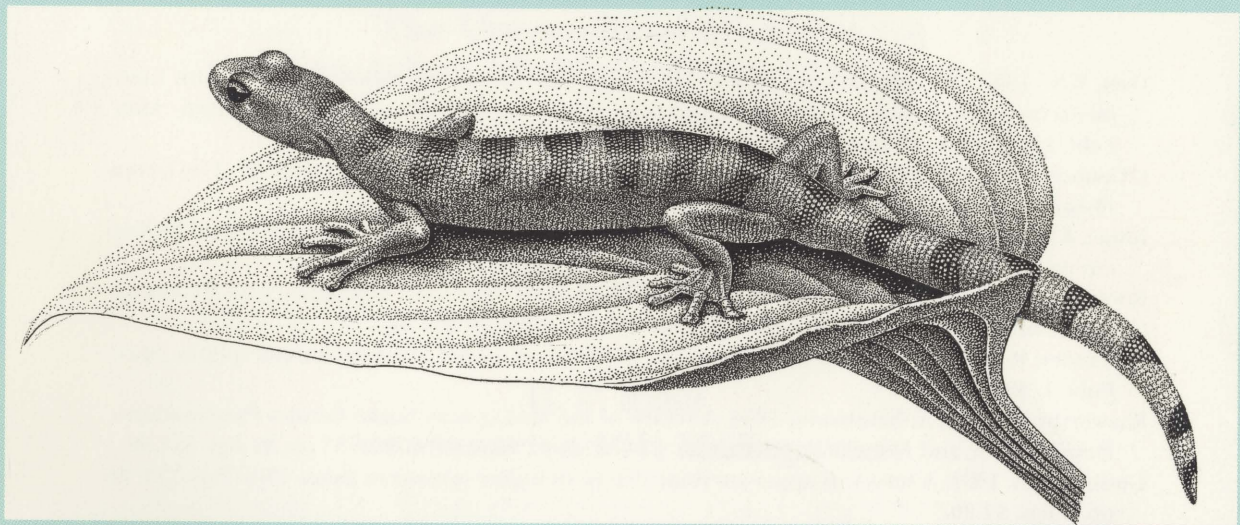


**THE GHOST GECKOS OF MADAGASCAR:
A FURTHER REVISION OF THE
MALAGASY LEAF-TOED GECKOS (REP-
TILIA, SQUAMATA, GEKKONIDAE)**

BY

**RONALD A. NUSSBAUM,
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AND OLAF PRONK**



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**The Ghost Geckos of Madagascar:
A Further Revision of the
Malagasy Leaf-toed Geckos
(Reptilia, Squamata, Gekkonidae)**

by

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ABSTRACT

Nussbaum, R. A., Raxworthy, C. J., and O. Pronk. 1998. *The ghost geckos of Madagascar: a further revision of the Malagasy leaf-toed geckos (Reptilia, Squamata, Gekkonidae)*. Misc. Publ. Mus. Zool. Univ. Michigan, 186:1-26, 25 figs., 5 tables. *Phyllodactylus brevipes* Mocquard, 1900, previously known from only two specimens collected prior to 1912 and erroneously believed to be a junior synonym of a well-known African species, *Phyllodactylus porphyreus*, was rediscovered near its type locality in the xeric regions of southwestern Madagascar. A new sister-species of *Phyllodactylus brevipes* from the rainforest region of southeastern Madagascar is described. The two species share character states that set them apart from all other species of phyllodactyle gekkonines, and a new genus, *Matoatoa*, is established to accommodate them. Two distinctive apotypic characters that diagnose *Matoatoa* are the presence of parallel transverse rings of body scales and ornamented bones in the snout region, which are covered by strongly adherent skin. Other distinctive characters of the genus are (1) homogeneous and smooth head, body, limb, and tail scales; (2) juxtaposed ventral scales; (3) absence of enlarged postmental scales; (4) 2-3 rows of slightly enlarged scales below and paralleling the infralabial scale rows; (5) presence of preloacal pores in males; and (6) adhesive tail tips in which the scansorial scales are not differentiated in size and shape from other tail scales nor modified into a ventral pad. The scansorial scales completely encircle the tail tip in *Matoatoa brevipes* and probably do so in the new species as well. In other geckos with scansorial tail tips, the scansors are restricted to the ventral surface of the tail tip. The two species are further characterized by the presence of a second ceratobranchial element and fused nasal bones, characters which vary among other gekkonine genera. *Phyllodactylus porphyreus* apparently does not occur in Madagascar, and, therefore, with the establishment of *Matoatoa*, the genus *Phyllodactylus* is eliminated from the Madagascan herpetofauna.

Matoatoa brevipes differs from the new rainforest species, *M. spannringi*, in size, coloration, nostril position, number of postrostral scales, number of subdigital lamellae on all digits, and the distribution and structure of the scansorial scales on the tail tip. *M. brevipes* is smaller, with a maximum snout-vent length of 40 mm, compared to a known size range of 53-58 mm SVL for *M. spannringi*. Females are the larger sex in *M. brevipes*; the sample size of *M. spannringi* is too small to determine whether or not sexual size dimorphism exists in this species. *M. brevipes* has a light grayish ground color with scattered, irregular flecks and streaks of darker pigment and a few small white spots, and completely lacks yellowish pigment; whereas *M. spannringi* has a lavender-brown ground color with a dorsal pattern of dark transverse bands or bars, a yellowish venter, suffusion of yellowish pigment on the head and dorsal surface of the distal tail, and bright yellow lip lines (yellow disappears in preservative). The nostril of *M. brevipes* lies posterior to the suture between the rostral and first supralabial scale and is separated from the rostral scale by part of the prenasal scale, whereas the nostril of *M. spannringi* is above the suture between the rostral and first supralabial and is in contact with the rostral scale. *M. brevipes* has 2-3 postrostral scales (very rarely one), compared to *M. spannringi* which has a single postrostral scale. *M. brevipes* has fewer subdigital scales on all digits than *M. spannringi*. The distribution of scansorial scales is more extensive on the tail tip of *M. brevipes*, and the setae of the scansors are taller and more elaborate in *M. brevipes* compared to *M. spannringi*.

The phylogenetic relationships of *Matoatoa* to other genera of phyllodactyles are unknown. The east-west disjunction of the two species of *Matoatoa* in desert and rainforest habitats is paralleled by similar disjunctions in the gecko genera *Paragehyra* and *Ebenavia*. The two species of *Matoatoa* are among the rarest reptiles in Madagascar, and further study is needed to determine their status.

Key words: *Reptilia, Squamata, Gekkonidae, Gekkoninae, Phyllodactylus, Matoatoa, Ghost Geckos, New Genus, New Species, Madagascar.*

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INTRODUCTION

The herpetofauna of Madagascar includes several species known from only one or few specimens collected many years ago. Because of massive deforestation and other continuing forms of habitat alteration, there is a strong possibility that some of these rare forms, especially the forest-adapted species, are extinct or in danger of extinction. Over the past eight years, our herpetofaunal surveys in Madagascar resulted in the rediscovery of some of these rare species. An example is the gecko *Paragehyra petiti* Angel of southwestern Madagascar, which was known from a single specimen collected in 1925 and not recorded again until we recently (1995) found additional specimens near the type locality at the mouth of the Onilahy River and in Bemaraha Reserve 540 km north of the type locality (unpublished). A similar situation exists for the enigmatic gecko *Phyllodactylus brevipes* Mocquard, also of southwestern Madagascar. This species was known only from the holotype and one other specimen, and had not been seen since 1911, when in 1991 we obtained specimens from near Belalanda, about 32 km southeast of the type locality.

The rediscovery of *Paragehyra petiti* and *Phyllodactylus brevipes* in the desert regions of southwestern Madagascar is remarkable for the nearly contemporaneous discovery in both cases of an undescribed sister-species in rainforest habitats in eastern Madagascar. *Paragehyra gabriellae*, the rainforest sister-species of *Paragehyra petiti*, was described by Nussbaum and Raxworthy (1994). The rainforest sister-species of *Phyllodactylus brevipes* is described in this paper, and these two "ghost geckos" are placed in a new genus.

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The drawings were done by John Megahan, and David Bay assisted with the photographs. We thank Marilee Sellers of the Electron Microscope Facility, Northern Arizona University for technical assistance in preparing the scanning electron micrographs, and Jim O'Reilly who also helped to prepare the scanning electron micrographs. We are indebted to Wulf Haacke for the loan of an important specimen in the Transvaal Museum and Ivan Ineich for information concerning the condition of the holotype of *Phyllodactylus brevipes*. Aaron Bauer and Anthony Russell reviewed the manuscript, and their suggestions improved it significantly. This research was made possible through the cooperation of the Malagasy Ministère de l'Enseignement Supérieur, the Ministère de la Production Animale et des Eaux et Forêts, and the Ministère de la Recherche Scientifique et Technologie pour le Développement. Our research was supported in part by grants (DEB 90-24505, DEB 93-22600, DEB 96-25873) from the National Science Foundation, the National Geographic Society (5396-94), and Earthwatch.

NOMENCLATURE HISTORY

The phyllodactyle geckos of Madagascar have had a tortuous history of discovery and systematic analysis. Mocquard (1909) made the first serious attempt to summarize the herpetofauna of Madagascar in an explicitly phylogenetic, albeit non-cladistic, framework. His arrangement of Madagascar geckos was similar to that of Boulenger (1885).

He placed Madagascar geckos with dilated digits in three groups, one of which included *Phyllodactylus* and *Ebenavia* and included species characterized by having a terminal pair of divided inferior lamellae without a free distal phalanx. *Phyllodactylus* was identified as having claws curving down between the pair of terminal lamellae, whereas *Ebenavia* was diagnosed as clawless. Nussbaum and Raxworthy (in press) showed, however, that females of *Ebenavia* have claws on their hind feet.

Mocquard (1909) recognized nine species of Madagascar *Phyllodactylus* Gray, including species that are today placed in the genera *Paroedura* Günther and *Phyllodactylus*. Angel's classic (1942) "Lézards de Madagascar" listed 11 *Phyllodactylus*, basically as recognized by Mocquard (1909), but accounting for certain synonymies and descriptions of new species. Guibé (1956) reviewed Madagascar species of *Phyllodactylus*, following the same arrangement as Mocquard (1909) and Angel (1942), but he recognized only ten species, as a result of synonymizing *Phyllodactylus brevipes* Mocquard with *P. porphyreus* (Daudin), a species otherwise known to occur in southern Africa.

Dixon and Kröll (1974) resurrected Günther's *Paroedura* and placed all Madagascar and Comoroan clawed, phyllodactyle geckos in it, with the exception of *Phyllodactylus brevipes*, which they seemingly resurrected from the synonymy of *P. porphyreus* without explanation nor mention of Guibé's treatment of *P. brevipes*. Dixon and Kröll stated that they would report on the status of *P. brevipes* in a later paper, but never did, perhaps because the holotype of *P. brevipes*, and the only specimen available to them, was fire damaged while on loan to Dixon (Brygoo, 1991; Dixon, in litt.)

The presence of *Phyllodactylus porphyreus* in Madagascar is problematic and seems highly doubtful. The first reference to this species in Madagascar is Duméril and Bibron (1836) who cited specimens collected by Quoy and Gaymard. Boulenger (1885) listed a specimen from Madagascar in the British Museum, which was purchased and without specific locality. Mocquard (1900a,b) compared *P. brevipes* to *P. porphyreus* without mentioning Madagascar specimens of the latter species, and he included both *P. brevipes* and *P. porphyreus* in his 1909 monograph on Madagascar amphibians and reptiles. Angel (1936, 1942) wrote that it is necessary to confirm the presence of *P. porphyreus* in Madagascar, because it possibly had been confused with *P. barbouri*, a species Angel (1936) described as a Madagascar endemic. Kluge (1965), however, showed that *P. barbouri* is based on a specimen of *Diplodactylus vittatus* (possibly *D. granariensis*, see Henle in Brygoo, 1991 and Bauer, 1994), presumably collected in Australia and wrongly recorded from Madagascar. Loveridge (1947) indicated without explanation that *P. porphyreus* is restricted to Africa and noted that Boulenger's (1885) reference to Madagascar should be omitted. Guibé (1956) believed that Mocquard's (1900a,b; 1909) *P. brevipes* is based on a specimen of *P. porphyreus* and included the latter in his list of Madagascar *Phyllodactylus*. Both Wermuth (1965) and Kluge (1993) listed *P. brevipes* as a junior synonym of *P. porphyreus*, which implies that the latter species occurs both in Africa and Madagascar.

Specimens obtained by us in 1992 and 1993 near Belalanda,

southwestern Madagascar (cited in Glaw and Vences, 1994) clearly fit Mocquard's (1900a,b) description of *Phyllodactylus brevipes* and are distinctly different from African specimens of *P. porphyreus*. We have not seen specimens of *P. porphyreus* from Madagascar and believe that species is restricted to Africa. *P. brevipes* and its new rainforest sister-species differ significantly from all other phyllodactyles, and we propose a new genus to accommodate them.

SYNOPSIS

Matoatoa new genus

Type species. *Phyllodactylus brevipes* Mocquard 1900a,b.

Diagnosis. Phyllodactyle gekkonines that have second ceratobranchials; fused nasals bones; precloacal pores in males; rugose or ornamented snout bones (premaxillae, maxillae, nasals, prefrontals, anterior frontal) strongly adhering to overlying skin; smooth postorbital skull bones not strongly adherent to overlying skin; homogeneous, flattened, smooth body scales arranged in parallel transverse rings; nonimbricate ventral scales; adhesive tail tip in which scansorial scales are not differentiated into distinct ventral pad, but rather consist of pilose scales of normal size and shape that nearly or completely encircle tail tip.

Description. Other distinctive characters of *Matoatoa*, not necessarily unique nor apotypic, include homogeneous and smooth head scales slightly raised in snout region, flattened in postorbital region; homogeneous, flattened, slightly imbricate scales on upper and lower surfaces of limbs and upper surfaces of digits; enlarged scales dorsally on the distal expansion of the digits; claws present on all digits of both sexes; homogeneous, flattened, very slightly imbricate scales on tail arranged in parallel transverse rings; lack of enlarged postmental scales; presence of 1-3 rows of slightly enlarged scales below and paralleling infralabials; 1-3 enlarged tubercles present at each side of cloaca, larger in males; postcloacal sacs present; cloacal bones present in males.

Content. Two species, *Matoatoa brevipes* (Mocquard) 1900a,b and a new species described below.

Distribution. Two restricted areas of southern Madagascar: southwestern coastal region between Morombe and the Fiherenana River near Toliara; southeastern rainforest belt near Tolongoina east of Fianarantsoa.

Etymology. The generic name "*Matoatoa*" is based on a Malagasy word "matoatoa" (pronounced "muh too uh too uh") which means "ghost", in reference to the elusive, mysterious, and secretive nature of the two species. We consider *Matoatoa* to be neuter in gender.

Remarks. Two synapotypic characters distinguish *Matoatoa* from the other phyllodactyle genera, *Asaccus*, *Ebenavia*, *Paroedura*, *Phyllodactylus*, *Ptyodactylus*, *Urocotyledon*, and *Uroplatus*. These are the arrangement of body scales into transverse parallel rings (Fig. 1A,B) and the presence of ornamented snout bones strongly adherent to the overlying skin (Fig. 2). The adjacent body scales of lizards in general, and of phyllodactyles in particular, overlap in the transverse plane so that alternate scales are aligned transversely or there is a

completely irregular pattern of alignment (Fig. 1C,D). The aligned transverse pattern of *Matoatoa* is almost certainly uniquely derived. Smooth skull bones and loosely adherent overlying skin is the presumed plesiotypic condition of lizards, including phyllodactyles. Although some other phyllodactyles of the genus *Paroedura* have ornamented skull bones and adherent skin (Dixon and Kroll, 1974), the pattern is entirely different from that observed in *Matoatoa*. In *Paroedura* species with ornamentation, the ornamentation occurs on all skull bones and not just those of the snout region. Ornamented skull bones may have evolved independently in *Matoatoa* and *Paroedura*, or some pattern of skull bone ornamentation may have been present in an hypothetical ancestor of these two genera with subsequent divergence toward the *Matoatoa* and *Paroedura* conditions. The shared condition of scansorial scales on the tail tip of the two species of *Matoatoa* also may prove to be uniquely derived, but the situation is confused by the presence of scansorial scales on the tail tips of other seemingly unrelated geckos (see below). In *Matoatoa*, the scansorial scales of the tail tip are not differentiated into a pad, and they are not restricted to the ventral surface. At least in this regard, the scansorial tail tip of *Matoatoa* spp. is unique.

Mocquard (1900a) noted that the skin of the head of *Matoatoa brevipes* is free from the underlying bones except on the snout, and, in the same publication, he noted that the skin of the cranium of *Phyllodactylus* (= *Paroedura*) *bastardi* is adherent to the underlying cranial bones. However, he overlooked the peculiar nature of the transversely aligned body scales and the adhesive tail tip in *M. brevipes*. He clearly believed that *M. brevipes* is closely related to *Phyllodactylus porphyreus*, and made comparisons only to the latter. This belief was probably partly due to geographic bias. Mocquard thought *P. porphyreus* was the only other slender-bodied, short-limbed *Phyllodactylus* in Madagascar. It now seems nearly certain that *P. porphyreus* is restricted to southern Africa.

Matoatoa brevipes (Mocquard)

Figure 3

Phyllodactylus brevipes Mocquard, 1900a,b, holotype MNHN (Museum National d'Histoire Naturelle, Paris) 1899.341, collected 25 June 1898 at "Ambolisatra" [almost certainly Ambolisaka on recent maps, about 10 km southeast of Morombe, 21°54'S, 43°35'E], Morombe Fivondronana, Toliara Province, Madagascar by G. Grandidier. Reported destroyed by Brygoo (1991); examined by Ivan Ineich in February, 1997, and reported (pers. com.) to be in relatively good condition with diagnostic characters intact, tail missing.

Specimens examined. TM 4025 ("Tsivanóá", see remarks); UMMZ 208367-208408, 218307 (8 km N Toliara near Belalanda); UMMZ 217046 (Ranobe). All specimens examined are from Toliara Fivondronana, Toliara Province. UMMZ 218381-3 are cleared and stained skeletal preparations, the remainder are preserved in alcohol. TM = Transvaal Museum; UMMZ = University of Michigan, Museum of Zoology.

Identification. A relatively small *Matoatoa*, not exceeding 40 mm snout-vent length; nostril posterior to suture between rostral and first supralabial scale, separated from rostral scale

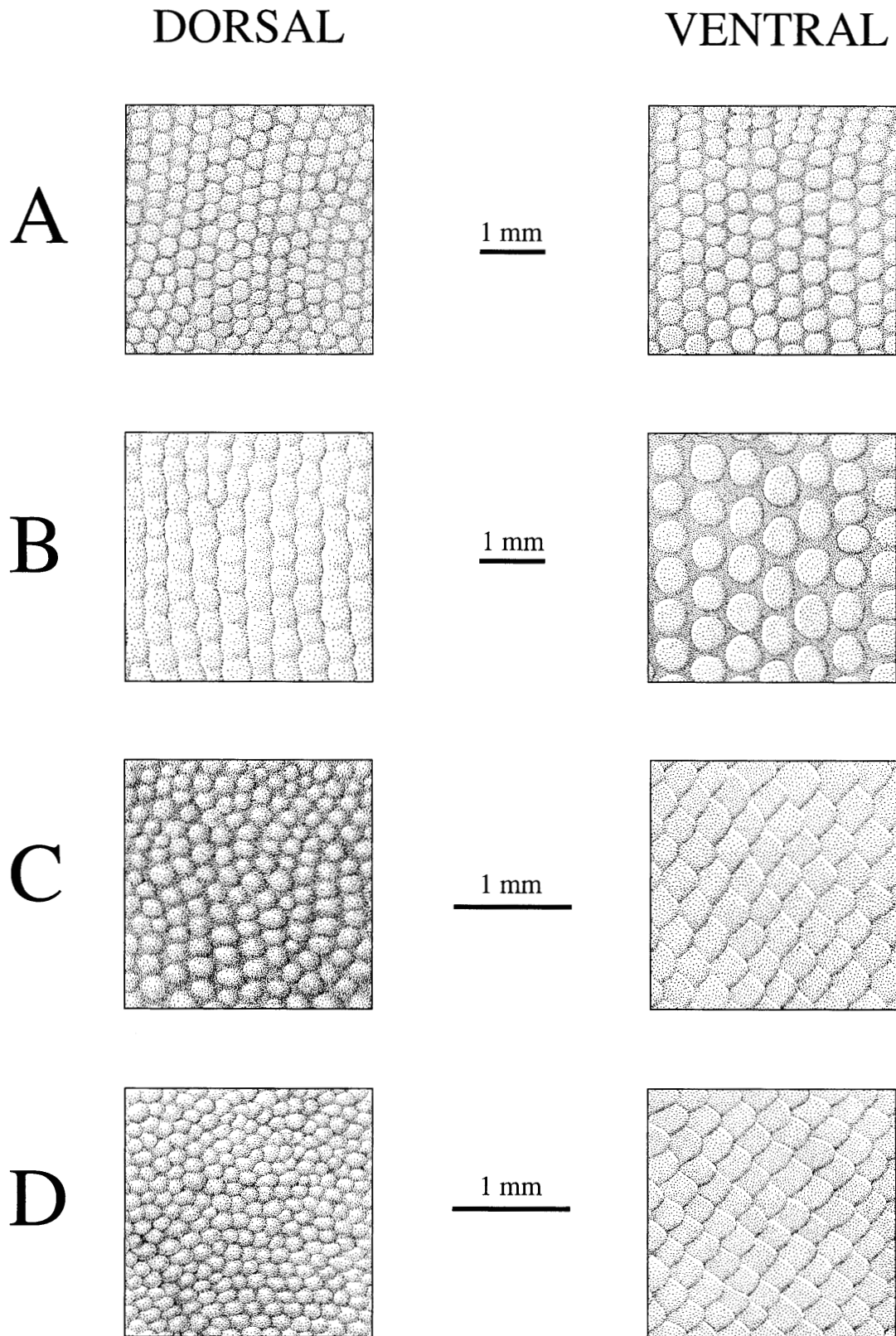


Figure 1. Dorsal and ventral scalation in (A) *Matoatoa brevipes* (UMMZ 208372), (B) *Matoatoa spannringi* (UMMZ 218374), (C) *Phyllodactylus porphyreus* (UMMZ 86210), and (D) *Urocotyledon inexpectata* (UMMZ 168098), illustrating the transverse scale rows in *Matoatoa*, compared to alternating or irregular transverse scale alignment and imbricate ventral scales in the other species.

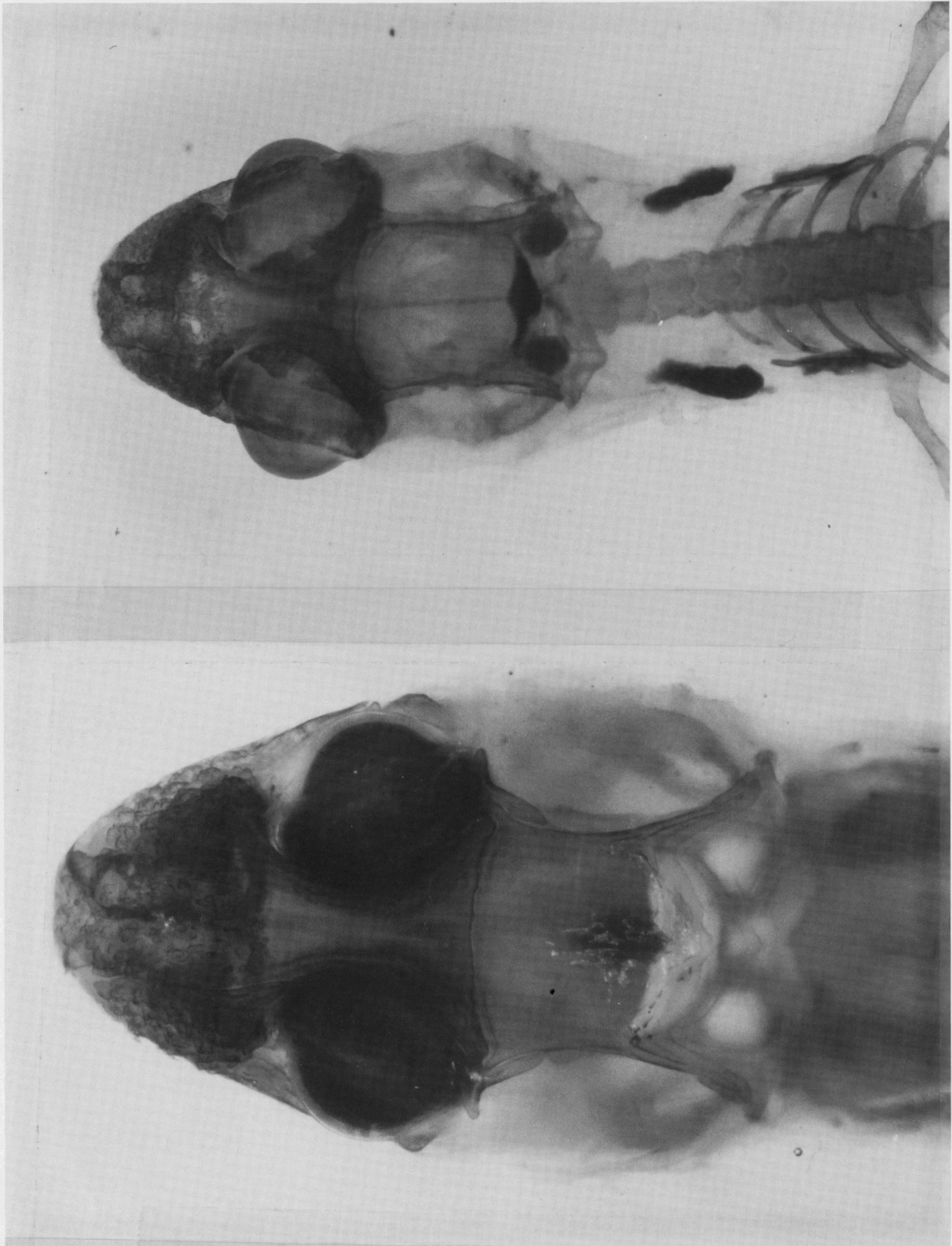


Figure 2. Skulls of (A) *Matoatoa brevipes* (UMMZ 218383) and (B) *Matoatoa spanringi* (UMMZ 218379) from cleared-and-stained specimens stored in glycerin. The rugose condition of the snout region, compared to the smooth posterior skull is evident in both specimens.

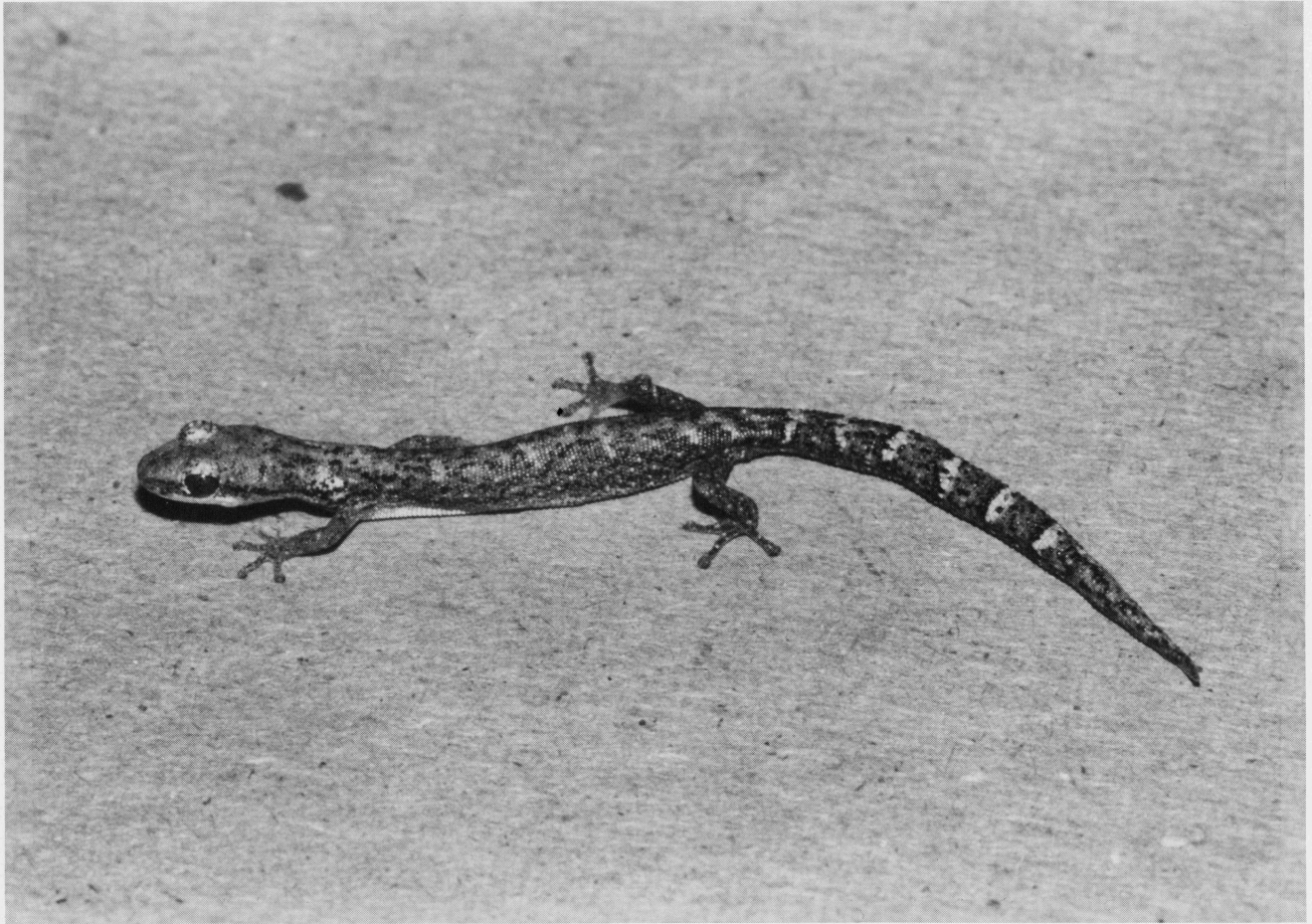


Figure 3. *Matoatoa brevipes* adult from near Belalanda, Toliara Fivondronana, Madagascar. Snout-vent length = 38 mm.

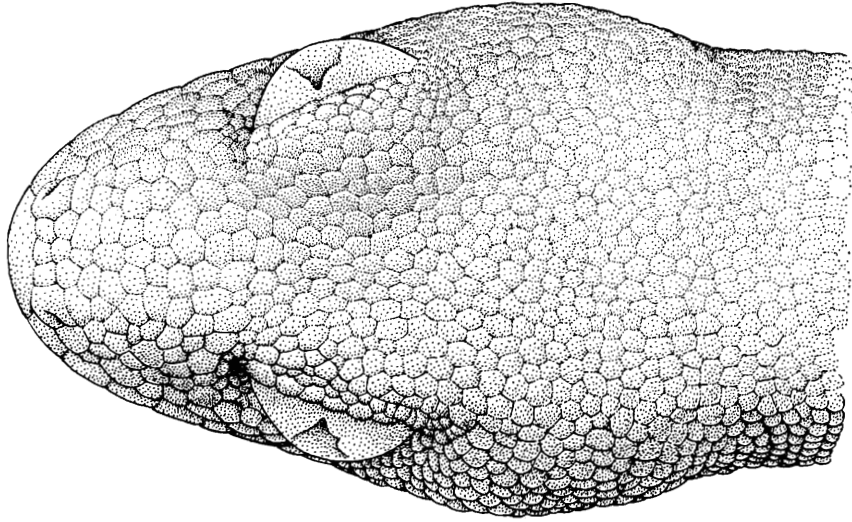
by interposition of prenasal; more than one postrostral scale between prenasals; scansorial scales of tail tip extensive, completely encircling distal one fifth of tail; pile (setae) of scansorial scales of tail tall and dense; dorsal color pattern of irregular, small dark spots and streaks on a grayish background; no yellow pigment.

Description. The following description is based on UMMZ 208383, but the drawings (Figs. 4A, 5A, 6A, 7A, 8A, 9A) are from UMMZ 208372. UMMZ 208383 is well preserved with small slit on left abdomen; tail original; ovaries white, right slightly anterior relative to left; one enlarged ovum, among several much smaller oocytes, measuring 1.7 mm diameter, in each ovary; oviducts slightly enlarged, white.

Counts and measurements in Tables 1 and 2. Head small, 0.21 times as long as snout-vent length, slightly wider than neck (Fig. 4A), slightly narrower than posterior body; snout 1.35 times longer than eye diameter, sides converge to a bluntly rounded tip, canthal ridges not evident, canthal bridge slightly convex; nostrils largely laterally oriented, easily visible from above; pupils vertical with broadly crenulate edges; ear opening tiny, round to slightly oval (Fig. 5A); body slender, slightly depressed, wider posteriorly; limbs small and short, forelimb reaches anteriorly to posterior border of eye, hindlimb extends forward to slightly less than half the axilla-groin dis-

tance, adpressed limbs fail to meet by 2-3 mm; digits short, increasing order of length I-II-III-V-IV; terminal pads moderate to narrow, 1.5 times wider than digit; tail 0.95 times as long as snout-vent length, round in cross-section, thicker in middle, terminal portion much narrower than proximal portion, tip sharp.

Rostral scale approximately rectangular, but dorsal border broadly convex, bordered dorsally by pair of prenasals and two smaller medial postrostrals; nostril (Figs. 6A, 7A) above first supralabial, entirely posterior to suture between rostral and first supralabial, bordered anterodorsally by large prenasal and posteroventrally by one postnasal, anteroventrally in contact with first supralabial, excluded from contact with rostral by prenasal; prenasal largest snout scale, postnasal second largest, remaining snout scales uniformly small; supralabials, pre- and postnasals smooth and nearly flat, remaining snout scales convex to slightly tuberculate; interorbital scales and posterior cranial scales increasingly flattened posteriorly compared to snout scales; supraoculars in five poorly defined rows of flat scales; superciliaries in one row of flat scales; mental scale slightly more than half as wide as rostral, much smaller than adjacent first infralabials, bordered posteriorly by two small postmentals slightly larger than posterior chin scales but not larger than scales lateral to them

A

2 mm

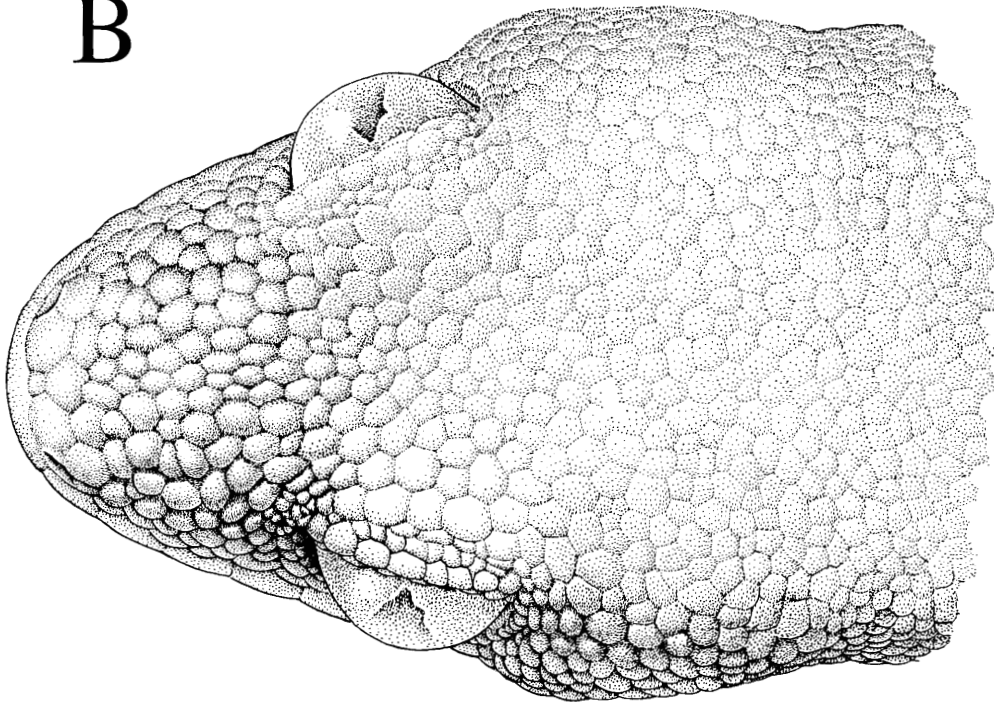
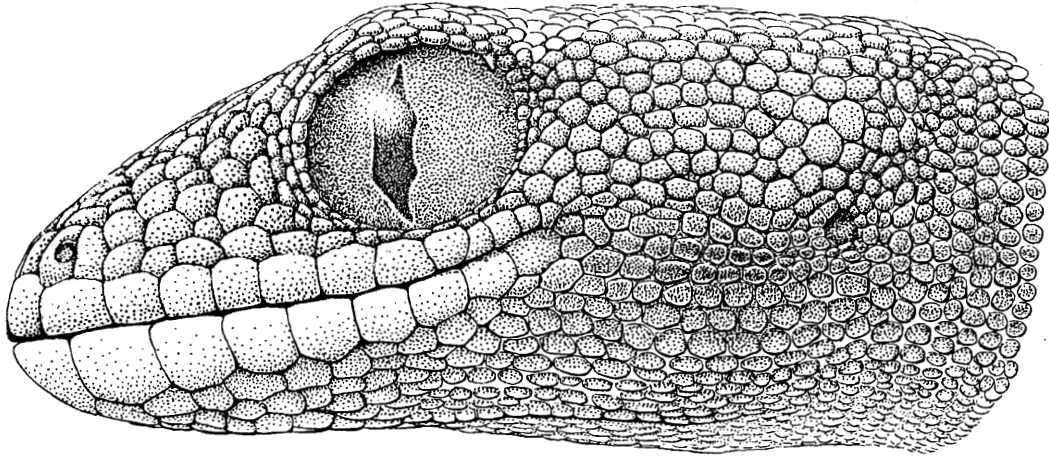
B

Figure 4. Dorsal view of heads of (A) *Matoatoa brevipes* (UMMZ 208372), and (B) *Matoatoa spanringi* (UMMZ 218374).

A



2 mm

B

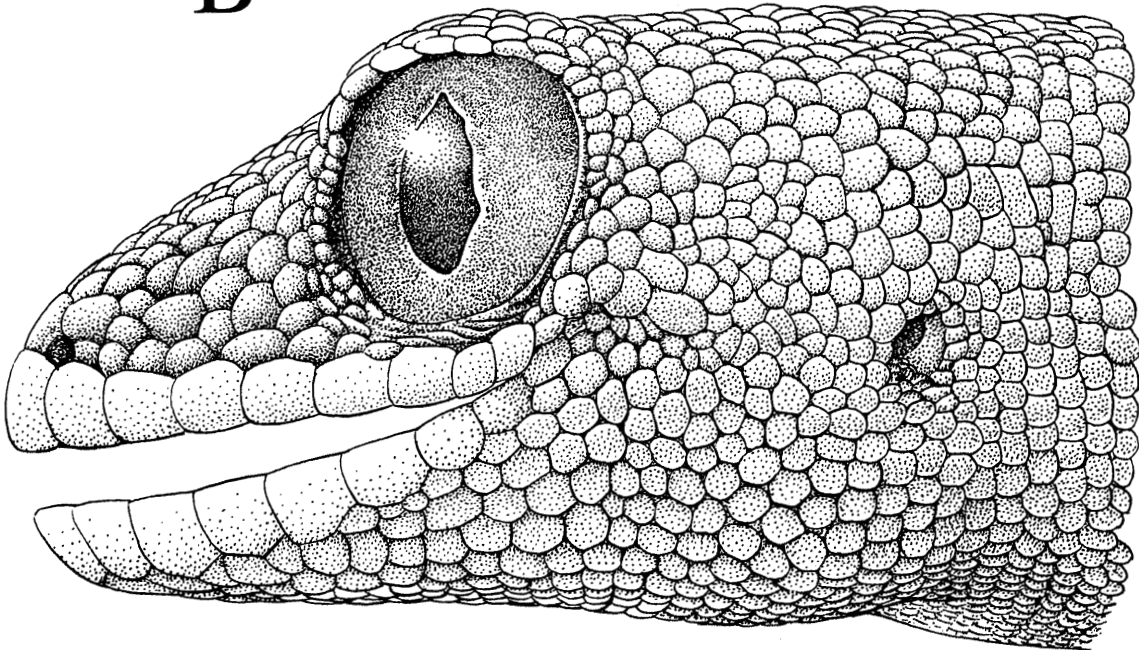


Figure 5. Lateral view of the heads of (A) *Matoatoa brevipes* (UMMZ 208372) and (B) *Matoatoa spannringi* (UMMZ 218734).

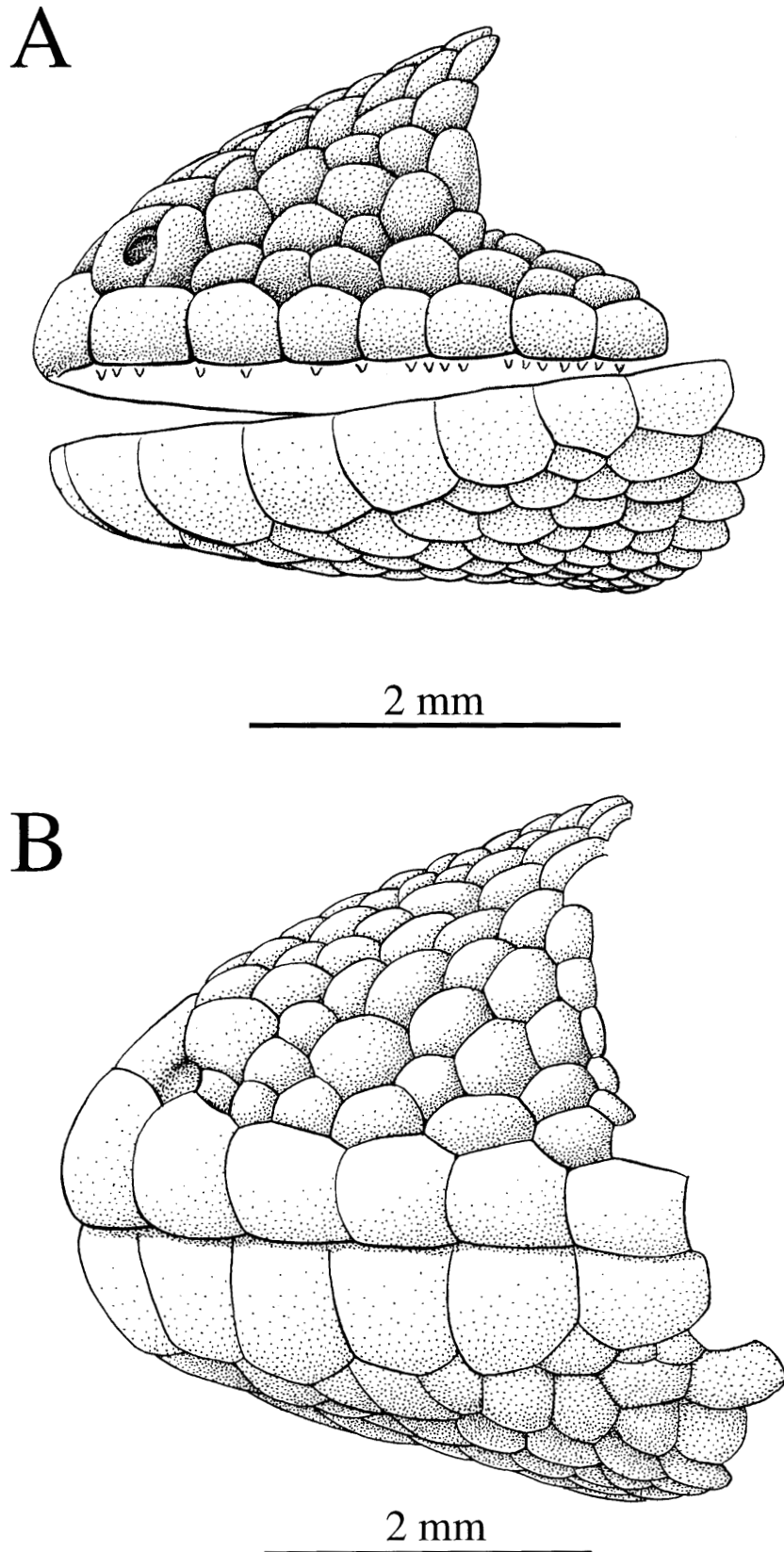
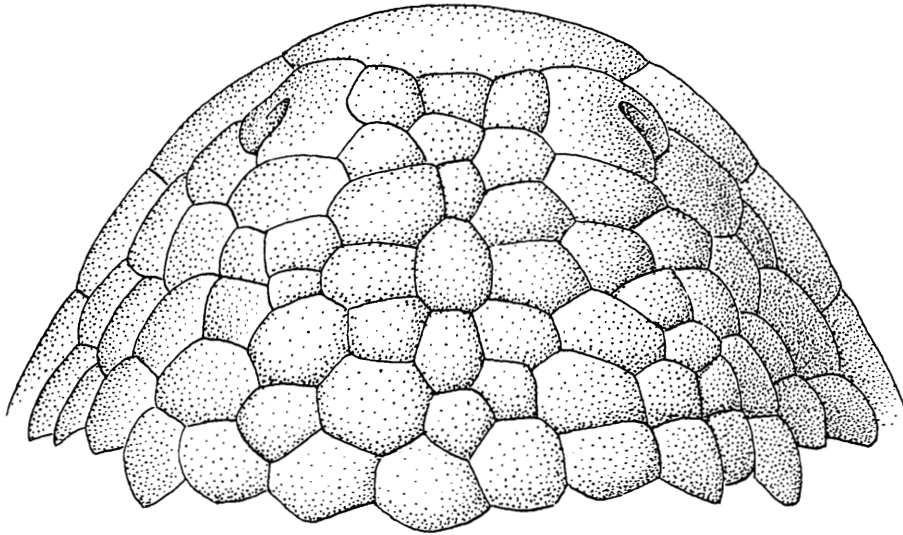
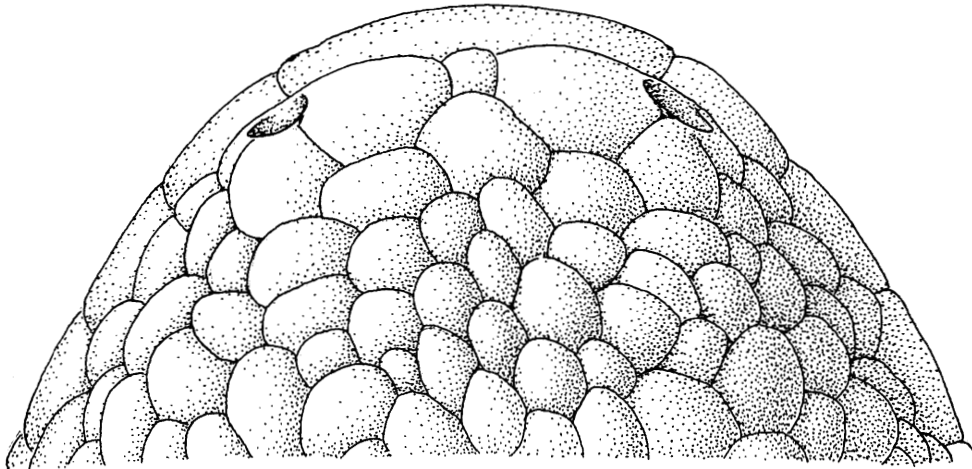


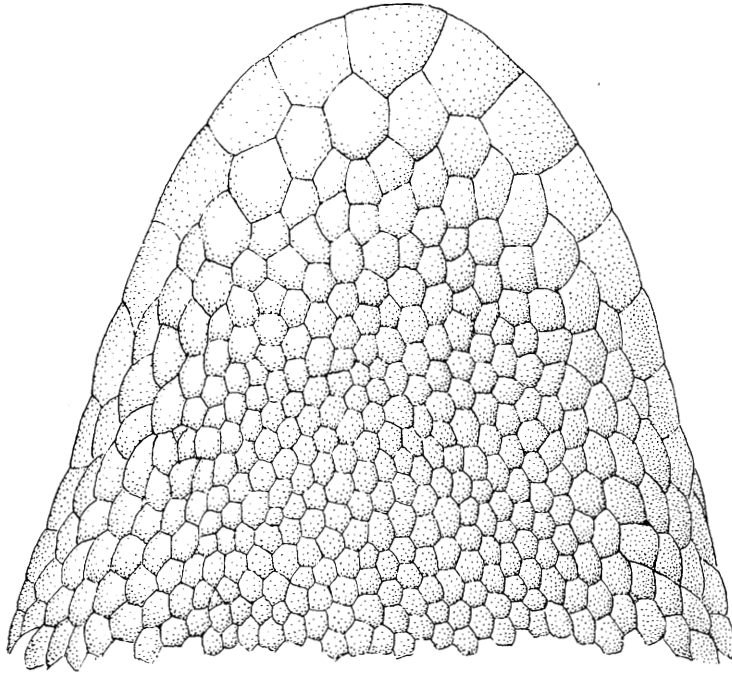
Figure 6. Lateral snout region of (A) *Matoatoa brevipes* (UMMZ 208372) and (B) *Matoatoa spannringi* (UMMZ 218374) illustrating different positions of the nostrils relative to the rostral scale and the suture between the rostral and the first supralabial scales.

A

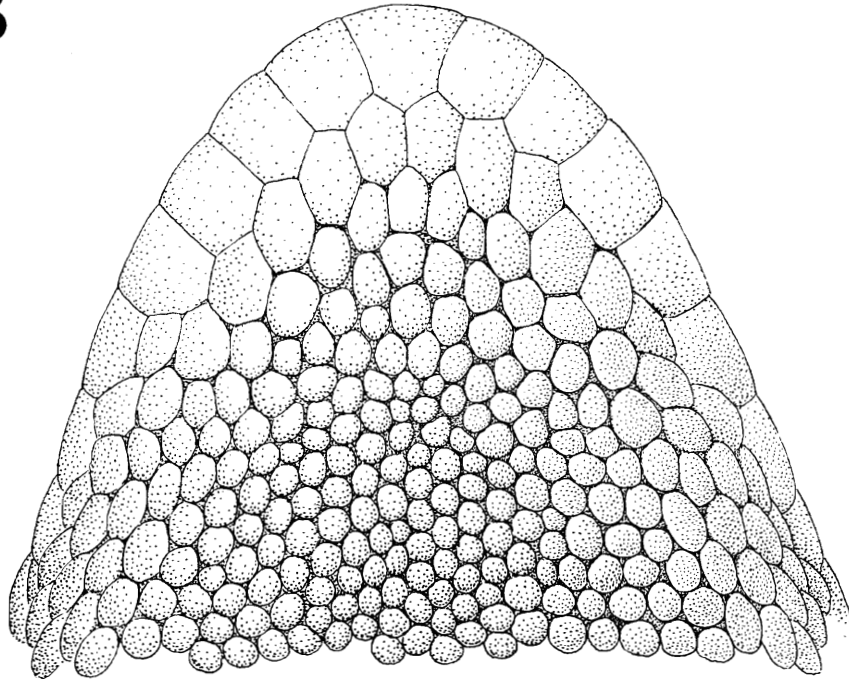
2 mm**B**

2 mm

Figure 7. Dorsal snout region of (A) *Matoatoa brevipes* (UMMZ 208372) and (B) *Matoatoa spannringi* (UMMZ 218374) showing different nostril positions and different number of postrostral scales.

A

2 mm

B

2 mm

Figure 8. Chin region of (A) *Matoatoa brevipes* (UMMZ 208372) and (B) *Matoatoa spannringi* (UMMZ 218374). Note the lack of enlarged postmental scales and the presence of rows of slightly enlarged scales between the infralabials and central chin scales in both species.

(Fig. 8A); infralabials bordered below by row of enlarged chin scales anteriorly that includes the two postmentals, more posteriorly there are two and then three rows of enlarged chin scales below the infralabials (Fig. 8A); chin and throat scales smooth, granular, slightly convex, throat scales smaller than anterior chin scales and posterior chest scales; dorsal and ventral body scales (Fig. 1A) homogeneous, smooth, juxtaposed, flattened to slightly convex, arranged in transverse rows or rings with irregularities dorsally caused by intercalation of short rows; upper scales of limbs, hands, feet, and proximal digits homogeneous, smooth, juxtaposed to slightly imbricate distally; terminal scales of digits enlarged (Fig. 9A), single large scale over each half of terminal pad, single large scale over base of claw; ventral scales of limbs similar to those of upper surfaces, slightly imbricate distally, those under tibiotarsal segment slightly enlarged; scales of palms and soles juxtaposed, irregular in shape, smooth, convex; subdigitals in single row, strongly pilose; each half of pilose terminal pad squarish with rounded corners (Fig. 9A), half pad of fourth toe 0.5 mm wide by 0.7 mm long; claw curves down between pads; single small tubercle on each side of cloacal opening; pair of postcloacal sacs present; tail scales homogeneous, squarish, arranged in parallel rings, last 28 rings including tip (covering 7 mm) consist entirely of pilose scales not otherwise differentiated in size or shape.

Coloration, after 38 months in preservative, has hardly changed, largely because there are no bright colors in life, which normally disappear in preservative. Dorsolateral surfaces of head, neck, and body light gray with numerous small, dark brown irregular markings and spots; faint brown stripe on side of head from nostril to just in front of shoulder where it bifurcates and continues posteriorly over shoulder along each side as pair of faint, brown stripes that fade in groin; middorsal region with fewer dark brown markings resulting in vague appearance of a middorsal light band; dorsolateral surfaces of tail colored similarly to body with light gray ground color dusted with light brown melanophores, and with numerous, irregular dark brown markings; upper surfaces of limbs, hands, feet, and digits heavily suffused with brown and with irregular bars or vermiculations of darker brown; iris black; white, calcified, subdermal endolymphatic sacs visible in lateral neck and otic regions; chin, throat, and chest white, but many scales have single, tiny melanophore visible with dissecting microscope; venter of anterior body white with scattered nearly microscopic melanophores increasing in density posteriorly; undersurfaces of limbs whitish gray dusted with brown; palms, soles, and subdigital region light brown; undersurface of tail heavily suffused with brown, increasingly so posteriorly.

Variation. Some morphometric and meristic variation is summarized in Tables 1 and 2. Morphometric variation is slight, and remarkable only in the number of postrostral scales, which varies from one to three in a sample of 43 specimens, one (2.3%) has one, 29 (67.4%) have two, and 13 (30.2%) have three postrostrals. The postrostral is unusually large in the single specimen with one postrostral, and probably represents a fusion of one or two other scales.

Males have three to five precloacal pores, a single male has three pores, 14 have four pores, and two have five pores.

Females lack precloacal pores. There is individual variation and sexual dimorphism in the number and size of tubercles on each side of the cloaca. Males have much larger tubercles, and the number on each side ranges from zero (five females, all adult males have at least two) to three, the modal number for both sexes being two.

Females are larger than males (t-test, $p < 0.001$). Females average 36.0 mm snout-vent length (range = 26-40, $n = 26$), whereas males average 32.5 mm (range = 29-35, $n = 17$).

There is no sexual dichromatism, except that males lack enlarged, white, calcified endolymphatic sacs under the skin between the side of the cranium and the shoulder. The dark stripe from nostril to shoulder is regularly present, but faintly expressed in a few individuals, and the continuation of the stripe as a double lateral line along the body is not evident in some individuals. Some individuals have a dorsal pattern of nearly uniformly distributed, small, dark speckles rather than the bolder pattern of larger markings. Small white spots, usually confined to a single scale, are scattered over the dorsal surfaces in varying density. Original tails may be a darker gray than the body, with a series of regularly spaced, white, dorsal spots or small cross bands (Fig. 3). Regenerated tails may be lighter in coloration and with less bold dark markings. The iris varies from black to heavily pigmented with light tannish gold pigment with black reticulations. In some specimens in life, the light gray dorsal ground color has a faint lavender tinge, especially anteriorly.

There is no ontogenetic variation in color or shape over the range of sizes available. Hatchlings have not been seen.

Distribution. Toliara Province between Morombe and the Fiherenana River in southwestern, coastal Madagascar. Specific localities include Ambolisaka (= Ambolisatra ?) in Morombe Fivondronana and Belalanda, Ranobe, and Tsivonoa in Toliara Fivondronana (Fig. 10).

Etymology. The specific name "*brevipes*" refers to the short feet of this species, which is manifested in its much shorter limbs relative to the other phyllodactyle geckos of Madagascar.

Habitat. Dry, open, spiny forests, generally on sandy coastal soils. Also in more mesic, denser forests near bodies of water. Specimens obtained by us were taken mainly from inside hollow, dead branches of standing trees.

Remarks. Methuen and Hewitt (1913) first reported this species from a locality other than the type locality. Their report was based on a single specimen (Transvaal Museum 4025) collected in 1911 by Methuen at "Tsivanóa in the southwest". Angel (1942) reported this locality as "Tsivanhoa". Glaw and Vences (1994) apparently interpreted this locality as "Tsivanaha" (or Tsinavahana), a locality near Cap Ste. Marie at the extreme southern tip of Madagascar. But "Tsivanóa" is almost certainly the region of Tsivonoa, which today includes the two coastal villages of Tsivonoabe and Tsivonoakely about 22 km NNW of Toliara near Ifaty. This area is between Belalanda and Ranobe, the other two known localities of this species in Toliara Fivondronana.

The pilose condition of the subdigital scales, the terminal pads of the digits, and tail tip cannot be seen in many preserved specimens because of the loss in preservative of the surface layer of beta keratin (Oberhäutchen). The

Table 1. Morphometric data (mm) for *Matoatoa brevipes* (all specimens are adults).

	UMMZ 208383	UMMZ 208385	UMMZ 208396	UMMZ 208398	UMMZ 208399	UMMZ 208405	UMMZ 208407	UMMZ 208408
Sex	female	female	female	male	male	male	female	male
Snout-vent length	38	38	40	29	34	33	39	34
Tail length	36	30*	29*	31	23*	26*	31*	28*
Head length	8.1	8.9	9.4	7.8	8.8	8.5	8.8	8.2
Head width	6.0	5.9	5.6	4.8	5.5	5.7	5.7	5.3
Snout length	3.1	3.5	3.6	2.8	3.1	3.0	3.5	2.9
Internarial distance	1.5	1.5	1.5	1.4	1.5	1.4	1.6	1.6
Eye-ear distance	3.0	3.1	3.0	2.5	2.5	2.5	2.8	2.6
Eye diameter	2.3	2.0	2.3	2.0	2.2	2.3	2.2	2.2
Ear opening diameter	0.3	0.3	0.4	0.3	0.4	0.4	0.4	0.3
Snout-axilla distance	14.2	14.5	15.8	13.0	13.9	14.2	14.6	14.1
Axilla-groin distance	19.7	19.9	20.9	14.6	17.3	17.0	20.7	17.5
Forelimb length	7.5	8.3	8.4	7.2	7.2	8.3	8.6	8.4
Hindlimb length	10.7	10.5	10.8	9.3	10.6	9.9	10.8	10.7

* Tail regenerated.

Table 2. Meristic data for *Matoatoa brevipes*.

	UMMZ 208383	UMMZ 208385	UMMZ 208396	UMMZ 208398	UMMZ 208399	UMMZ 208405	UMMZ 208407	UMMZ 208408
Supralabials (L,R)	9-10	8-8	9-8	8-9	7-8	8-8	8-9	8-9
Infralabials	9-10	8-8	9-8	8-9	9-8	7-8	9-10	8-9
Postrostrals ¹	2	2	2	2	3	3	3	2
Sdm I (L,R) ²	5-5	5-5	4-5	5-5	5-5	5-5	5-5	5-5
Sdm II	7-7	7-8	7-7	7-7	7-7	7-8	7-7	7-7
Sdm III	9-9	9-8	9-9	8-9	9-9	9-8	9-9	9-10
Sdm IV	10-11	11-9	10-10	10-10	9-10	9-9	10-10	11-10
Sdm V	8-8	7-8	7-8	8-8	8-9	7-8	8-7	7-8
Sdp I (L,R) ³	5-5	6-5	5-5	5-5	5-5	5-5	5-5	5-5
Sdp II	8-7	7-7	7-7	7-7	8-7	7-7	7-8	7-7
Sdp III	10-10	9-8	9-9	9-8	9-9	9-9	9-9	9-9
Sdp IV	12-12	12-11	12-12	11-12	12-12	10-10	12-12	11-12
Sdp V	11-10	10-10	10-10	9-10	10-10	10-10	10-10	10-10

¹ number of scales bordering rostral dorsally exclusive of supranasals

² number of subdigital lamellae on digits I-V of manus, exclusive of terminal pad

³ number of subdigital lamellae on digits I-V of pes, exclusive of terminal pad

scansorial region of the tail tip is unique in that the pilose scales are not confined to the ventral surface as in all other reported cases of adhesive tails, but instead completely encircle the tail. The tail tip is further distinctive in that the pilose scales are not differentiated in shape or size from the other scales of the tail, forming a distinct pad, as in most other geckos with adhesive tails. Pilose scales redevelop on the tips of fully, or nearly fully, regenerated tails.

The majority of specimens of both sexes have regenerated tails (9 of 12 males; 15 of 23 females). The condition of the tail (whether regenerated or original) of eight of the remaining sample of 43 individuals is unknown, because the tails were broken and lost when captured. Although males have a higher frequency of broken tails than females, larger samples are needed to verify this difference. The unusually high frequency of tail loss in *M. brevipes* is unexplained, as nothing is known about their predators and social interactions.

Most specimens were collected during the day by removing them from refugia. The specimen from Ranobe was collected fully exposed and active at night, suggesting this species is nocturnal.

Matoatoa spanringi new species

Figures 11 and 12

Holotype. UMMZ 218371 (RAN 57225), mature male, collected 9 April 1996 between Ambohimananana and Fiadanana, 21°28.61'S, 47°33.83'E, 690 m, Ikongo Fivondronana, Fianarantsoa Province, Madagascar by Jürgen Spannring.

Paratopotypes. UMMZ 218372-9 (RAN 48010, 48079, 56001, 57226-30), collected April, 1996 by Jürgen Spannring and Malagasy assistants.

Other specimens. UMMZ 218380 (RAN 56242), from the type locality.

Identification. A relatively large *Matoatoa* with known size

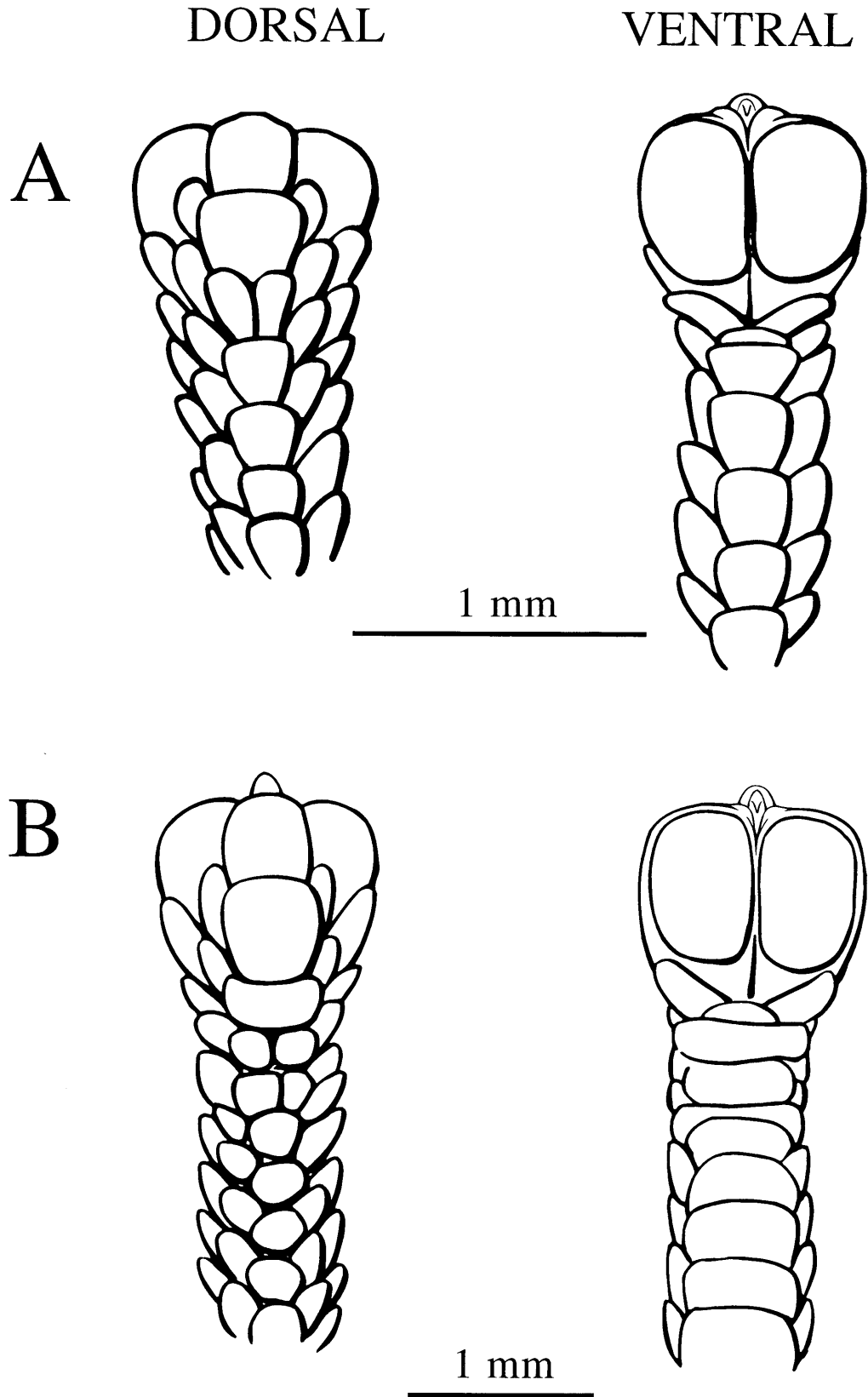


Figure 9. Dorsal and ventral scalation of digit IV of the manus of (A) *Matoatoa brevipes* (UMMZ 208372) and (B) *Matoatoa spannringi* (UMMZ 218374) showing the enlarged scales over the claw and scansorial pads.

range of 53 to 58 mm snout-vent length; nostril positioned above suture between rostral and first supralabial scale, in contact with rostral scale; single postrostral between prenasals; scansorial scales on ventrolateral tail tip, relatively restricted, occurring on less than one fifth of distal tail; dorsal coloration lavender brown with darker transverse bars; venter yellowish; yellow suffusion dorsally on distal tail and head; bright yellow lips (yellow pigment disappears in preservative).

Description of the holotype. Specimen in excellent condition, small slit on left abdominal region; tail complete, unregenerated; hemipenes extruded; testes ellipsoidal, 4.7 by 2.2 mm, pure white, right testis slightly anterior to left testis; vasa deferentia highly coiled, unpigmented.

Measurements and counts in Tables 3-4. Head small to medium, 0.25 times snout-vent length, barely wider than neck (Fig. 4B), nearly same width as body; snout 1.68 times eye diameter, sides converge sharply to a rounded tip, canthal

ridges not strongly expressed, canthal bridge nearly flat with very slight depression; nostrils laterally oriented, barely visible from above; pupils vertical with crenulate borders; ear openings tiny, nearly circular (Fig. 5B); body slender, slightly depressed; limbs moderately robust, short, forelimb extends forward to nearly half way between ear and posterior margin of eye, hindlimb extends forward to midbody, adpressed limbs fail to meet by 5 mm; digits slightly webbed at base, moderately long, increasing order of length I-II-III-V-IV; terminal pads small to medium, less than twice as wide as digit; tail 1.06 times snout-vent length, round to slightly depressed in cross-section, greatest diameter about one third of distance to tip, tapering to blunt tip which is slightly flattened on ventral surface.

Rostral scale rectangular, with small dorso-medial notch, bordered dorsally by nostrils, one pair of prenasals and one postrostral between prenasals (Fig. 7B); nostril above suture

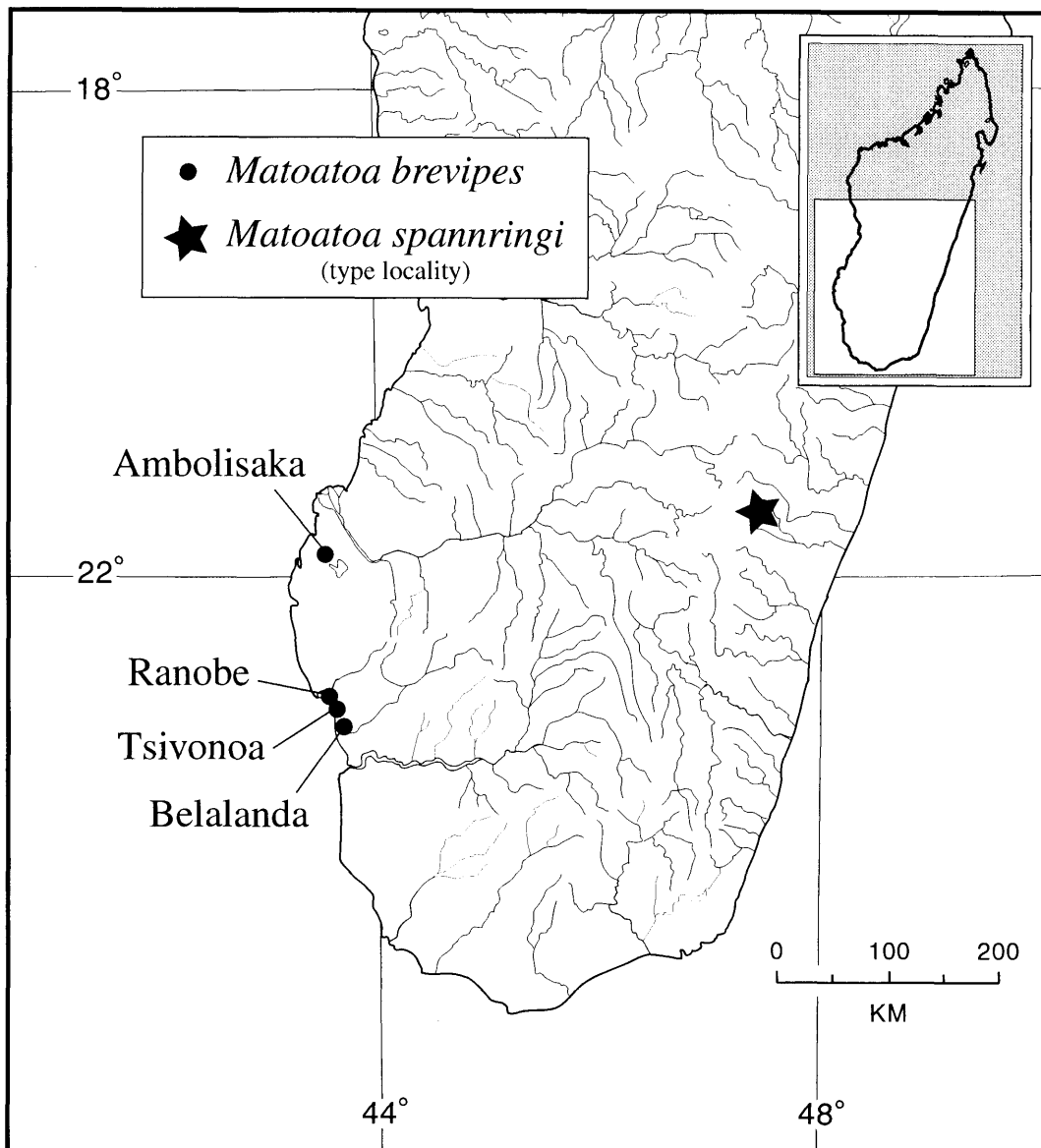


Figure 10. Distribution of *Matoatoa brevipes* and *Matoatoa spannringi*.

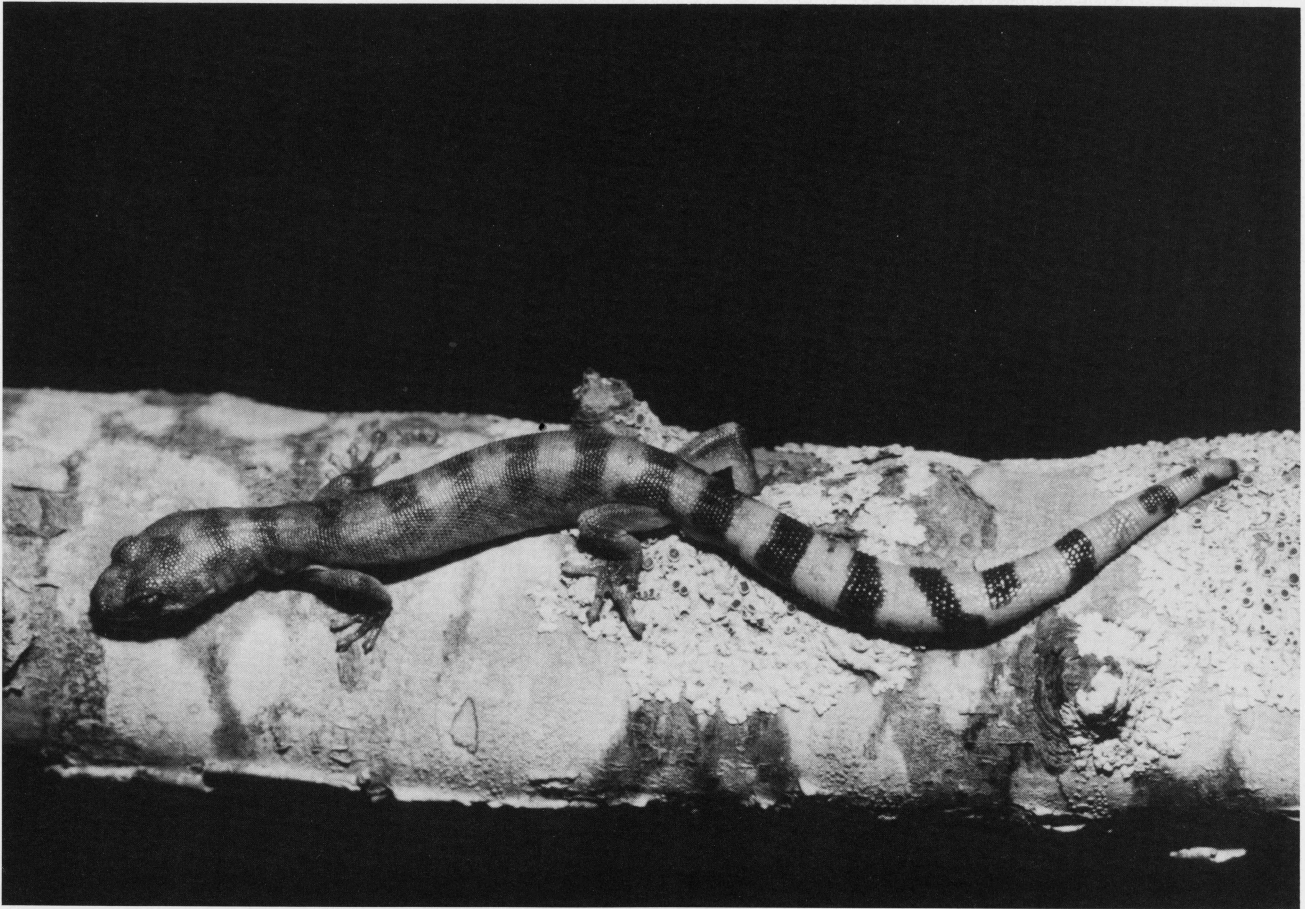


Figure 11. Male holotype (UMMZ 218371) of *Matoatoa spannringi* in life with original tail and lacking enlarged, subdermal, endolymphatic sacs in front of the forelimb.

between rostral and first supralabial (Figs. 6B, 7B), contacts first supralabial below, rostral and prenasal anteriorly, prenasal and one large supranasal dorsally, and one small postnasal; prenasals are largest snout scales, nearly smooth but roughened with several small tubercles; remaining snout scales tuberculate; supralabials and rostral each with multiple low tubercles; supraocular scales large, smooth, flat, in four rows; superciliaries smooth, flat to slightly rounded, aspinous, in two rows, scales of outer row much larger; interorbital and anterior postorbital scales slightly tuberculate changing to smooth and flat posteriorly on cranium; mental half as wide as rostral, equal in size to first infralabial (Fig. 8B), roughly triangular; two small postmentals not differentiated from adjacent scales; row of scales medial to infralabials including postmentals larger than remaining chin scales; chin and throat scales small, juxtaposed, flat to slightly rounded; throat scales smaller than chin and chest scales; dorsal scales homogeneous, small, round to squarish, flat, juxtaposed, arranged into distinct transverse rows (rings) with irregularities caused by intercalated, short scale rows (Fig. 1B); ventral scales like dorsals, also in parallel transverse rows continuous with dorsal rows, and with fewer irregularities caused by intercalated rows (Fig. 1B); dorsal scales of limbs, hands, and feet smooth, flat, slightly imbricate; ventral scales of limbs

smooth, juxtaposed or slightly imbricate proximally, more strongly imbricate distally, scales on ventral surface of tibiotarsal segment enlarged; scales of palms and soles smooth, largely juxtaposed, of irregular size and shape; dorsal scales of hands, feet, and digits smooth, imbricate, uniformly small except on tips of digits where scales dorsal to scansorial pads and claw bases are enlarged (Fig. 9B); subdigital scales in single row, densely pilose with low pile where Oberhäutchen intact; terminal subdigital scale at base of scansorial pads V-shaped; pair of terminal scansorial pads on each digit with taller and coarser pile compared to pilosity of subdigitals, pad sub-trapezoidal (Fig. 9B) with longer outer and shorter inner borders, nearly uniform in size across toes and fingers, pad of left 4th toe 1.5 mm long by 1.1 mm wide (right 4th toe, 1.6 by 1.1); well-developed claw curves down between scansorial pads; six precloacal pores; two enlarged tubercles at each side of cloacal opening; pair of postcloacal sacs; scales of tail homogeneous, smooth, flat, squarish, arranged in parallel rings, scales of terminal 10 rings densely pilose ventrolaterally with low pile (where Oberhäutchen is intact).

Coloration in life: Dorsal ground color of neck, body, and anterior one fifth of tail brownish lavender to flesh, posterior tail light yellow suffused with brown; seven dark brown, transverse bands on neck and body, six similar dorsal

Table 3. Morphometric data (mm) for holotype and paratypes of *Matoatoa spannringi* (all are adults; missing data due to distortion as a result of drying of specimen).

Holotype	Paratypes							
	UMMZ 218371	UMMZ 218372	UMMZ 218373	UMMZ 218374	UMMZ 218375	UMMZ 218376	UMMZ 218377	UMMZ 218378
Sex	male	male	male	female	female	male	female	female
Snout-vent length	53	55	57	58	58	56	57	54
Tail length	56	39*	35*	45*	**	**	18*	49
Head length	13.3	13.3	13.8	11.8	12.5	12.3	13.3	12.5
Head width	9.0	8.9	8.8	9.0	9.1	9.1	—	—
Snout length	4.7	4.3	4.6	4.6	5.0	4.8	—	—
Internarial distance	2.2	2.1	2.2	2.2	2.3	2.1	—	—
Eye-ear distance	4.0	3.7	3.9	3.9	4.1	4.1	—	—
Eye diameter	2.8	2.9	3.1	3.0	2.7	2.8	—	—
Ear opening diameter	0.6	0.6	0.5	0.5	0.6	0.5	—	—
Snout-axilla distance	22.0	22.0	22.7	21.8	22.1	22.1	—	—
Axilla-groin distance	30.4	29.7	30.9	32.2	31.5	31.4	—	—
Forelimb length	12.7	12.7	14.4	12.6	13.7	14.6	12.8	12.5
Hindlimb length	18.8	17.0	16.6	16.8	17.9	17.9	17.7	16.0

* Tail regenerated.

** Tail recently broken, detached portion missing.

Table 4. Meristic data for holotype and paratypes of *Matoatoa spannringi* (missing data resulting from specimen damage).

Holotype	Paratypes							
	UMMZ 218371	UMMZ 218372	UMMZ 218373	UMMZ 218374	UMMZ 218375	UMMZ 218376	UMMZ 218377	UMMZ 218378
Supralabials (L,R)	9-10	9-9	7-9	9-9	9-9	9-10	10-9	10-9
Infralabials	9-9	9-9	7-8	9-10	9-9	9-10	9-9	9-8
Postrostrals ¹	1	1	1	1	1	1	1	1
Sdm I (L,R) ²	7-7	7-7	6-7	7-7	7-8	7-7	7-	7-8
Sdm II	11-10	9-10	9-10	9-9	10-10	10-10	9-	10-9
Sdm III	11-12	12-11	11-12	12-11	11-12	11-	11-	11-12
Sdm IV	12-14	13-14	13-13	12-14	15-14	14-14	13-	12-14
Sdm V	10-10	10-10	9-10	10-10	10-10	10-10	9-	10-10
Sdp I (L,R) ³	8-7	7-7	7-7	7-7	7-8	7-8	7-	7-7
Sdp II	10-11	10-9	9-9	10-11	11-12	11-11	10-	9-9
Sdp III	13-12	13-12	-13	13-13	14-13	13-13	13-	13-12
Sdp IV	16-17	16-16	-17	17-17	16-16	16-17	16-	15-15
Sdp V	14-14	13-13	14-14	14-14	14-14	14-14	13-	13-13

¹ number of scales bordering rostral dorsally exclusive supranasals² number of subdigital lamellae on digits I-V of manus, exclusive of terminal pad³ number of subdigital lamellae on digits I-V of pes, exclusive of terminal pad

crossbands on proximal three fourths of tail with few, irregular, large, brown spots distally on dorsal tail; lower sides of body and tail brownish yellow; pre- and postaxial surfaces of limbs brownish lavender to flesh, dorsal surfaces brown; upper surfaces of hands, feet, and digits brownish lavender to flesh; head light yellow dorsolaterally with suffusion of darker melanophores, dark brown dorsal band at junction of cranium and neck, large brown spot medially on cranium behind eyes, supraocular and interorbital region brown, dark brown U-shaped band on snout above supralabials and rostral extending from eye through nostrils to other eye; iris metallic gold with black reticulations; bright yellow upper and lower lip lines on supralabials and rostral above and on

infralabials and mental below; chin yellow; venter of throat, neck, body, tail, and limbs pale yellow.

The color of living individuals changes dramatically at night: ground color lightens to creamy white or grayish, brown bands and spots lighten but pattern is unchanged.

Coloration after nine months in alcohol: Brownish lavender to flesh ground color has dulled to light tan, all yellow pigment has faded to white, and brown bands and spots have lightened only slightly.

Variation. Hatchlings and older juveniles are unknown. Morphometric and meristic variation among the adults is slight, and is noted in Tables 3-4. All available specimens have a single postrostral scale separating the prenasals. One male

has three instead of the usual two enlarged tubercles at side of the cloaca, and one female has cloacal tubercles only on the right side. A few individuals in life have grayish pigment on the head rather than the yellow suffusion, although these individuals nevertheless have the bright yellow lip lines. This variation is not apparent in preserved specimens because the yellow suffusion fades to grayish. The dark brown, transverse, dorsal bands are less regular in some specimens, compared to the holotype. These individuals have some bands broken or fused or connected by narrow bridges of brown pigment.

The two largest specimens are females, but one male is only 1 mm shorter than the two largest females, and the sample size is too small to determine whether there is significant size dimorphism between sexes. Males have either four (two individuals) or six (two individuals) precloacal pores, whereas females lack pores. The cloacal tubercles of females are much smaller than those of males. Females have prominent, calcified, subdermal endolymphatic sacs extending from the shoulders to the cranium on each side, which are lacking in males. There is no apparent sexual dichromatism.

Regenerated tails have a dorsolateral pattern of dark brown spots and streaks instead of the regular pattern of dark brown, dorsal crossbands characteristic of original tails. In addition, regenerated tails lack yellow pigment and have a gray-

ish ground color.

Distribution. Known only from the type locality (Fig. 10).

Etymology. The name "*spannringi*" is a personal noun in the genitive case, given in honor of Jürgen ("Nero") Spannring who succeeded in finding this species while many others failed. The first known specimen of *Matoatoa spannringi*, found in 1992, was lost by an assistant soon after it was captured and photographed. Two subsequent expeditions to the region of the type locality led by Nussbaum in 1993 and Raxworthy in 1995 failed to yield additional specimens of *Matoatoa spannringi*. Occupied elsewhere in Madagascar, we asked our capable friend Nero to help us find this elusive "ghost" gecko. Through the months of March and April, 1996, Nero lived in the region of the type locality with the sole purpose of obtaining specimens. Toward the end of his quest, his perseverance, hard work, and skill were rewarded, and we take great pleasure in naming this species after him.

Habitat. The region of the type locality was originally rainforest, but today consists largely of rice paddies, scrub brush, and other degraded agricultural habitats (Figs. 13, 14). Specimens were taken from a single patch of degraded primary forest about 3,000 m² in size, which was surrounded by rice paddies and cassava plantations. All specimens were found in holes in small to medium size trees known locally as "lalona" (probably *Weinmannia* sp., Family Cuconiaceae).



Figure 12. Female paratopotype (UMMZ 218374) of *Matoatoa spannringi* in life, with regenerated tail; enlarged, subdermal, endolymphatic sac visible in front of forelimb.



Figure 13. Habitat near the type locality of *Matoatoa spannringi*. Only a few, small, isolated patches of degraded rainforest like the one shown exist in this region. Most of the original forest has been removed to establish agricultural plots.

Associated species of amphibians and reptiles include several rainforest forms that persist in isolated patches of degraded forest. These include the mantellid frog, *Mantella bernhardi*, and the hyperoliid frog, *Heterixalus alboguttatus*.

Remarks. The major differences between *Matoatoa spannringi* and *M. brevipes* are summarized in Table 5. The extent of pilose scales under the tail tip of *M. spannringi* is uncertain, because all available specimens have lost in preservative the Oberhäutchen of a significant number of scales in this region. From the information available, it appears that *M. spannringi* has fewer pilose scales on the tail tip and that the development of the pilose structures is less elaborate (lower, denser, and less ornamented pile) compared to *M. brevipes*. It may also be that the pilose scales are found only ventrolaterally on the tail tip, compared to completely encircling the tail as in *M. brevipes*. This needs to be confirmed with additional material. Behavioral observations in terraria show that the tail of both *Matoatoa spannringi* and *M. brevipes* is somewhat prehensile and that the tail tip serves as a scansorial organ, which aids locomotion.

Almost nothing is known about the life history of *Matoatoa spannringi*. They are active only at night in captivity, hiding by day, so presumably they are nocturnal in nature. Some

females have two enlarged eggs, one in each ovary, suggesting the clutch size is two.

MICROSTRUCTURE OF SCANSORIAL SCALES IN *MATOATO*A

The micropile, or setae, of scales with intact Oberhäutchen is not visible to the naked eye. The setae of scansorial scales can barely be seen under high magnification with a dissecting microscope, and only when the preserving fluid has dried so that the micropile fluffs up (setae do not adhere to each other) and lightens in color. Scanning electron microscopy (SEM) has been used successfully to examine the microstructure of epidermal setae of lizards (see Bauer, 1986, and Schleich and Kästle, 1986, for geckos), and that technique was used here.

All subdigital lamellae and the ventral surfaces of the paired terminal pads of both species of *Matoatoa* are entirely covered with dense micropile, which has an adhesive function in scansorial locomotion. The subdigital lamellae of *Matoatoa* are single ranked except for the distalmost one, which is paired; each member of the pair rests at the base of one of the terminal

Table 5. Summary of character state differences between *Matoatoa brevipes* and *M. spannringi*.

	<i>Matoatoa brevipes</i>	<i>Matoatoa spannringi</i>
Size	Small, maximum size 40mm snout-vent length.	Large, known size range 53-58mm snout-vent length.
Color	Light gray ground color with irregular, small, dark brown or black spots and streaks on dorsolateral surfaces.	Light brownish lavender ground color with dark brown dorso-lateral cross bands on neck, body, and tail; distal tail, sides, venter, and head with yellowish suffusion; bright yellow lip lines.
Nostril	Nostril behind suture between rostral and first supralabial, excluded from contact with rostral by interposition of prenasal scale.	Nostril above suture between rostral first supralabial, contacts rostral.
Postrostrals	2-3 postrostral scales; one of 41 specimens has a single postrostral.	Single postrostral scale.
Ventral scales of tibiotarsal segment	Slightly enlarged compared to other ventral limb scales.	Greatly enlarged compared to other ventral limb scales.
Subdigital scales	Fewer subdigital scales on all fingers and toes; 4-6 on first finger and first toe; 10-12 on fourth toe (see Tables 2 and 4).	More subdigital scales on all fingers and toes; 6-8 on first finger and toe; 15-17 on fourth toe (Tables 2 and 4).
Pilosity	Pile of subdigital scales and tail tip relatively tall and conspicuous.	Pile much lower and less conspicuous.

toe pads. At low magnification (Fig. 15A,B), the micropile of the distalmost pair of subdigital lamellae and the proximal portion of the terminal toe pads appears as a thick carpet of setae. At medium magnification (Fig. 16A,B), the micropile of the toe pad is revealed as densely packed setae with slightly curved and expanded tips. The expanded setal tips resolve into complex branched heads at magnifications greater than 1,000 (Fig. 17A,B). At yet higher magnification (18A,B), the terminus of each branchlet of the setal heads is revealed to be dilated. Presumably, the expanded termini of these branchlets provide the adhesive surfaces that are functional in scansorial locomotion.

Scales on the ventral surface of the tail base of *Matoatoa* are without scansorial micropile (Fig. 19A,B). Usually three distinct, naked, apical pit organs can be seen near the distal edge of each scale of the ventral tail base of *M. brevipes* (Fig. 19A). The apical pit organs of *M. spannringi*, in this same region of the tail base, are positioned differently, compared to *M. brevipes*. They are on the distal edge of the scale, facing posteriorly (Fig. 19B). They differ further from those of *M. brevipes* in that they are covered by setae, which are shorter than the setae of scansorial scales, unbranched, and seem-

ingly have no scansorial function (Fig. 20B). The apical pit organs of the tail scales of *M. brevipes* are also setose further distally on the tail where the scales are largely covered with scansorial micropile. In this region, the entire distal edge of the scale as well as the surfaces of the apical pit organs are covered with short, unbranched setae, and the center of each pit organ supports two elongate, unbranched setae (Fig. 20A).

Toward the tip of the tail, micropile begins to appear as patches restricted to the distal portion of each scale (Fig. 21A), and further distally, at the tail tip, these patches expand to occupy the entire surface of each scale (Fig. 21B). At about 214-412 X (Fig. 22A,B), the density and character of the micropile of the scansorial tail scales is revealed. Subjectively, it appears that the micropile of the tail tip scales is somewhat less dense than that of the toe pads (compare Figs. 17A,B and 23A,B), and the setae of the tail tip scansors are more slender and have less complex branching (compare Figs. 18A,B and 24A,B). It also appears that the branchlets are not so greatly expanded at the tips (Figs. 25A,B), compared to the toe pads (Figs. 18A,B). Overall, however, the scansorial setae of the toe pads and tail tips of both species



Figure 14. Degraded secondary forest and abandoned agricultural plots near the type locality of *Matoatoa spannringi*. Secondary forest is being burned to establish new fields.

are similar, and it seems certain that the genetical-developmental pathway of the toe pad and tail tip adhesive structures are nearly the same.

DISCUSSION

Phylogenetic Affinities of *Matoatoa*

Dixon and Kroll (1974) believed *Matoatoa brevipes* is more closely related to African species of *Phyllodactylus* than to other phyllodactyles that occur in Madagascar, which invokes the idea of relatively recent dispersal of ancestral *M. brevipes* from Africa to Madagascar. This same view was held by Mocquard (1900a,b; 1909), who compared *M. brevipes* only to *Phyllodactylus porphyreus*, presumably because he believed the latter species also occurred in Madagascar. Although *M. brevipes* superficially resembles some African species of *Phyllodactylus*, including African and Seychellean species that are now placed in the genus *Urocotyledon*, its phylogenetic relationships have never been carefully assessed. This is at least partly because of lack of material and because between 1956 and 1992 it was considered to be a junior synonym of *P. porphyreus*.

The discovery of *Matoatoa spannringi* is important, because

its sister-species relationship to *M. brevipes* and their radically different habitats, the latter in southwestern deserts and the former in southeastern rainforest, strongly suggests they are descendants of a lineage of phyllodactyles that have inhabited Madagascar for a very long period of time. The other theory, that *M. brevipes* relatively recently colonized the dry regions of southwestern Madagascar from ancestors in southeastern Africa is no longer tenable.

The phylogenetic affinities of *Matoatoa* are currently unknown, and will have to be determined in the context of a cladistic analysis of the remaining phyllodactyles, including the remaining Old and New World species of *Phyllodactylus*, *Ebenavia*, *Paroedura*, *Urocotyledon*, and *Uroplatus*. At present, there are no known apotypic character states that link *Matoatoa* unambiguously with any of the latter genera. Although *Matoatoa* shares with *Urocotyledon* and *Phyllodactylus europaeus* the derived condition of having adhesive tail tips, there is good reason not to place undue weight on this character.

Adhesive Tail Tips in Lizards

Adhesive tail tips in lizards are known only among geckos, and have been recorded within two gecko subfamilies, the Diplodactylinae and Gekkoninae. Among diplodactylines,

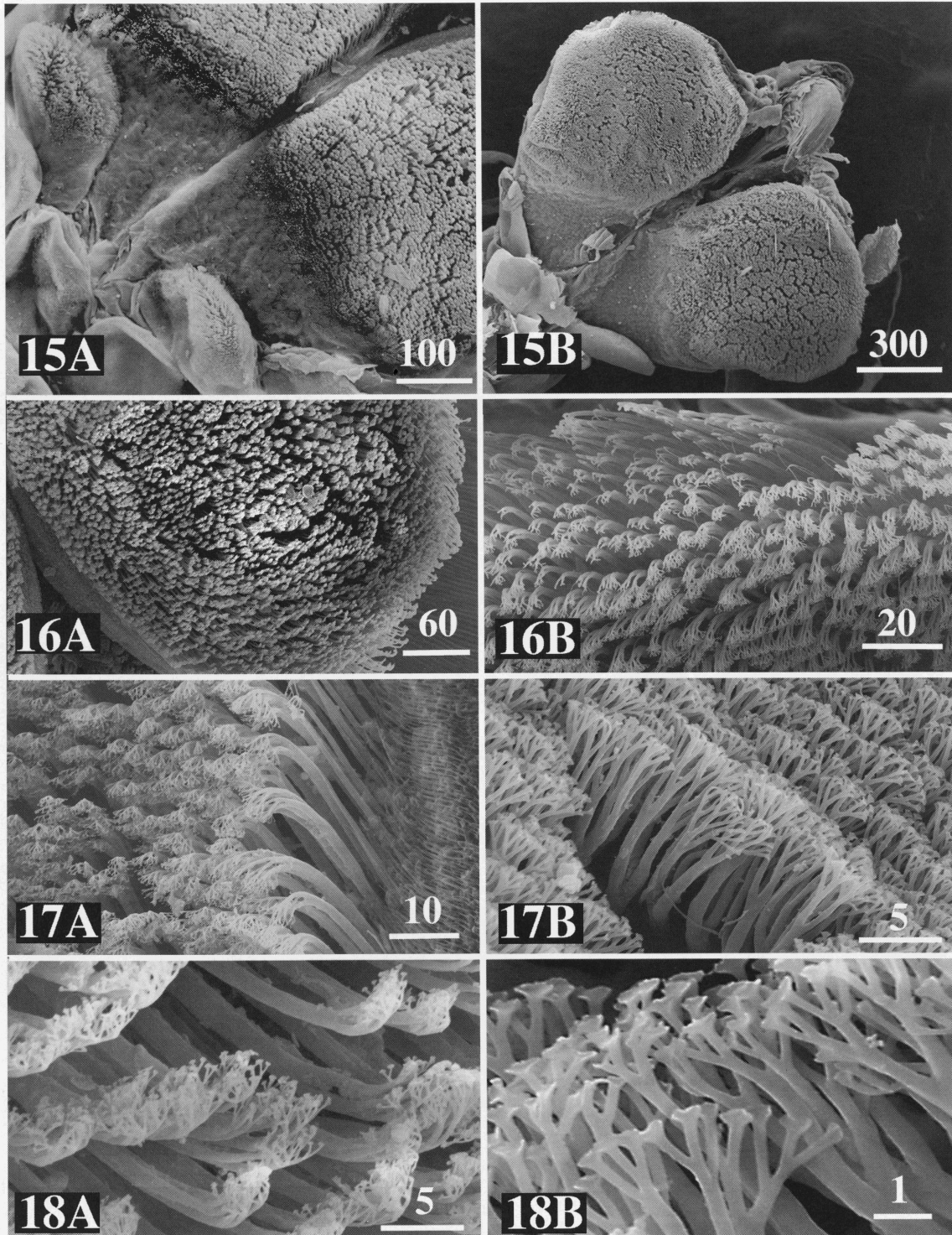


Figure 15. (A) Scanning electron micrograph (126 X) of distal pair of subdigital lamellae and proximal, ventral portion of the paired terminal toe pads (digit IV, pes) of an adult *Matoatoa brevipes* (UMMZ 218307); the dense micropile is visible at this low magnification, but the structure of the setal tips is not. (B) Similar view (47 X) of ventral toe tip (digit IV, pes) of *M. spannringi* (UMMZ 218380). Scales in micra.

Figure 16. (A) Scanning electron micrograph (182 X) of ventral surface of distal portion of one toe pad of *Matoatoa brevipes* (UMMZ 218307); distal curvature of setae and expanded setal heads are visible at this magnification. (B) Similar view (660 X) for *M. spannringi* (UMMZ 218380). Scales in micra.

Figure 17. (A) Scanning electron micrograph (1170 X) of setae of toe pad of *Matoatoa brevipes* (UMMZ 218307); the complex branching of the tips of the setae is visible at this magnification. (B) Similar view (2720 X) for *M. spannringi* (UMMZ 218380). Scales in micra.

Figure 18. (A) Scanning electron micrograph (2760 X) of setae of toe pad of *Matoatoa brevipes* (UMMZ 218307); the expanded termini of the setal branchlets are visible. (B) Similar view (9900 X) for *M. spannringi* (UMMZ 218380). Scales in micra.

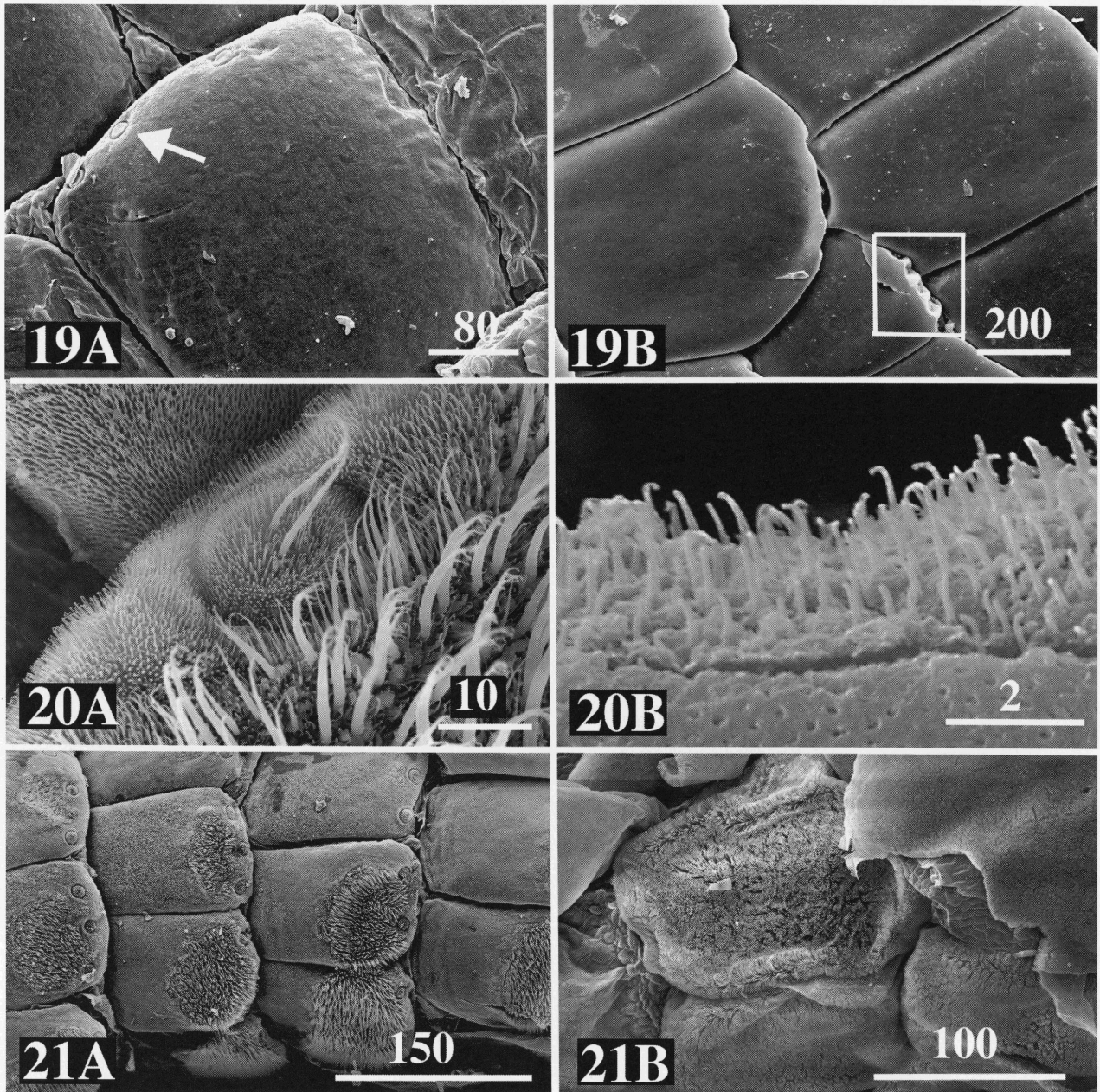


Figure 19. (A) Scanning electron micrograph (179 X) of ventral scale of the tail base of *Matoatoa brevipes* (UMMZ 218307); the apical pit organs (arrow) can be seen distally; scales in this region of the tail are without pilose adhesive structures. (B) Similar view (77 X) for *M. spannringi* (UMMZ 218380); the apical pit organs (within square) face posteriorly in this species. Scales in micra.

Figure 20. (A) Scanning electron micrograph (1500 X) of posterior edge of tail tip scale of *Matoatoa brevipes* (UMMZ 218307); posterior edge of scale including the apical pit organ is covered with short, non-branched setae without expanded tips, which are unlikely to have a scansorial function; two elongate, unbranched setae project from the center of the apical pit organ; longer, branched, scansorial setae are visible proximally. (B) SEM (11,100 X) of distal edge of tail base scale of *M. spannringi* (UMMZ 218380) showing the short, unbranched setae covering the apical pit organ; there are no scansorial setae on scales in this region of the tail. Scales in micra.

Figure 21. (A) Scanning electron micrograph (207 X) of tail scales near the ventral tip of the tail of *Matoatoa brevipes* (UMMZ 218307); at this intermediate position, pilose patches begin to appear distally on each scale; three apical pit organs are also visible on each scale. (B) SEM (304 X) of ventral tail tip scale of *M. spannringi* (UMMZ 218380); entire scales of this region are covered with micropile. Scales in micra.

Figure 22. (A) Scanning electron micrograph (214 X) of tail tip scales of *Matoatoa brevipes* (UMMZ 218307). (B) SEM (412 X) of ventrolateral tail tip scale of *M. spannringi* (UMMZ 218380). Scales in micra.

Figure 23. (A) Scanning electron micrograph (1000 X) of setae of tail tip scansorial scale of *Matoatoa brevipes* (UMMZ 218307) illustrating density of setae. (B) SEM (3740 X) of setae of scansorial scale of *M. spannringi* (UMMZ 218380). Scales in micra.

Figure 24. (A) Scanning electron micrograph (8333 X) of setae of scansorial scale of tail tip of *Matoatoa brevipes* (UMMZ 218307) illustrating the branching pattern of the setal termini. (B) SEM (8050 X) of setae of scansorial tail tip scale of *M. spannringi* (UMMZ 218380). Scales in micra.

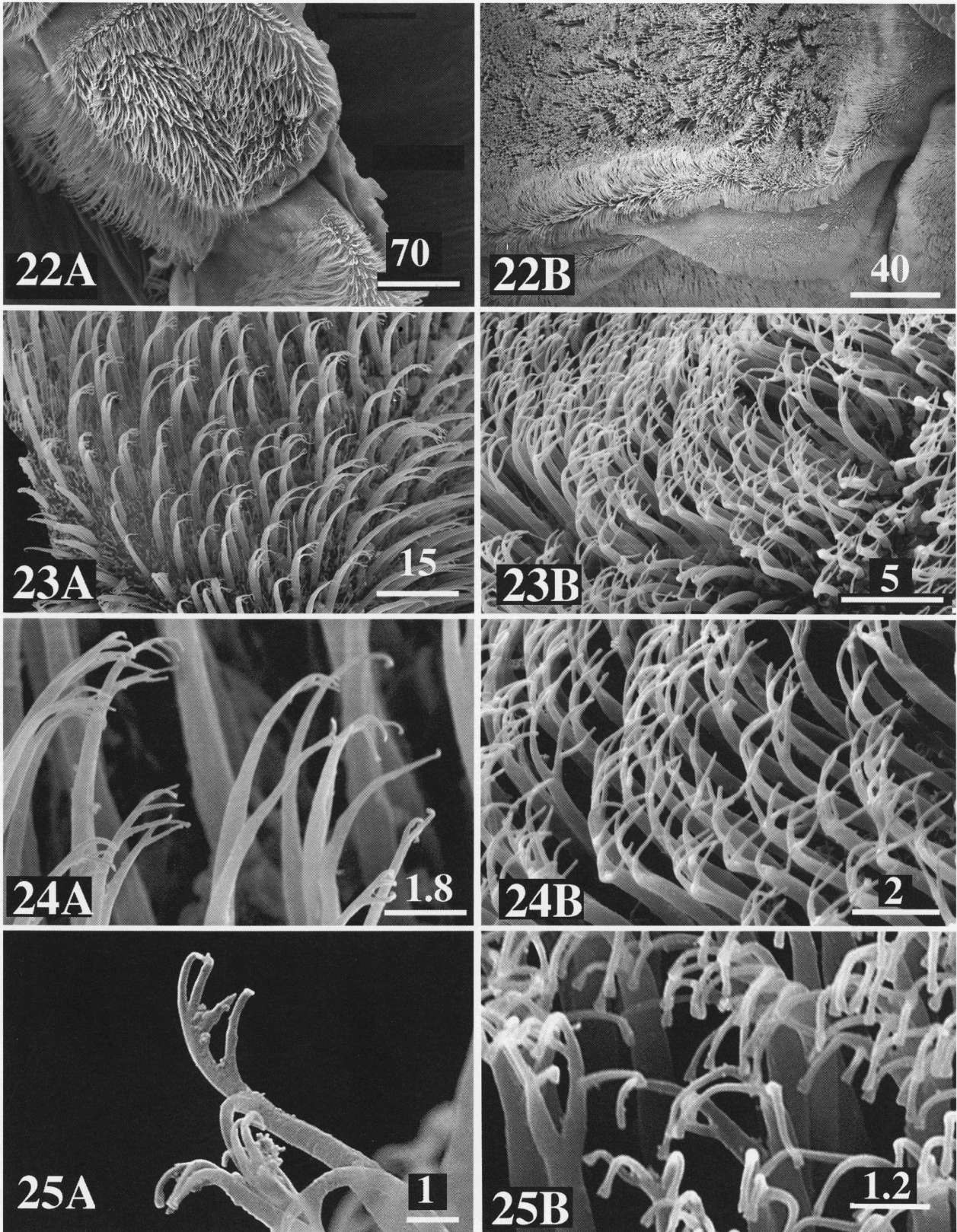


Figure 25. (A) Scanning electron micrograph (9,500 X) of setal termini of scansorial tail tip scale of *Matoatoa brevipes* (UMMZ 219307) illustrating the slightly expanded condition of the branchlets. (B) Similar view (12,083 X) of setal termini of tail tip scale of *M. spannringi* (UMMZ 218380). Scales in micra.

adhesive tail tips have been reported only among members of the tribe Carphodactylini, including the genera *Bavayia* and *Eurydactylodes* (Bauer, 1986; Meier, 1979), *Hoplodactylus* and *Naultinus* (Bauer, 1986), *Pseudothecadactylus* (Cogger, 1975; Bauer 1986), and *Rhacodactylus* (Bauer, 1986; Bocage, 1881; Boulenger, 1878, 1879, 1883; Guichenot, 1866; Mertens, 1964; Roux, 1913; Woodland, 1920). Bauer (1986) showed that, while the New Zealand carphodactylines of the genera *Hoplodactylus* and *Naultinus* lack well-defined tail pads visible by gross examination, scanning electron microscope study reveals dense aggregations of complex setae on parts of scales under the tail tip, which probably have an adhesive function.

Among gekkonines, adhesive tail pads are known in *Lygodactylus* (Fitzsimons, 1943; Greer, 1967; Loveridge, 1947; Mertens, 1964; Pasteur, 1964, 1977; Vitt and Ballinger, 1982; Tornier, 1899), *Matoatoa* (original observations), *Microscalabotes* (Pasteur, 1964), *Phelsuma* (Mertens, 1964), *Phyllodactylus* (Angel, 1946; Boulenger, 1878, 1879; Eijdsden, 1983; Fitzinger, 1843; Freytag, 1975; Lataste, 1877; Mertens, 1964; Mourgue, 1910; Rieppel and Schneider, 1981; Schreiber, 1912; Wiedersheim, 1876), and *Urocotyledon* (Eijdsden, 1962; Kluge, 1983; Mertens, 1964; Müller, 1910; Perret, 1963). All species of *Lygodactylus*, *Matoatoa*, *Microscalabotes*, and *Urocotyledon* are reported to have adhesive tail pads. Among *Phyllodactylus*, as currently recognized, only *P. europaeus* is reported to have adhesive tail pads. Mertens (1964) suggested that many species of *Phelsuma* have adhesive tail tips, but he presented convincing data for only *P. madagascariensis*, and we have confirmed his observations for the latter species.

In all reported cases of adhesive tail tips, with the exception of *Matoatoa*, the adhesive scales are restricted to the ventral surface of the tail tip. And, in most cases, the scansorial scales are modified into a distinctive pad which may resemble the scansorial pads of the digits. This is especially true of *Lygodactylus*, wherein the tail tip scansors are arranged in two rows separated by a central sulcus. The similarity between the tail and toe pads is so similar in *Urocotyledon palmata* that Loveridge (1947) mistakenly used a figure of a tail tip pad taken from Müller (1910) to represent the toe pad of that species. In most reported cases, as in *Matoatoa*, regenerated tails of geckos with adhesive tail tips have adhesive scales, but usually less well developed than in original tails.

The adhesive tail tip of *Matoatoa* spp. differs from that of other geckos in that the scansorial scales are not restricted to the ventral surface, but instead nearly or completely encircle the tail tip. Furthermore, with the possible exceptions of *Hoplodactylus*, *Naultinus*, and *Phelsuma madagascariensis*, *Matoatoa* differs from the other forms with adhesive tails in that the tail tip scansors are not differentiated in size, shape, and arrangement from other tail scales. The only gross indications of adhesiveness in the tail tip of *Matoatoa* are the velvety gray appearance (reduced light reflection) of the tail tip, the prehensile movement of the tail tip in life, and the appearance of dense micropile on the scansorial scales, which are just barely visible using a dissecting microscope.

The phylogenetic significance of scansorial scales on the tail tips of gekkonids is uncertain. Their universal presence in *Lygodactylus* and the apparently closely related *Microscalabotes*,

and in *Matoatoa*, *Urocotyledon*, and the carphodactyline genera of the southwestern Pacific region indicates a strong phylogenetic component at the generic or tribal levels. However, it seems certain that adhesive tail tips have evolved independently at least twice and probably more times within gekkonids. *Lygodactylus* and *Microscalabotes* may share a most recent common ancestor, as may the latter pair with *Phelsuma*, and all three genera contain species with adhesive tail tips. The relationships within the phyllodactyle genera are obscure, and at present there is no basis other than adhesive tail tips for arguing that *Matoatoa* and *Urocotyledon* are sister genera, and their relationships to *Phyllodactylus europaeus* are equally unclear. Furthermore, the extent of the distribution of adhesive tail tips within the currently recognized assemblage of *Phyllodactylus* species is poorly studied, and it may be that species other than *P. europaeus* will prove to have adhesive tail tips.

The independent evolution of adhesive tail tips seems especially likely in light of what is known about their structure and development. Maderson (1965, 1966) and Ruibal (1968) showed that the body scales of geckos in general are covered with small, scattered setae, which are derivatives of the Oberhäutchen. These setae, through developmental modification (elongation, compaction, increased branching complexity), form the surface structures (micropile) of the adhesive toe and tail pads. As suggested by Underwood (1954) and Bauer (1986), if the Oberhäutchen of body scales of geckos is generally competent to develop into adhesive pads, then given a common induction stimulus (e.g., friction, pressure), similar adhesive pads may evolve in parallel in independent lineages obscuring phylogenetic relationships.

Distributional Patterns

A fascinating pattern of geographical distribution shared by species-pairs of Madagascan geckos is emerging, which suggests that rainforest may have been the ancestral habitat for most gecko lineages, and perhaps other vertebrate lineages in Madagascar as well. This would be the case if all of Madagascar was once blanketed in rainforest, and if the expansion of the xeric habitats in southwestern Madagascar coincided with loss of rainforest in this region as a result of climatic change. The evidence for this scenario stems from the distributional patterns of three species-pairs of three endemic genera of Madagascan geckos.

Nussbaum and Raxworthy (1994) described a new species of *Paragehyra*, *P. gabriellae*, from the rainforests of southeastern Madagascar, which they concluded was the sister-species of the only other known species of *Paragehyra*, *P. petiti*, from the desert region of southwestern Madagascar. Because *P. gabriellae* has a higher number of presumed ancestral character states than *P. petiti*, Nussbaum and Raxworthy (loc. cit.) hypothesized that the common ancestor of the two species was a rainforest form and that ancestral *P. petiti* invaded the xeric habitats of southwestern Madagascar with the expansion of this relatively new kind of environment. The distributional pattern of *Matoatoa* and a preliminary assessment of the character states of the two species follows this same pattern. The desert form, *M. brevipes*, is smaller, has fewer

subdigital lamellae, more extensive and elaborate scansorial pilosities on the tail tip, and more extensive and prominent ornamentation of the snout bones, compared to *M. spannringi*, all of which are likely to be derived character states.

The genus *Ebenavia* was thought to include a single species, *E. inunguis*, distributed largely in the eastern rainforests of Madagascar. However, Nussbaum and Raxworthy (in press) found a new diminutive species in the southwestern deserts of Madagascar, which, in addition to small size, has several derived character states compared to its rainforest sister-species.

There are several other genera of amphibians and reptiles in Madagascar with east-west disjunctions, which when analyzed cladistically will provide a test of the generality of the pattern shared by *Paragehyra*, *Matoatoa*, and *Ebenavia*. Candidates include the mantellid genera *Mantella* and *Mantidactylus*, the microhylid genus *Scaphiophryne*, the gekkonine genera *Lygodactylus* and *Paroedura*, the chameleon genera *Brookesia* and *Furcifer*, the scincid genus *Amphiglossus*, and the colubrid genera *Liophidium* and *Lycodryas* (*Stenophis*). Exceptions to this pattern are the oplurid lizards, species of the scincid genus *Voeltzkowia*, and the tortoise genera *Geochelone* and *Pyxis*, the species of which are restricted to xeric environments.

Population Status and Conservation

The status of the two species of *Matoatoa* is unknown, and, because of their elusive character, it will be difficult to determine their distribution and abundance. *M. brevipes* is known from four localities, three of which are represented by a single specimen, and they are difficult to find at the fourth locality. These four localities occur along a narrow coastal strip 150 km long extending from a site about 10 km southwest of Morombe southward to the Fiherenana River. Our surveys in surrounding areas (Lac Tsimanampetsotsa, Anakao, Sept Lacs, St. Augustin, Kirindy, Zombitsy, Analavelona) and at many additional sites within its known range did not reveal additional populations. The habitat within the known range of *M. brevipes* has been subjected to human disturbance for many hundreds of years. Disturbance involves clearing of land to establish villages, roads, and agricultural plots; but more serious perhaps is the cutting of trees for firewood and charcoal production and the grazing of cattle and goats. It might be argued that *M. brevipes* has survived in spite of this and must, therefore, be a species that can adapt to human-modified habitat. However, there is no evidence that *M. brevipes* is truly anthropophilic, and its small range and seemingly spotty distribution and rarity at sites where it is known to occur suggest that its survival is uncertain, especially when weighed against the increasing human demand for resources in the region.

Matoatoa spannringi is known from only 10 specimens collected at a single locality in a small patch of degraded rainforest in an area almost completely denuded of natural vegetation. In addition, the species has proven almost impossible to collect, either because of rarity or secretiveness or both. Our surveys in surrounding areas (Andringitra Reserve, Ranomafana National Park, Manombo Reserve) failed to yield

M. spannringi, but there are many rainforest remnants within 300 km of the type locality, especially to the north along the rain forest belt that extends as far north as Perinet, that have not been surveyed and which may possibly harbor this species. Current data suggest, however, that this is one of the rarest geckos in Madagascar and that it deserves special consideration for protection.

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