taxa; node 5: undescribed genus of mostly East African pholcids previously assigned to *Spermophora*, including Comoran and one Malagasy species; node 6: *Paramicromerys* Millot.



APPENDIX 5

The two alternative resolutions of pholcines as represented in the 15 most parsimonious cladograms obtained by NONA. For numbered clades and terminal taxa see Appendix 4.

