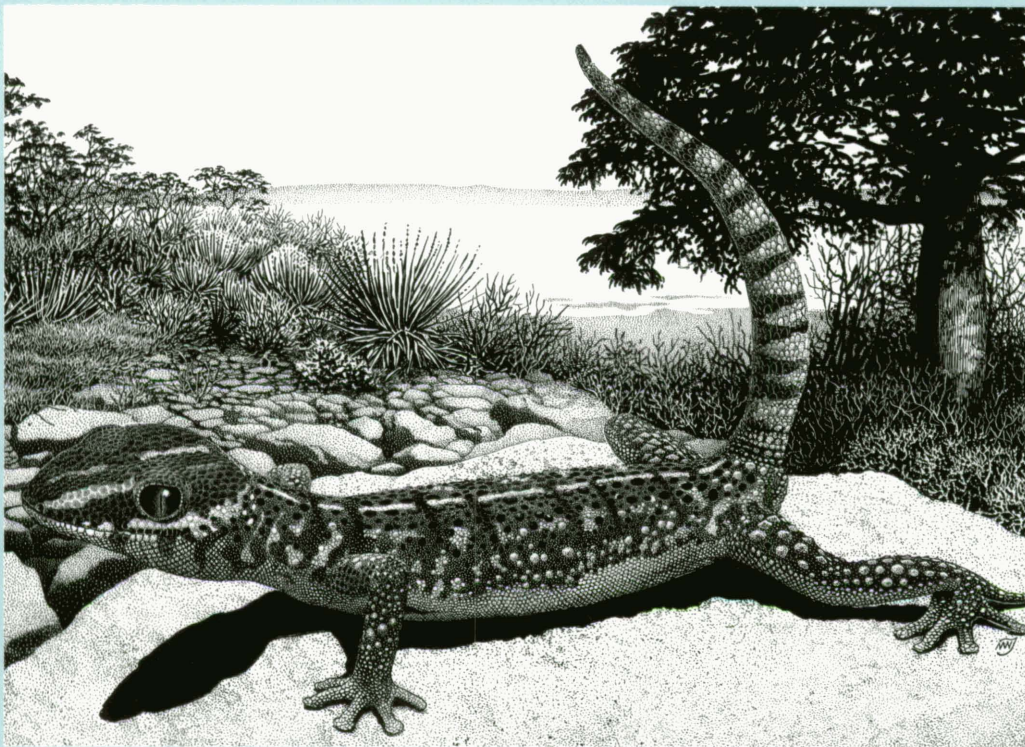


**SYSTEMATIC REVISION OF THE
GENUS *PAROEDURA* GÜNTHER (REPTILIA:
SQUAMATA: GEKKONIDAE), WITH THE
DESCRIPTION OF FIVE NEW SPECIES**

BY

RONALD A. NUSSBAUM AND CHRISTOPHER J. RAXWORTHY



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**Systematic Revision of the Genus
Paroedura Günther (Reptilia: Squamata:
Gekkonidae), with the Description of
Five New Species**

by

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ABSTRACT

Nussbaum, R.A. and Raxworthy, C.J. 2000. Systematic revision of the genus *Paroedura* Günther (Reptilia: Squamata: Gekkonidae), with the description of five new species. *Misc. Publ. Mus. Zool. Univ. Michigan*, 189: 1-26, 12 figs, 7 tables. The gekkonine genus *Paroedura* Günther, endemic to Madagascar and the Comoro Islands, previously contained ten species divided into two subgroups. The first group consisted of a largely northern enclave of species defined by having the nostril in contact with the rostral scale. This group included the type species, *P. sanctijohannis*, found only in the Comoros, and six Madagascan species including *P. gracilis*, *P. guibeeae*, *P. homalorhina*, *P. masobe*, *P. oviceps*, and *P. stumpffi*. The second group, defined by having the nostril excluded from contact with the rostral scale by interposition of a prenasal scale, included three southern species, *P. androyensis*, *P. bastardi*, and *P. picta*.

Examination of type material and recently collected specimens yielded considerable new information about the distribution and taxonomic relationships within the genus. *Paroedura guibeeae* is shown to be a junior synonym of *P. bastardi*. Five new Madagascan species are described, including three in the *sanctijohannis*-Group and two in the *picta*-Group, bringing the total species for the genus to 14. These new species occur in northern, west-central, and southwestern Madagascar, for the most part in transitional and dry forest habitats. A distribution map for the new species and a key to the species of *Paroedura* is presented.

Key words: Reptilia, Squamata, Gekkonidae, *Paroedura*, systematics, Madagascar, *P. maingoka* n.sp., *P. karstophila* n.sp., *P. tanjaka* n.sp., *P. vahiny* n.sp., *P. vazimba* n.sp.

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INTRODUCTION

Dixon and Kroll (1974) resurrected *Paroedura* Günther, 1879, a genus of Madagascar-Comoroan geckos, from the widely distributed and heterogeneous genus *Phyllodactylus*, described a new species, and provided the most recent review of the group. They recognized nine species of *Paroedura*: *P. androyensis* (Grandidier), *P. bastardi* (Mocquard), *P. gracilis* (Boulenger), *P. guibae* Dixon and Kroll, *P. homalorhina* (Angel), *P. oviceps* (Boettger), *P. picta* (Peters), *P. sanctijohannis* Günther, and *P. stumpffi* (Boettger). One of these, *P. sanctijohannis*, the type species of *Paroedura* by monotypy, is endemic to the Comoros. The remaining eight species are Madagascar. Nussbaum and Raxworthy (1994) described a tenth species, *P. masobe*, from Zahamena Reserve, Madagascar and briefly summarized ecological data for the Madagascar forms.

When Dixon and Kroll (1974) revived *Paroedura* (feminine) from *Phyllodactylus* (masculine), they failed to account for the gender change in their spelling of specific names. Most subsequent authors (e.g., Nussbaum and Raxworthy, 1994; Glaw and Vences, 1994) also did not correct the spellings. The names affected are *P. "homalorhinus,"* which should be *P. homalorhina*, and *P. "pictus"* corrected to *P. picta*.

Mocquard (1909) and subsequent authors (Angel, 1942; Guibé, 1956) recognized that *Paroedura* can be divided into two groups by the position of the nostril relative to surrounding scales. In one group, here referred to as the *picta*-Group, the nostril is excluded from contact with the rostral scale by the position of the prenasal (= supranasal) scale. This group includes *P. androyensis*, *P. bastardi*, and *P. picta*. In the second group, here named the *sanctijohannis*-Group, the nostril contacts the dorsolateral corner of the rostral scale. This group includes *P. gracilis*, *P. homalorhina*, *P. masobe*, *P. oviceps*, *P. stumpffi*, and *P. guibae*. In general, the *picta*-Group is restricted to south-southwestern Madagascar and occurs in drier habitats, whereas the *sanctijohannis*-Group is distributed in west-central and northern Madagascar and generally occurs in wetter, often rainforest, habitats. Other than the nostril position, there is no evidence that either of these two groups is monophyletic.

Our field studies in Madagascar yielded five new species of *Paroedura* and additional data on the distribution, variation, and systematics of the genus. We describe the new species and present other new information on *Paroedura* in this paper.

METHODS AND MATERIALS

General field techniques are described in Raxworthy and Nussbaum (1994). Specimens were euthanized by injection with chlorobutanol, fixed in 10% buffered formalin, soaked in water to remove the formalin, and stored in a final solution of 75% ethanol. The following abbreviations are used in the tables for morphometric and meristic characters. SVL = snout-vent length; TL = tail length; HL = head length; HW = head width, at widest point; HD = head depth, at mid-orbit; SL = snout length, anterior edge of eye to tip of snout; ED = horizontal eye diameter; EO = ear opening diameter; AGL = axilla-groin length; Forelimb = forelimb length, from axilla to tip of longest finger; Hindlimb = hindlimb length, from groin to tip of longest toe; Supralab = number of supralabial scales; Infralab = number of infralabial scales; Sdlm = number of subdigital lamellae on digits I-V of

manus; Sdlp = number of subdigital lamellae on digits I-V of pes. Counts are listed left-right. Snout-vent and tail lengths were measured with a ruler to the nearest 1 mm; other measurements were done with dial calipers and recorded to the nearest 0.1 mm. Maturity was estimated by direct examination of the gonads. Females with yolked or slightly yolked ova, whether ovarian or oviductal, were considered to be mature. Males with enlarged testes and coiled and enlarged vasa deferentia were considered to be mature. Smaller individuals with unyolked follicles or undeveloped testes and vasa deferentia were considered to be immature. Latitudes and longitudes were recorded to the nearest 0.001' when determined by satellite communication and to the nearest 0.10' when estimated from maps. Specimens are identified by catalog numbers of the Museum of Zoology, The University of Michigan (UMMZ), the Museum National d'Histoire Naturelle, Paris (MNHN), and by field numbers (RAN, RAX).

Status of *Paroedura guibae* Dixon and Kroll

Dixon and Kroll (1974) established *Paroedura guibae* on the basis of a series of specimens from near Betroka in southern Madagascar. They apparently believed these specimens represented the mainland form of *P. stumpffi*, and that the latter species was otherwise confined to its type locality on the northern satellite island named "Nosy Be." This was erroneous, however, because *P. stumpffi* had long been known from the northern mainland adjacent to Nosy Be (Guibé, 1956). Betroka, on the other hand, is 1,150 km south of the northern rainforest habitat of *P. stumpffi* in xeric vegetation.

Dixon and Kroll's (1974) photograph of the holotype and their description of *Paroedura guibae* led us to suspect it is based on specimens of *P. bastardi*, the major difference being the position of the nostril in regard to the rostral scale. In *P. bastardi*, the nostril is separated from the rostral scale by interposition of a small prenasal scale, whereas *P. guibae* was described as having the nostril in contact with the rostral scale, as in *P. stumpffi* and several other northern species of the genus. We examined all of the type material of *P. guibae* and found that in every case the nostril is clearly excluded from the rostral by the prenasal as in *P. bastardi* and two other southern species, *P. androyensis* and *P. picta*. It is unclear why Dixon and Kroll (1974) thought the nostril of the Betroka specimens contacts the rostral, but it is clear that this error was the reason they compared the specimens in detail only to *P. stumpffi* and missed the otherwise obvious similarities to *P. bastardi*. Because we could not find characters to distinguish the types of *P. guibae* from *P. bastardi*, a species common in the area of the type locality of *P. guibae*, we consider *P. guibae* to be a junior synonym of *P. bastardi*.

Paroedura maingoka n. sp.

Figures 1 and 2

Holotype. UMMZ 211210 (RAN 51098), adult male collected 10 December 1995, east side of Lac Tsimanampetsotsa, Tsimanampetsotsa Reserve, 24°5.274'S, 43°45.229'E, 50 m elevation, Betioky Fivondronana, Toliara (Tuléar) Province, Madagascar, by R. A. Nussbaum, C. J. Raxworthy, and Angelin and Angeluc Razafimanantsoa.

Paratypes. UMMZ 211211-20 (RAN 50984-5, 51092-7, 50935-



Figure 1. Holotype (UMMZ 211210; RAN 51098) of *Paroedura maingoka* in defensive posture.

6), collected 8-10 December 1995 at the type locality by the same collectors.

Other specimens. UMMZ 224237-9 (RAN 57408-10), 14 November 1997, coastal limestone cliffs 8 km S Itampolo, 24°43.18'S, 43°59.10'E, 160 m elevation, Ampanihy Fivondronana, Toliara (Tuléar) Province, Madagascar, R. A. Nussbaum.

Identification. A medium-sized *Paroedura* (adult size range 47-71 mm SVL); nostril excluded from contact with rostral by interposition of prenasal; dorsal tubercles trihedral to weakly tetrahedral; larger dorsal body tubercles arranged in about 12 longitudinal rows, larger tubercles separated by 2-3 small flat scales and/or smaller tubercles; light transverse band across back of head extending anteroventrally, ending below eye; neck and body with 5 transverse, dorsolateral, dark bands alternating with 5 light bands edged by narrow dark brown lines; white vertebral stripe on neck and body interrupted by narrow dark brown lines that border light transverse bands; unregenerated tail with 8-9 white bands alternating with 8-9 dark brown bands; prominent vertical or anteriorly curved tail display when disturbed.

Description of holotype. See Fig. 1. Well preserved, small slit posterolaterally on venter. Hemipenes extruded. Large white testes (5.8 x 4.7 mm); enlarged, white vasa deferentia.

Measurements and counts in Table 1. Head wider than neck, about as wide as body. Snout short, nearly as long as postorbital portion of head, angled steeply downward to tip, slight

depression between prominent canthal ridges. Posterolateral borders of occiput squared. Ear opening vertical slit. Body very slightly depressed. Tail 0.72 times snout-vent length, nearly round in cross section anteriorly, increasingly laterally compressed posteriorly, sharply pointed tip; ventral pygal section with pair of postcloacal sacs. Forelimb laid forward reaches to midway between eye and nostril, hindlimb to about 5 mm behind axilla. Digits slightly expanded at tips.

Rostral scale rectangular, wider than tall, slightly wider than mental. Nostril in contact with large prenasal anteriorly, smaller second supranasal dorsally, four small postnasals, and dorsal process of first supralabial. First supralabial largest, labials smooth. Snout and interorbital scales juxtaposed, some slightly raised, scale row in front of orbits tuberculate, as are larger lateral occipital scales. Dorsal occipital skin co-ossified with skull. Dorsolateral neck and body scales heterogeneous with about 12 longitudinal (midbody) rows of enlarged tetrahedral tubercles, enlarged tubercles separated mostly by small flat scales and fewer small tubercles. Dorsal scales of forelimb largely flat and weakly imbricate, except larger scales of radio-ulnar segment, which are slightly tuberculate. Dorsal scales of hindlimb strongly tuberculate with small, granular, interposed scales. Pre- and postaxial scales of forelimb not differentiated from ventral scales. Preaxials of hindlimbs large, flat, slightly imbricate; postaxials smaller, granular. Dorsal pygal scales like dorsal body scales; lateroventral pygals flat, slightly imbricate, with a pair of lateral



Figure 2. Juvenile *Paroedura maingoka* from type locality, in life, illustrating juvenile color pattern (compare to Fig. 1).

tubercles. First four postpygal tail segments each with transverse row of tubercles dorsolaterally; posteriorly tail with slightly imbricate, flattened scales.

Mental pentagonal, bordered posteriorly by pair of elongate postmentals. Postmentals contact mental, first infralabial, one enlarged lateral gular, one smaller posterolateral gular, and one enlarged central gular. First three infralabials significantly larger than others, second infralabial largest. Gulars, except as noted, small, granular. Ventrals of chest and abdomen flat, slightly overlapping, posterior abdominals largest. Ventral scales of limbs granular to increasingly larger and slightly imbricate distally. Scales of palms and soles rounded, juxtaposed. Proximal subdigitals in rows of 2-3, distally two narrow leaf-like rows of scales followed by enlarged row supporting terminal pads. Pair of squarish, terminal, pilose pads, each pad about 1 mm across. Well-developed claws curving downward between terminal pads of all digits. Prominent elongate scale above base of each claw.

Color after three months in alcohol (nearly the same as in life): Head and snout tannish brown dorsally with irregular flesh markings; prominent, white, subcanthal stripe from eye to lip, passing downward just below nostril and along suture between rostral and first supralabial; irregular white stripe across back of head continuing forward and downward on each side, ending below anterior edge of eye on 7th supralabial; supralabials 1-6 largely brown, but lighter along ventral margins; triangular brown patch in front of each eye, includes scales below

subcanthal white stripe and most of supralabials 1-6; anterior ciliaries bright white, forming a conspicuous white line in front of eye. Lateral region of lower jaw largely white with some brown spots on infralabials; three light brown streaks running posteroventrally from infralabials onto sublabials, first beginning below anterior orbit, third beginning below posterior orbit. Dorsum of neck and body brown, with prominent white vertebral stripe from base of skull to pygal vertebrae interrupted by eight dark cross lines; prominent white shoulder collar across top of shoulders extending downward and slightly forward ending in front of each forelimb insertion; dorsolateral region of neck and body with scattered white markings and isolated white tubercles; lower sides grayish with light brown marbling grading to white venter; upper surfaces of forelimbs gray with some enlarge white scales on distal segment; upper surfaces of hindlimbs dark brown with large white tubercles; tail with alternating white and dark brown bands dorsolaterally, dark bands fainter across underside of tail; ventral surfaces of head, body, limbs, and pygal portion of tail white.

Variation. Morphometric and meristic variation are summarized in Table 1. Among the small, male-biased sample of types, males are the larger sex, but one female is only 6 mm SVL smaller than the largest male. Larger samples are needed to determine whether the size difference is real. Males have a more swollen ventral pygal region of the tail with larger lateral pygal tubercles, and larger postcloacal sacs than females. There

Table 1. Morphometric and meristic variation among the holotype (holo) and paratypes (para) of *Paroedura maingoka*. Measurements in mm.

	UMMZ	211210	211211	211212	211213	211214	211215	211216	211217	211218	211219	211220
		holo	para	para	para	para	para	para	para	para	para	para
Sex		male	male	female	male	male	male	female	female	male	female	male
Maturity		mature	mature	immature	mature	mature	mature	mature	immature	mature	immature	mature
SVL		71	68	50	67	58	60	65	50	59	48	47
TL		51	49	36	41*	47	35*	50	39	32*	—	—
HL		24.9	23.1	18.9	23.2	19.4	22.0	21.7	18.0	22.4	19.7	18.5
HW		16.8	16.3	12.1	15.7	13.4	14.3	15.5	11.6	13.9	11.5	11.0
HD		11.3	11.8	8.7	10.2	8.6	9.9	9.8	7.4	9.2	8.2	7.7
SL		8.8	9.4	6.6	8.1	7.3	7.5	7.7	6.6	7.1	6.5	6.9
ED		5.3	4.9	3.9	4.7	3.7	4.8	4.6	3.8	4.3	3.8	3.4
EO**		3.1x1.2	3.0x0.7	2.3x0.8	3.2x1.2	2.4x0.6	2.6x0.9	2.7x0.9	1.7x0.7	2.6x0.8	2.0x0.8	2.1x0.6
AGL		28.8	31.3	20.5	28.2	25.9	26.9	28.0	23.0	25.0	21.0	21.4
Forelimb		22.8	22.8	17.1	22.0	19.0	19.8	21.7	16.8	18.6	17.0	16.1
Hindlimb		30.1	29.1	21.7	28.0	25.7	25.5	25.7	22.6	25.4	22.8	21.4
Supralab		10-10	10-9	10-10	9-10	9-9	9-9	11-10	9-9	9-10	10-10	8-8
Infralab		9-9	9-8	8-8	9-8	8-8	8-8	9-9	8-8	9-8	8-8	8-8
Sdlm I		8-9	10-10	9-10	10-9	10-10	8-8	11-10	9-9	9-10	10-10	8-8
Sdlm II		12-11	12-11	12-12	13-12	12-11	10-11	13-13	12-11	11-11	12-11	10-10
Sdlm III		14-13	13-12	14-14	14-13	13-13	12-12	14-15	12-12	12-13	12-12	12-12
Sdlm IV		12-12	13-13	13-13	12-12	12-12	12-12	13-14	12-11	12-11	12-12	12-12
Sdlm V		11-12	10-10	10-9	11-11	11-11	10-10	11-12	10-11	11-10	11-11	11-11
Sdlp I		9-9	9-9	9-9	10-10	9-9	8-9	10-10	9-9	10-10	9-10	9-9
Sdlp II		12-12	12-12	12-12	11-12	13-12	11-11	13-14	11-11	11-11	12-12	10-11
Sdlp III		14-14	14-15	14-15	15-14	15-15	13-14	17-16	13-13	14-14	15-15	13-13
Sdlp IV		16-16	16-17	16-16	15-15	17-17	15-14	17-17	14-13	14-14	15-15	14-14
Sdlp V		17-16	16-16	16-15	15-15	16-16	15-15	17-17	15-15	14-15	16-17	15-15

*Tail regenerated or broken with part missing

**height x length

are no other obvious sexual differences in coloration and morphology.

The most important variation in coloration concerns the expression of light and dark bands on the neck and body. In some individuals, these bands are boldly expressed (Fig. 2) and in others they are nearly completely obscured (Fig. 1). Regenerated tails may have a variegated brown and white color pattern rather than a banded pattern.

Hatchlings and small juveniles are unknown, but smaller individuals tend to be more brightly colored with greater contrast between light and dark markings. This is especially noticeable in the banding of the tail and body. Bolder and brighter color patterns of young are also typical of *Paroedura bastardi* and *P. picta*.

Etymology. The specific name, “*maingoka*” (mine goo kuh), a Malagasy word for “scorpion”, is used as an unlatinized specific epithet. It refers to the striking behavior of individuals of this species when confronted, in which the tail is immediately curved anteriorly over the back in a scorpion-like manner (Fig. 1).

Distribution. Known only from the type locality at Tsimanampetsotsa and near Itampolo (Fig. 3).

Habitat. Individuals were found only at night (20:30-23:50 hr) on the ground among limestone boulders or on limestone rocks in xeric vegetation dominated by baobabs and baobab-like leguminous trees of short stature.

Remarks. *Paroedura maingoka* differs from *P. gracilis*, *P. homalorhina*, *P. karstophila* n. sp., *P. masobe*, *P. oviceps*, *P. sanctijohannis*, *P. stumpffii*, *P. tanjaka* n. sp., and *P. vazimba* n. sp. in having the nostril excluded from contact with the rostral scale

by interposition of a large prenasal scale (nostril contacts rostral in latter seven species). *Paroedura maingoka* shares the nostril position with *P. bastardi*, *P. picta*, *P. vahiny* n.sp., and *P. androyensis*. *Paroedura maingoka* differs from the latter four species in having a boldly banded tail and fully expressed defensive tail display. *Paroedura maingoka* differs further from *P. picta* in having larger terminal pads that are wider than the proximal portion of the digits (not wider in *P. picta*), dorsal tubercles separated by a mixture of smaller tubercles and small flat scales (separated by flat scales only in *P. picta*), and in having vertically transverse dark and light body and neck bands (angled sharply anteroventrally in *P. picta*); further from *P. bastardi* in having large dorsal tubercles separated by smaller scales (large dorsal tubercles juxtaposed in *P. bastardi*), and a white vertebral stripe and light and dark, transverse neck and body bands (missing in adult *P. bastardi*); further from *P. androyensis* and *P. vahiny* in larger size (71 compared to 47 mm maximum SVL), presence of white vertebral stripe and body and neck bands (lacking in the latter two forms), and absence of multicarinate scales (present in *P. androyensis* and *P. vahiny*).

The tail display of *Paroedura maingoka* is undoubtedly a defensive behavior, which has been reported for other lizards, especially geckos (Bustard, 1967; Arnold, 1988). A striking parallel to the present case was reported for the Chinese gecko, *Teratoscincus roborowskii* (Autumn and Han, 1989). The latter authors believed the behavior is involved in Batesian mimicry of scorpions. It is also possible, however, that in association with the vividly banded color pattern, the tail acts as a lure to attract the attention of predators to the most expendable part of the

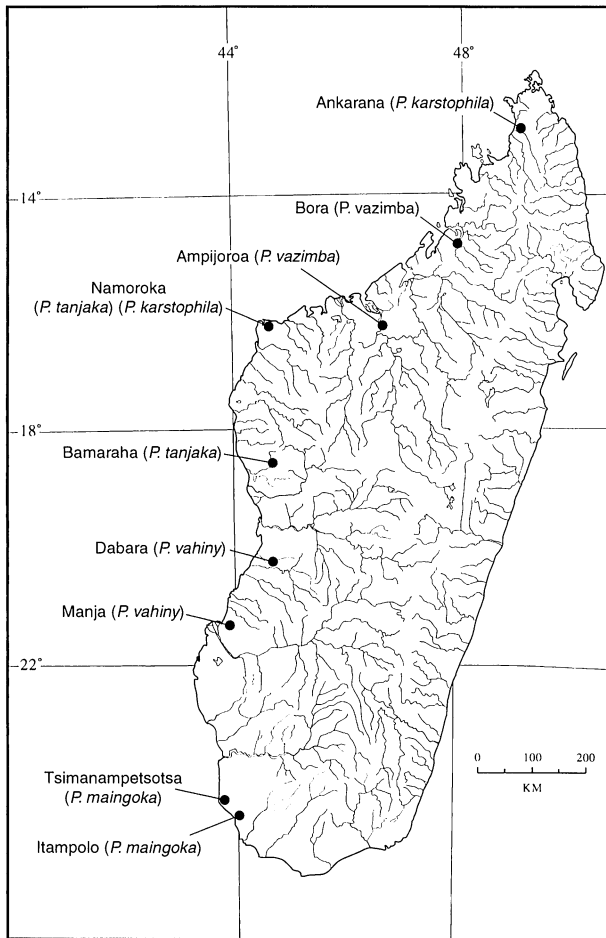


Figure 3. Geographic distribution of five new species of Madagascan *Paroedura*.

body, which is readily autotomized (Johnson and Brodie, 1974). In the case of *P. maingoka*, we observed no obvious animals, scorpions or otherwise, at the type locality that might serve as banded models. However, uniformly colored scorpions of many species are abundant on the limestone slopes and plateaux of southwestern Madagascar.

Paroedura maingoka was recently found near Itampolo, 70-80 km SE of the type locality, in limestone habitat and scrub forest. This species probably occurs throughout much of the largely unsurveyed, calcareous Mahafaly Plateau along the southwestern coast. Although rare in collections, its occurrence in a reserve (Tsimanampetsotsa), its secretive habits, and its preference for rough terrain, which is difficult for humans to spoil, provide some protection for this species. *P. maingoka* is probably not currently threatened with extinction.

Paroedura karstophila n. sp.
 Figures 4, 5, and 6

Holotype. UMMZ 219252 (RAN 55600), mature male, collected 4 July 1996 at Amboronaomby, Namoroka Reserve, 16°28.321'S, 45°20.825'E, 150-180 m elevation, Soalala Fivondronana, Mahajanga Province, Madagascar by J. Rafanomezantsoa, L. Rakotozafy, and J. B. Ramanamanjato.

Paratypes. UMMZ 219248-51 (RAN 55595, 55597-9), same data

as holotype. UMMZ 219280-1 (RAN 55614-5), 3 July 1996, Ambinorabe-Belaka, Namoroka Reserve, 16°28.225'S, 45°19.515'E, 150-180 m elevation, Soalala Fivondronana, Mahajanga Province, Madagascar, J. Rafanomezantsoa, L. Rakotozafy, and J. B. Ramanamanjato. UMMZ 219282-7 (RAN 55652-7), 8 July 1996, Beritra Lake, Namoroka Reserve, 150-180 m elevation, Soalala Fivondronana, Mahajanga Province, Madagascar, J. Rafanomezantsoa, L. Rakotozafy, and J. B. Ramanamanjato. UMMZ 222020-37 (RAX 29-31, 91-4, 152-6, 193, 264, 271-4), 2-7 December 1996, Namoroka Reserve, 16°28.189'S, 45°20.906'E, 150-180 m elevation, Soalala Province, Mahajanga Province, Madagascar, J. B. Ramanamanjato, C. J. Raxworthy, and Angelin and Angeluc Razafimanantsoa. UMMZ 219245-7 (RAN 55035, 55037, 55039), 26 April 1996, Campement des Anglais, Ankarana Reserve, Ambilobe Fivondronana, Antsiranana Province, Madagascar, A. P. Raselimanana, J. B. Ramanamanjato, A. Razafimanantsoa.

Identification. A small *Paroedura* up to 55 mm SVL; nostril in contact with rostral scale; eye large, horizontal diameter equal to or slightly greater than distance between eye and ear opening; snout relatively long, 61-74% as long as head width; no vertebral crest or ridge with double row of closely spaced tubercles; limbs and digits moderate length; appressed hindlimb does not reach anterior to axilla; forelimb laid forward extends to loreal region or nostril, never extending beyond tip of snout; double row of subdigital lamellae; 10-14 lamellae beneath 4th digit of manus, 13-17 beneath 4th digit of pes; large dorsal tubercles of body trihedral, separated by smaller tubercles, arranged into longitudinal rows; four distinct, dark, dorsal transverse band on neck and body separated by lighter patches of ground color; light patch between first and second dark dorsal bands extends ventrally and slightly anteriorly on each side to anterior forelimb insertions; no dark eye mask (Fig. 5).

Description of holotype. Well preserved, no damage, small posterolateral slit in body wall, tail original, attached to specimen. Mature male, enlarged white testes, enlarged white vasa deferentia.

Measurements and counts in Table 2. Head oviform, wider (9.8 mm) than neck (6.1 mm), same width as body. Posterior cranium flat, shelf-like. Snout long, slightly longer than postorbital segment of skull, sloping moderately downward anteriorly; shallow, narrow concavity between distinct canthal ridges. Eyes large, horizontal diameter equal to distance between eye and ear, 0.63 times snout length; directed slightly anteriorly. Ear vertical, oval slit; small, not visible from above. Limbs moderate length; forelimb extends forward to point between eye and nostril; hindlimb reaches forward to forelimb insertion. Fingers and toes of moderate length; third finger longest, only slightly longer than fourth; third toe longest, only slightly longer than fourth. Tips of digits slightly expanded with small toe pad; no separate claw-bearing segment. Claws small, not visible from above, curving down between terminal lamellae. Original tail 0.92 times SVL, postpygal portion rounded in cross-section proximally, slightly laterally compressed distally, tapering gradually to a sharp tip.

Nostril contacts rostral, first supralabial, two supranasals, and four postnasals. Supranasals adjacent to rostral separated by single granular scale. Rostral rectangular, wider than tall, with pair of dorsolateral processes that contact nostrils. Supraoculars keeled. Superciliaries weakly keeled on lateral edges. First

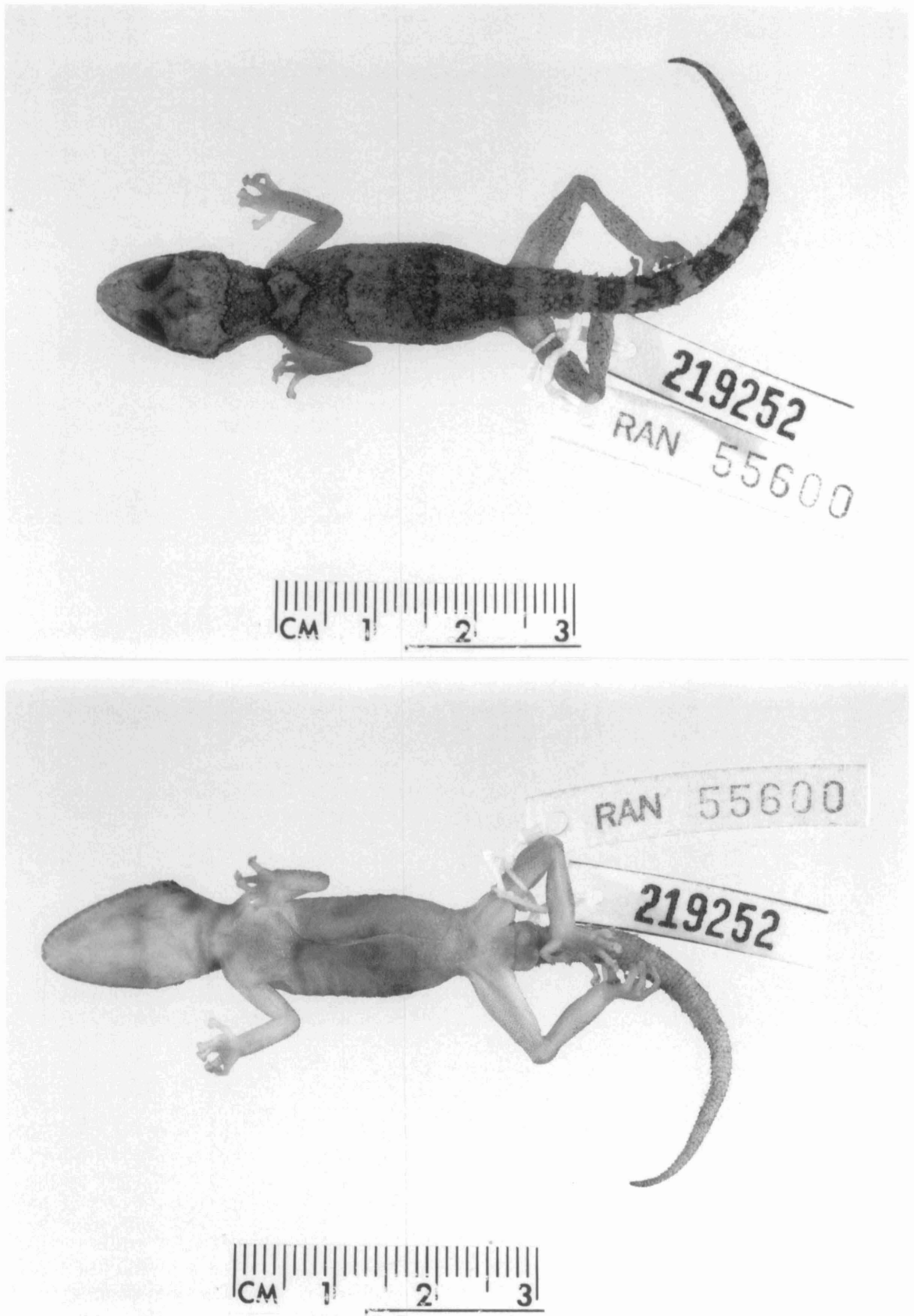


Figure 4. Holotype (UMMZ 219252; RAN 55600) of *Paroedura karstophila*.

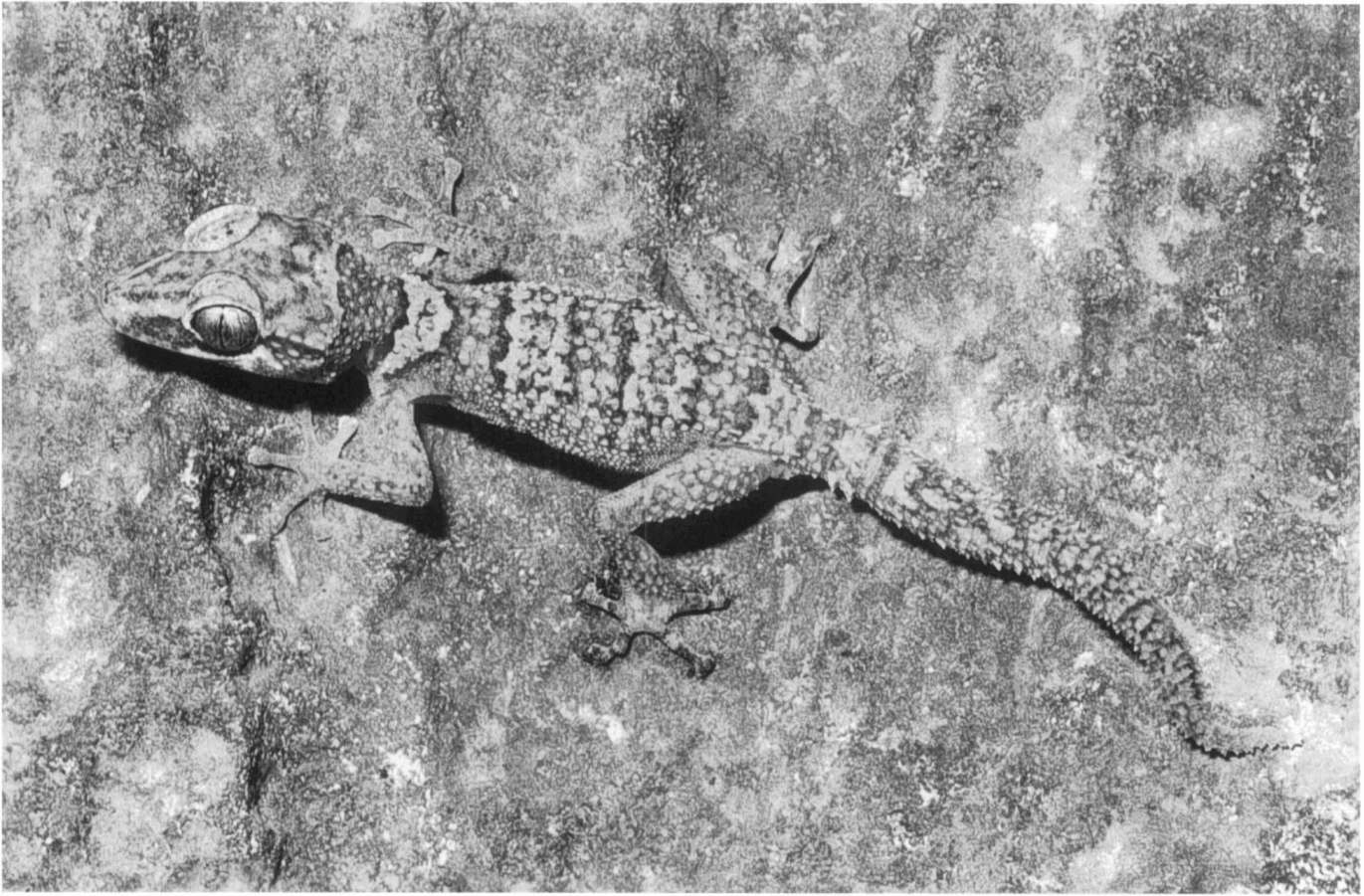


Figure 5. *Paroedura karstophila* from Namoroka; light color phase with fully expressed dorsal markings. Note that the first dorsal light mark (above the forelimb) extends down the side to the area near the forelimb insertion. This is an important key characteristic that distinguishes *P. karstophila* from *P. vazimba* (see Fig. 12).

supralabial tallest. Supra- and infralabials smooth, without central raised area. Mental triangular, same width anteriorly as rostral, nearly contacting first supralabial when mouth closed. Postmentals paired, longer than wide, irregularly shaped; contact each other medially, mental anteriorly, first and second infralabials laterally, and enlarged chin shields posterolaterally and posteriorly.

Cranial skin co-ossified with underlying bones. Tubercles of snout, interorbital region, and anterior dorsal cranium homogeneous. Tubercles of lateral cranium and dorsolateral neck, body, and tail heterogeneous with smaller tubercles interspersed among larger prominent tubercles. Prominent tubercles of body trihedral, arranged into 12 longitudinal rows at midbody, fewer rows anteriorly and posteriorly on body. Upper surfaces of proximal segment of forelimb with large, homogeneous, trihedral tubercles; distal segment heterogeneous, with smaller tubercles among the larger tubercles. Both proximal and distal segments of hindlimbs with heterogeneous tubercles. Tops of hands, feet, and digits covered with smooth, imbricate scales. Dorsolateral surface of postpygal tail with transverse rows of spiny tubercles diminishing in size posteriorly. Ventral scales regionally homogeneous. Chin scales small, granular, juxtaposed. Posterior throat and ventral scales of body larger than chin scales, smooth, flattened, slightly imbricate. Undersurfaces of limbs and tail with small, slightly imbricate scales. Palms and soles with juxta-

posed granular scales. Ventral surface of digits with two rows of lamellae. Pair of pilose terminal pads on each digit, each pad about 0.5 mm wide.

Color (after 36 months in alcohol): Top of head tannish brown; narrow dark brown line extending posteriorly from each nostril, ending above ear. Iris black with faint brassy cast. Supra- and infralabials whitish, heavily dusted with brown melanophores. Dorsum of neck and body with four dark brown transverse bands on lighter tannish ground color. Anterior-most dorsal band just behind head, covering most of neck; second over shoulders; third at midbody; fourth above groin. Light ground color separating first and second dark dorsal bands on neck extends ventrally and slightly anteriorly on each side to point near anterior edge of forelimb insertion. Tail with alternating light and dark bands dorsolaterally. Upper surfaces of limbs nearly uniform light tan. Ventral surfaces of head, neck, body, and limbs whitish; microscopic examination reveals numerous tiny, brown melanophores on ventral surfaces. Underside of postpygal tail white, heavily dusted with brown.

Variation. Morphometric and meristic variation among types is summarized in Tables 2-3. There is little within population (Namoroka and Ankarana) variation. The size of the dominant dorsal trihedral tubercles varies among individuals, as does the distinctiveness of the longitudinal rows formed by the large tubercles on the dorsum. Analysis of interpopulation variation is

Table 2. Morphometric and meristic variation among Namoroka types of *Paroedura karstophila*. Measurements in mm.

UMMZ	219248 para	219249 para	219250 para	219251 para	219252 holo	219280 para	219281 para	219282 para	219283 para	219284 para	219285 para
Sex	male	male	male	male	male	female	female	female	male	male	female
Maturity	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature
SVL	50	40	47	48	48	43	48	49	42	47	49
TL	31*	39	15*	35*	44	—	33*	28*	—	25*	—
HL	16.4	13.0	16.6	16.4	16.5	15.2	16.6	16.5	14.9	16.2	16.4
HW	10.4	8.6	9.8	10.5	9.8	9.5	10.0	9.9	8.9	10.1	10.4
HD	6.2	5.0	5.9	6.2	6.0	5.6	5.7	5.7	5.6	6.3	6.3
SL	6.8	6.0	6.4	6.7	6.5	6.2	7.0	6.8	6.0	6.8	6.9
ED	4.2	3.4	4.4	4.3	4.1	4.0	4.3	4.3	3.8	4.2	4.2
EO**	1.3x0.4	1.3x0.7	1.7x1.1	1.8x0.8	1.8x1.0	1.3x0.9	1.4x1.0	1.9x1.0	1.4x0.8	1.6x1.1	1.5x1.0
AGL	24	17	22	21	21	17	20	20	18	18	20
Forelimb	19	16	17	20	18	18	19	17	18	18	20
Hindlimb	26	24	27	28	27	25	27	26	23	25	28
Supralab	19-18	19-20	17-17	19-17	18-17	19-19	18-17	17-18	17-18	17-16	17-17
Infralab	12-11	11-13	12-12	12-12	13-12	14-13	12-12	12-12	13-12	13-13	13-14
Sdlm I	7-7	7-7	7-6	7-7	8-8	7	8-8	7-7	8-7	7-7	7-7
Sdlm II	10-9	9-9	8-7	10-11	9-9	10-10	11-10	8-9	9-8	10-9	9-10
Sdlm III	11-11	12-12	10-10	12-13	13-12	11-11	12-12	10-	11-10	12-12	12-14
Sdlm IV	11-11	13-13	11-11	12-13	11-11	11-12	11-11	11-	11-11	11-10	13-10
Sdlm V	10-9	10-10	9-8	10-10	10-10	10-9	10-10	9-9	10-10	9-10	9-10
Sdlp I	8-8	7-7	7-7	7-8	8-8	7-7	7-7	7-7	7-7	7-7	7-7
Sdlp II	11-10	9-12	9-9	11-10	12-11	10-10	12-11	10-9	10-9	10-9	12-10
Sdlp III	14-14	14-13	11-11	15-15	14-13	15-15	14-15	14-12	13-13	13-14	14-13
Sdlp IV	14-16	13-15	13-13	15-15	16-13	16-15	15-15	14-14	15-15	14-15	16-15
Sdlp V	13-13	14-14	13-13	15-15	14-15	14-15	14-15	12-13	14-14	14-14	14-15

*Missing part or regenerated.

**height x length

(Continued below.)

Table 2. (Continued.) Morphometric and meristic variation in Namoroka *Paroedura karstophila*.

UMMZ	219286 para	219287 para	222020 para	222021 para	222022 para	222023 para	222024 para	222025 para	222026 para	222027 para	222028 para
Sex	female	female	male	male	male	male	female	female	male	male	female
Maturity	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature
SVL	47	47	45	46	44	49	48	49	45	48	48
TL	—	36	16*	47	51*	—	34*	—	36*	—	—
HL	16.0	15.7	16.0	16.7	15.7	16.0	16.5	16.3	15.0	16.9	16.5
HW	9.9	9.8	10.0	10.1	9.4	10.2	9.4	10.2	9.8	10.2	10.4
HD	5.9	5.7	5.4	5.7	5.7	5.8	5.9	6.2	5.9	6.1	5.7
SL	6.7	6.0	6.6	6.5	6.0	7.0	6.9	6.7	6.2	6.9	6.7
ED	4.1	4.2	4.1	4.2	4.4	4.5	4.1	4.4	4.3	4.6	4.4
EO**	1.4x1.0	1.5x0.9	1.5x1.0	1.7x0.8	1.8x0.7	1.8x0.9	1.7x0.8	2.0x0.8	1.5x0.9	1.7x1.0	1.8x1.2
AGL	20	21	18	18	19	20	22	24	20	22	21
Forelimb	19	17	18	18	18	19	18	19	19	19	19
Hindlimb	25	24	26	25	26	27	26	26	24	28	25
Supralab	17-17	17-17	18-17	17-17	17-17	16-16	16-17	16-16	16-17	16-16	18-17
Infralab	11-11	11-12	14-13	12-12	12-11	12-12	11-11	11-11	12-11	11-10	12-11
Sdlm I	7-7	7-7	7-7	6-7	7-7	7-8	8-8	8-8	7-7	7-7	7-
Sdlm II	10-10	8-9	9-9	9-8	9-9	10-10	10-10	9-9	9-10	10-9	9-9
Sdlm III	12-13	10-11	12-11	11-11	11-11	13-13	11-11	12-11	12-12	11-11	12-12
Sdlm IV	11-13	11-11	11-11	11-11	12-11	11-13	11-11	12-12	13-12	11-11	10-
Sdlm V	10-11	9-9	10-9	9-8	10-9	10-10	10-9	10-9	11-10	9-10	9-
Sdlp I	8-7	7-7	7-7	7-7	8-7	7-8	8-8	7-7	8-7	7-7	7-7
Sdlp II	11-10	10-9	10-10	10-9	10-11	10-11	10-11	11-11	10-11	9-10	9-9
Sdlp III	15-15	13-12	14-15	12-13	14-14	14-14	13-14	14-13	14-	13-14	15-13
Sdlp IV	15-16	14-15	15-15	14-13	14-14	16-15	15-15	14-15	15-16	14-15	15-15
Sdlp V	15-16	13-13	15-14	12-14	13-13	15-14	15-15	14-13	15-15	15-15	14-15

*Missing part or regenerated.

**height x length

(Continued on next page.)

Table 2. (Continued.) Morphometric and meristic variation in *Namoroka Paroedura karstophila*.

UMMZ	222029 para	222030 para	222031 para	222032 para	222033 para	222034 para	222035 para	222036 para	222037 para
Sex	male	male	male	female	male	male	male	female	female
Maturity	mature	mature	mature	mature	mature	mature	mature	mature	mature
SVL	45	45	44	46	46	46	46	48	47
TL	38*	43	46	—	—	27*	32*	32*	39*
HL	16.4	15.1	15.9	15.9	15.5	15.5	16.3	15.7	16.5
HW	10.9	9.5	9.6	10.0	9.9	10.0	10.1	10.0	9.9
HD	6.2	5.6	5.5	5.7	6.0	6.0	5.9	6.0	6.4
SL	6.9	6.4	6.5	6.6	6.5	6.3	6.3	6.7	6.8
ED	4.1	4.5	3.9	4.4	4.0	4.4	4.1	3.4	4.5
EO**	1.6x0.8	1.5x0.8	1.3x0.8	1.6x0.8	1.4x0.9	1.6x0.5	1.3x0.4	1.5x0.6	1.3x0.8
AGL	19	18	20	20	20	21	21	23	22
Forelimb	19	18	18	18	21	20	18	20	21
Hindlimb	25	26	25	25	27	25	26	24	26
Supralab	18-19	18-17	17-17	19-17	17-18	18-17	17-17	14-15	18-18
Infralab	11-11	12-12	12-11	11-12	13-13	12-12	13-12	12-12	12-13
Sdlm I	7-7	8-7	8-7	8-8	7-7	7-7	7-7	7-7	8-7
Sdlm II	10-9	10-10	10-10	10-9	10-9	9-8	9-9	10-10	10-10
Sdlm III	11-10	12-12	12-13	11-11	11-12	10-12	11-11	11-11	12-12
Sdlm IV	10-11	12-13	13-12	10-13	11-11	11-12	11-	11-13	12-12
Sdlm V	9-10	10-9	10-10	9-10	9-9	9-10	9-9	9-9	10-10
Sdlp I	7-7	8-7	7-7	7-7	8-8	7-7	6-6	7-7	9-8
Sdlp II	10-11	11-12	11-10	10-10	10-10	9-10	9-10	10-12	12-11
Sdlp III	12-13	14-14	14-14	14-14	12-14	13-13	13-12	14-13	15-15
Sdlp IV	14-14	15-14	15-15	14-15	14-14	14-13	13-15	15-14	16-17
Sdlp V	14-14	15-15	14-14	14-15	14-14	13-14	14-13	13-14	16-17

*Missing part or regenerated.

**height x length

Table 3. Morphometric and meristic variation in *Paroedura karstophila* from Ankarana.

UMMZ	219245 para	219246 para	219247 para
Sex	female	female	male
Maturity	mature	mature?	mature
SVL	51	44	55
TL	32*	—	44*
HL	18.1	15.3	18.0
HW	10.8	8.8	10.9
HD	6.6	5.9	6.7
SL	7.5	6.5	7.6
ED	4.6	4.0	4.5
EO**	2.0x1.3	1.7x0.7	2.1x0.8
AGL	23	17	23
Forelimb	18	16	18
Hindlimb	27	21	27
Supralab	18-18	18-16	17-16
Infralab	14-13	15-14	13-14
Sdlm I	9-9	9-10	10-9
Sdlm II	11-12	12-12	12-11
Sdlm III	12-12	13-13	12-14
Sdlm IV	13-12	13-13	13-14
Sdlm V	11-10	12-12	12-12
Sdlp I	9-8	9-9	10-10
Sdlp II	12-12	13-12	12-12
Sdlp III	14-14	15-15	15-14
Sdlp IV	16-16	16-16	17-16
Sdlp V	16-16	16-17	18-16

*Missing part or regenerated.

**height x length



Figure 6. *Paroedura karstophila* from Namoroka; dark phase with faintly expressed dorsal markings.

hampered by the small size of the Ankarana sample. The largest individual, 55 mm SVL, is a male from the Ankarana population ($n = 3$). The largest individual among the Namoroka sample ($n = 31$), also a male, is only 50 mm SVL. These data strongly suggest that the northern population has a larger average size. Although the two largest individuals are males, several females from Namoroka are nearly as large (49 mm SVL) as the largest male (50 mm) from that population. The single female from the Ankarana population is only 4 mm shorter than the largest of the two males. It seems unlikely that significant sexual dimorphism in size exists in this species. There is no detectable morphometric and meristic variation between the two populations.

Some individuals within population are more darkly colored, dorsally and ventrally than others, and the distinctiveness of the transverse, dark, dorsal bands varies from slightly expressed to prominent (Figs 5-6). The light band separating the first and second dorsal bands, which extends ventrally along the sides to the insertions of the forelimbs, is consistently present and is an important identifying feature of the species.

Hatchlings and small juveniles are unknown. Over the size range of the samples, there is no evidence of ontogenetic variation in coloration, nor is sexual dichromatism evident.

Distribution. Known only from the karst habitats of Namoroka

and Ankarana Reserves in northwestern Madagascar (Fig. 3).

Etymology. The name "*karstophila*" refers to the apparent preferred habitat of this species.

Remarks. *Paroedura karstophila* is most similar to *P. vazimba* n. sp., and the two species differs from other species of *Paroedura* by many of the same character states (see the "Remarks" section below for *P. vazimba*).

All individuals were collected at night, 19:30-23:30 hr, when they were active on the surface. All were first observed on tsingy rock, 0.5-7.0 m above ground in open deciduous forest.

***Paroedura tanjaka* n. sp.**

Figures 7 and 8

Holotype. UMMZ 224225 (RAN 54507), mature male, collected 18 March 1996, Bemaraha Reserve, Ambalarano Tsingy, 18°59.230'S, 44°45.566'E, 100-140 m elevation, Antsalova Fivondronana, Mahajanga Province, Madagascar by J. B. Ramanamanjato, A. P. Raselimanana, C. J. Raxworthy, and Angelin and Angeluc Razafimantsoa.

Paratypes. UMMZ 224232-3 (RAN 54468, 54527), 17-19 March 1996, Ambalarano (see data for holotype). UMMZ 224226-31 (RAN 54202, 54205-6, 54242, 54324, 54439), 8-12 March 1996, Bemaraha Reserve, Antranopasasy River, 18°42.481'S, fade to

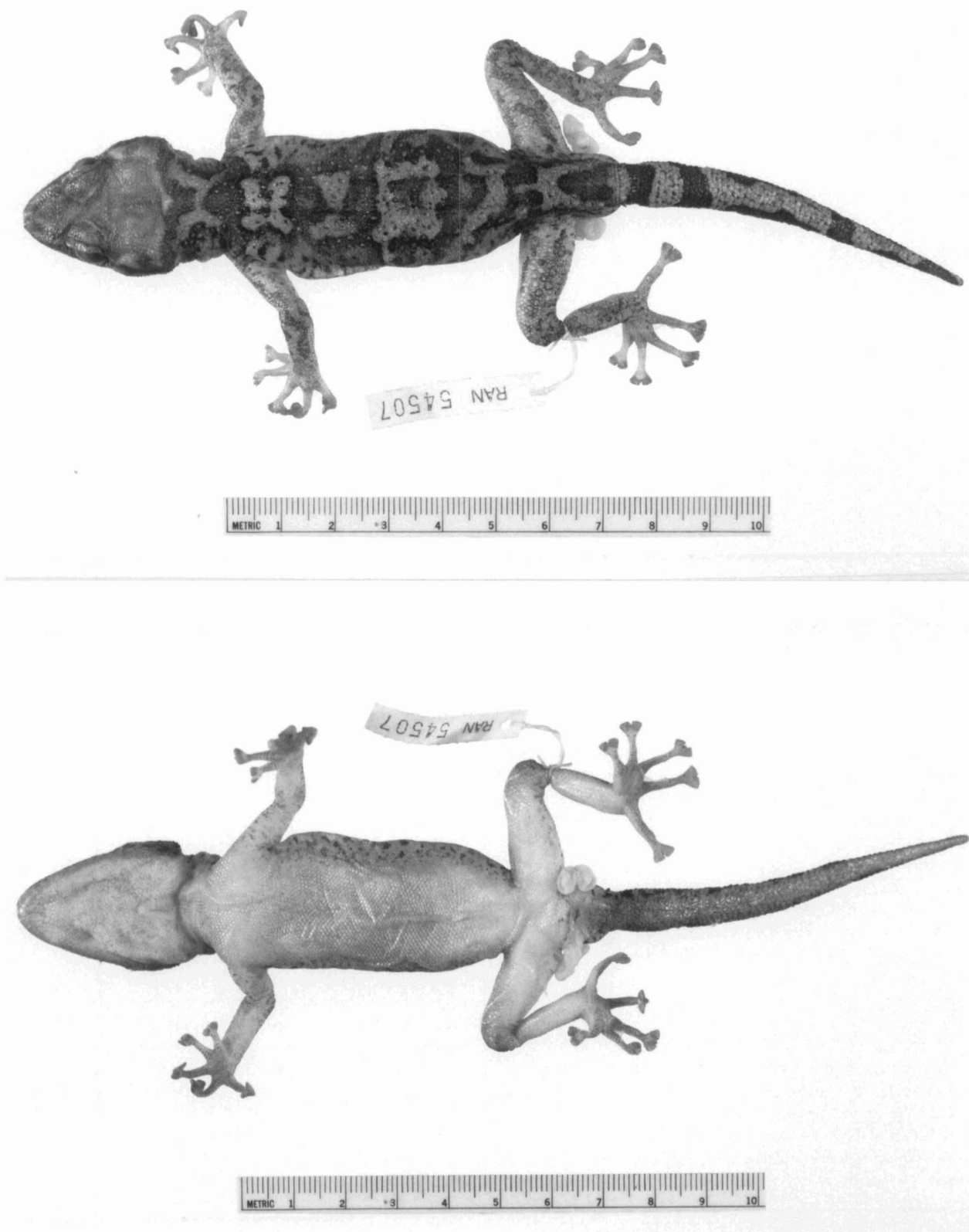


Figure 7. Holotype (UMMZ 224225; RAN 54507) of *Paroedura tanjaka*.

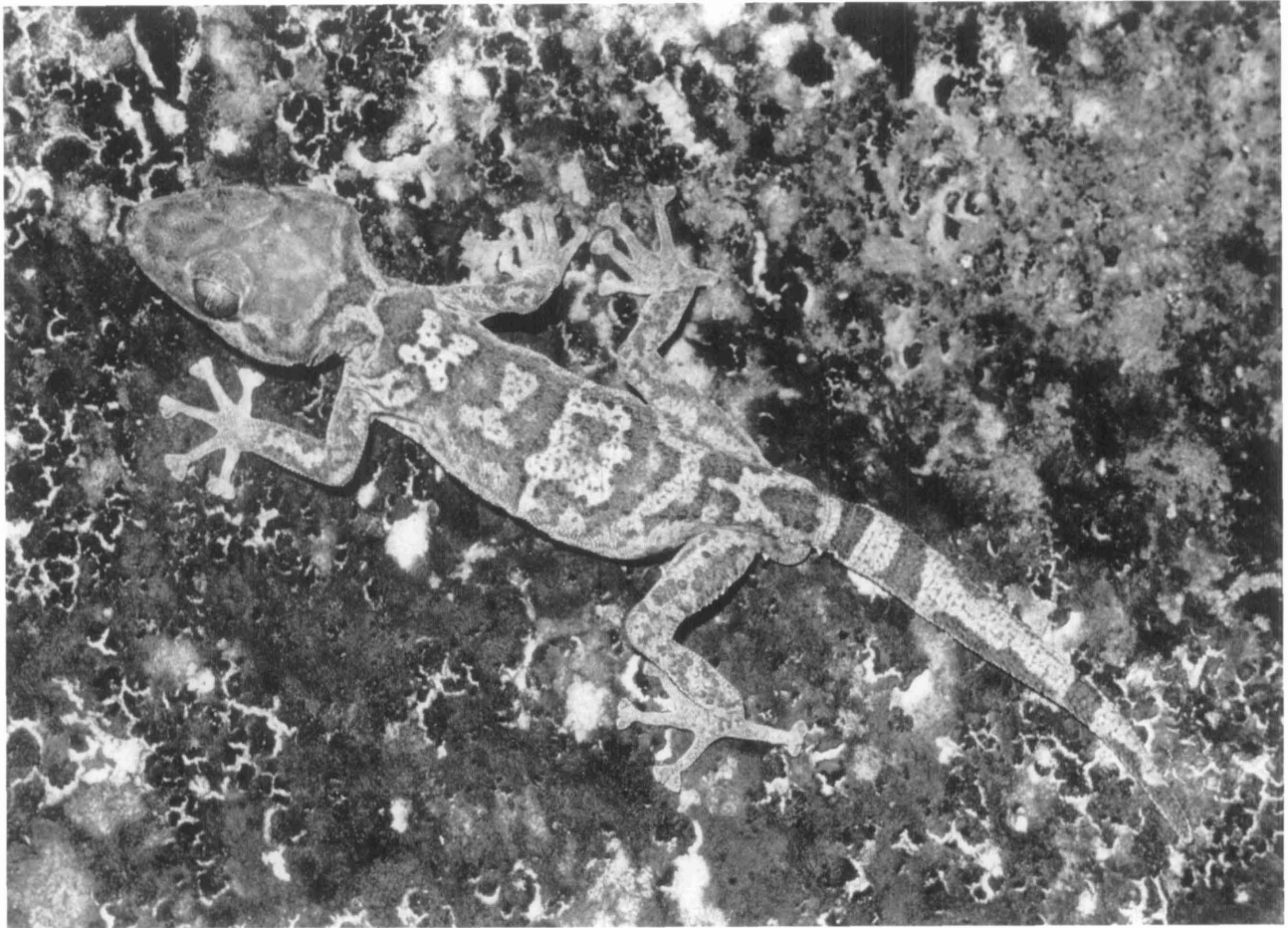


Figure 8. *Paroedura tanjaka* holotype in life.

44°42.981'E, 130-200 m elevation, Antsalova Fivondronana. UMMZ 224234-5 (RAN 54585-6), 20 March 1996, Bemaraha Reserve, Manambolo, 19°08'S, 44°50'E, 100-300 m elevation, Antsalova Fivondronana. UMMZ 219232-8 (RAN 55593-4, 55623-7) 4-7 July 1996, Namoroka Reserve, Ambovonaomby, 16°28.32'S, 45°20.82'E, 150-180 m elevation, Soalala Fivondronana. UMMZ 219239-43 (RAN 55647-51), 8 July 1996, Namoroka Reserve, Beritra Lake, Soalala Fivondronana. UMMZ 221987-99, (RAX 34, 36, 95-6, 148, 150-1, 191-2, 232, 267, 270, 275), UMMZ 222038-44 (RAX 32-3, 35, 37, 149, 233, 269); 2-7 December 1996, Namoroka Reserve, 16°28.189'S, 45°20.906'E, 150-180 m elevation, Soalala Fivondronana. All paratypes collected in Mahajanga Province, Madagascar.

Identification. A large, (up to 102 mm snout-vent length), robust, big-headed *Paroedura*; nostril contacts dorsolateral projection of rostral scale; dorsum with small to moderate-size trihedral tubercles, not arranged in obvious longitudinal rows, separated by smaller tubercles and small flat scales; supraoculars and superciliaries flattened, acarinate; large terminal pads more than twice the width of digits at base of pads; dorsolateral coloration of adults, irregular pattern of light brown blotches, marbling and transverse bands on lighter grayish ground color; cranium distinctly different in coloration from neck and body, immaculate tan, delimited posterolaterally by light line; hatchlings dark brown to black dorsolaterally with three vivid white crossbands; distinct crossbands and blackish dorsolateral color of hatchlings

adult pattern during ontogeny of juveniles and subadults; unregenerated tails with alternating light and dark bands that usually do not cross ventral surface; regenerated tail less distinctly banded, usually with irregular light and dark markings; cranium light tan dorsally, bordered posterolaterally by light line.

Description of holotype. Excellent condition, small slit posteriorly on left side; tail complete, regenerated; hemipenes extruded; testes ellipsoidal (5 mm long), white; vasa deferentia enlarged, white.

Measurements and counts in Table 4. Head large, 0.34 times snout-vent length, much wider than neck, as wide as body; cranium square, flat on top; snout slopes steeply downward in front of eyes, 1.45 times longer than horizontal eye length; canthal ridges prominent, canthal bridge concave in front of eyes, flat near nostrils; nostrils visible from above; ear openings nearly vertical slit, slanted slightly posteriorly at upper end, positioned below posterolateral corner of cranium, not visible from above; body stout, slightly depressed; limbs stout, moderately long, forelimb reaches nostril, hindlimb reaches axilla; digits long, terminal pad large, more than twice width of digits at base of pads; tail 0.75 times as long as snout-vent length, regenerated, round in section, tapers gradually to blunt point.

Rostral scale rectangular with dorsolateral projections contacting nostrils, bordered dorsally by pair of prenasals, the latter separated by one small internasal (postrostral); nostril bordered by prenasal, rostral, first supralabial, four small, infra- and

Table 4. Morphometric and meristic variation in *Paroedura tanjaka*: holotype and paratypes from Bemaraha. Measurements in mm.

UMMZ	224225 holo	224231 para	224232 para	224233 para	224234 para	224235 para	224226 para	224227 para	224228 para	224229 para	224230 para
Sex	male	female	female	female	female	female	female	male	female	male	female
Mat	mature	mature	mature	mature	mature	mature	?	?	?	?	?
SVL	102	91	97	91	92	90	78	70	71	74	75
TL	76*	81*	65*	84**	84**	84**	68	37*	—	69	54*
HL	34.9	32.2	35.3	31.5	32.5	32.3	27.0	26.4	25.2	26.0	26.8
HW	24.4	21.9	28.2	22.8	23.5	23.1	17.9	16.4	16.3	17.7	16.4
HD	13.7	12.0	15.6	13.4	11.7	11.8	10.6	9.0	8.5	10.3	9.0
SL	13.3	12.3	13.7	12.2	12.2	12.3	10.5	10.1	9.5	10.3	9.9
ED	9.2	7.1	7.5	8.6	7.5	7.4	6.8	5.9	5.8	6.0	5.9
EO**	5.0x2.2	4.1x1.4	4.6x1.0	4.8x1.7	4.8x1.8	4.8x1.6	3.4x1.8	3.4x1.7	3.4x1.7	3.5x1.7	3.1x1.3
AGL	44	42	42	40	41	40	34	29	32	31	33
Forelimb	38	35	35	36	36	35	28	28	26	28	28
Hindlimb	50	49	49	46	47	52	41	36	37	42	39
Supralab	12-14	14-12	13-13	13-14	14-15	14-12	14-14	12-12	13-12	13-12	13-10
Infralab	11-12	10-10	11-10	12-12	11-10	10-10	12-12	10-11	10-10	10-10	13-11
Sdlm I	9-9	9-9	9-9	10-9	10-10	9-9	8-8	9-9	8-8	8-8	10-9
Sdlm II	13-13	14-13	12-13	14-14	14-13	13-13	12-11	12-12	12-11	12-12	13-12
Sdlm III	15-15	16-16	14-15	16-17	15-16	15-16	13-14	14-14	13-14	13-14	13-14
Sdlm IV	15-16	15-16	14-16	16-18	16-16	16-15	13-14	15-14	15-15	14-15	14-14
Sdlm V	13-12	12-12	11-12	12-12	12-12	12-12	12-11	10-10	11-11	12-11	11-11
Sdlp I	9-9	10-9	9-9	9-9	9-9	9-9	8-8	8-9	8-8	8-8	8-8
Sdlp II	15-15	15-14	15-14	15-14	13-14	14-14	11-12	12-12	13-13	14-12	13-12
Sdlp III	19-18	17-17	16-16	17-19	17-17	17-18	14-15	16-16	17-17	17-16	17-17
Sdlp IV	20-20	18-18	18-19	19-18	19-18	18-19	16-16	18-17	19-18	18-17	17-17
Sdlp V	21-21	19-21	20-21	20-19	20-19	19-20	17-15	18-17	19-18	20-18	18-17

* Missing part or regenerated.

**height x length

postnasals, one larger supranasal; scales around nostrils and canthal bridge near nostrils flat, smooth; remaining head scales above supralabials and row of small scales bordering supralabials weakly tuberculate, those of cranial table especially weakly tuberculate, some flat; supralabials largely smooth, faintly tuberculate posteriorly; supraoculars flat; outer superciliaries large, rectangular, flat, smooth, arranged in single uniform row; inner ciliaries square, flat, aspinous anteriorly and anterodorsally, but each bearing single short spine beginning at posterodorsal corner of eye and behind eye; mental triangular, as wide as rostral; pair of elongate postmentals in medial contact, each bordered laterally by one elongate chin shield; three slightly enlarged chin scales behind postmentals, central one largest; first four infralabials much larger than posterior infralabials; posterior infralabials weakly tuberculate; scales directly below infralabials slightly larger than chin and throat scales; dorsolateral neck and body with scattered, moderately enlarged trihedral tubercles separated by much smaller tubercles and small flat scales, enlarged tubercles not arranged in obvious parallel, longitudinal rows; upper surfaces of limbs with some enlarged trihedral tubercles; upper digits with flat, slightly overlapping scales; large central scale over claw; pygal region tuberculate dorsally, bearing pair of conical tubercles, one on each side, above lateral edges of cloaca; tail scales squarish, flat, smooth, juxtaposed, lacking spines and tubercles (regenerated); ventral scales smooth, granular and juxtaposed on chin and throat, larger and flatter posteriorly on venter; scales under limbs smooth, flat, increasing in size and slightly imbricate distally; scales of palms and soles smooth, small, slightly raised, juxtaposed; subdigital lamellae generally in double row, but with

fusions and other irregularities, smaller near terminal pad, but ultimate subdigital enlarged, lying at base of pad; pair of terminal pilose pads large, each pad rhombic, nearly as long as wide, sides of single pad measuring 2.1-2.4 mm, minimum digit width at base of pad 1.7 mm, width of both pads 4.9-5.1 mm including space between them.

Color after 30 months in alcohol: cranial table and canthal bridge immaculate light yellowish tan, cranial table delimited behind and on sides by lighter border; sides of head light grayish brown with white markings; eyelids white anteriorly; iris light tannish gold; dorsolateral neck and body light gray with distinct light brown marbling and crossbands; lower sides grayish white with brown spots; upper surfaces of limbs colored similarly to body; tail grayish dorsolaterally with few bold light brown crossbands and bars; upper digits gray; venter of head, neck, and body nearly white, heavily dusted with tiny brown spots on chin and throat, lightly dusted with brown posteriorly on venter and under limbs; palms and soles brown, subdigital scales brown; ventral surface of tail uniform, light grayish brown.

Variation. Meristic and morphometric variation for the paratypes from Bemaraha and Namoroka Reserves are summarized in Tables 4 and 5, respectively. Six of 11 specimens from Bemaraha are 90 mm SVL or longer, whereas the largest of 32 specimens from Namoroka is only 84 mm SVL. This strongly suggests that the Bemaraha population has larger average adult body size than the Namoroka population. Because there is an obvious allometric increase in stoutness with size, the adults of Bemaraha appear to be more robust than the larger Namoroka adults. With current samples sizes, there is no detectable geographic variation in meristic and coloration charac-

Table 5. Morphometric and meristic variation in *Paroedura tanjaka*: paratypes from Namoroka. Measurements in mm.

UMMZ	219232 para	219233 para	219234 para	219235 para	219236 para	219237 para	219238 para	219239 para	219240 para	219241 para	219242 para
Sex	female	female	male	female	male	male	female	female	female	female	female
Maturity	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature
SVL	81	79	75	81	74	84	76	65	75	77	78
TL	—	—	58*	54*	68	78	67	58	—	—	69
HL	26.3	26.9	25.2	27.4	26.2	27.2	25.0	23.3	25.4	27.0	25.4
HW	17.4	18.3	17.5	18.1	16.7	18.1	16.5	14.4	16.3	16.8	17.3
HD	10.1	11.0	10.5	10.4	9.8	10.9	10.1	8.6	9.8	9.7	10.1
SL	10.3	11.3	10.8	10.7	10.2	10.6	10.3	9.4	9.7	10.6	10.4
ED	6.5	7.3	6.2	6.9	5.5	7.0	6.4	5.6	5.6	6.1	5.8
EO**	3.8x2.5	4.2x1.5	3.5x1.4	3.2x1.0	3.8x1.5	4.0x1.8	3.4x1.6	3.4x1.7	3.0x1.5	3.8x2.1	3.5x1.1
AGL	38	38	31	36	31	35	34	30	37	34	38
Forelimb	33	32	32	33	30	32	31	30	31	30	32
Hindlimb	43	46	44	47	43	46	45	40	40	43	44
Supralab	13-13	14-14	14-13	12-13	13-14	15-15	14-15	13-14	13-12	13-12	13-14
Infralab	9-11	11-11	11-10	10-10	12-11	11-11	11-12	10-11	10-11	11-10	11-11
Sdlm I	9-9	8-7	10-11	9-9	9-9	9-9	9-10	8-9	9-9	9-9	9-9
Sdlm II	12-10	12-11	11-11	11-11	11-11	12-12	11-11	11-12	11-11	11-11	11-10
Sdlm III	13-14	14-13	14-13	13-14	14-14	14-13	14-13	13-13	13-13	14-13	12-12
Sdlm IV	13-14	13-13	15-15	13-14	14-14	15-15	13-12	13-13	13-14	14-14	13-14
Sdlm V	11-12	11-11	13-12	14-11	13-13	12-12	12-12	10-11	11-11	12-12	12-12
Sdlp I	9-9	10-9	10-10	10-10	9-9	10-9	9-9	9-7	8-9	8-9	9-8
Sdlp II	14-14	14-13	15-14	13-13	12-13	12-12	13-13	11-12	11-12	12-12	12-11
Sdlp III	15-15	16-14	16-16	16-14	14-15	16-15	15-15	15-15	15-14	15-15	15-16
Sdlp IV	17-18	16-17	17-18	17-16	17-17	17-16	16-16	17-17	15-16	17-16	18-16
Sdlp V	16-18	18-16	18-17	18-16	17-17	17-18	18-18	15-15	16-16	16-17	16-16

*Missing part or regenerated.

**height x length

(Continued below.)

Table 5. (Continued.) Morphometric and meristic variation in *Paroedura tanjaka*: paratypes from Namoroka.

UMMZ	219243 para	221987 para	221988 para	221989 para	221990 para	221991 para	221992 para	221993 para	221994 para	221995 para	221996 para
Sex	male	female	male	male	male	male	male	female	male	male	male
Maturity	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature
SVL	77	75	78	79	75	77	79	63	62	78	79
TL	71	69	70	—	—	—	—	—	43*	71*	—
HL	26.2	25.3	27.1	28.5	25.2	27.0	26.4	22.9	21.1	24.9	26.2
HW	18.4	16.3	16.8	18.7	16.9	17.5	18.0	14.1	13.7	17.1	17.3
HD	11.4	9.2	9.1	10.8	10.0	11.1	10.8	9.4	9.1	10.5	11.0
SL	10.6	10.6	10.6	10.8	10.0	11.1	10.8	9.4	9.1	10.5	11.0
ED	6.6	5.9	6.4	6.4	6.4	6.3	6.5	5.7	4.8	6.2	6.4
EO**	3.5x1.5	3.4x1.2	3.7x1.2	3.8x1.4	3.8x1.1	3.8x1.1	3.6x1.4	3.2x1.3	3.0x1.2	3.1x1.0	3.8x1.3
AGL	34	35	36	39	36	39	38	27	30	36	35
Forelimb	35	30	32	36	31	30	30	28	26	32	32
Hindlimb	45	43	46	49	46	42	45	40	35	45	46
Supralab	13-14	13-14	15-15	—	14-14	15-15	15-15	15-14	14-13	15-14	14-14
Infralab	11-12	11-12	12-12	—	11-12	12-11	12-12	11-11	10-11	12-12	11-11
Sdlm I	9-8	9-9	9-9	9-	9-9	9-8	8-9	9-8	8-9	10-9	9-9
Sdlm II	11-11	11-12	10-11	12-12	11-12	11-12	11-12	12-11	12-12	12-12	11-12
Sdlm III	13-13	13-14	13-14	15-15	14-14	12-14	13-14	14-12	13-13	14-15	15-14
Sdlm IV	13-13	14-14	13-14	15-15	14-15	13-15	13-15	13-12	13-13	13-15	14-14
Sdlm V	11-13	12-12	12-12	12-12	12-12	11-12	12-12	10-10	12-11	11-11	12-12
Sdlp I	9-9	9-9	9-9	9-8	8-8	8-8	9-8	7-8	9-8	10-9	9-9
Sdlp II	11-13	13-13	11-11	12-12	12-12	12-12	12-11	11-12	12-13	13-11	11-12
Sdlp III	15-15	15-15	14-15	15-15	15-16	15-15	15-15	15-13	15-15	15-15	16-15
Sdlp IV	17-16	17-17	16-15	15-15	17-17	15-16	16-16	15-15	15-16	16-17	17-18
Sdlp V	17-18	17-15	17-16	17-17	15-15	16-16	17-16	16-17	16-16	17-17	18-18

*Missing part or regenerated.

**height x length

(Continued on next page.)

Table 5. (Continued.) Morphometric and meristic variation in *Paroedura tanjaka*: paratypes from Namoroka.

UMMZ	221998 para	221999 para	222038 para	222039 para	222040 para	222041 para	222042 para	222043 para	222044 para
Sex	male	male	female	male	female	female	female	female	female
Maturity	mature	?	mature	mature	mature	mature	mature	mature	mature
SVL	76	62	76	83	75	82	73	81	82
TL	69*	55	68	65*	51*	70*	—	58*	73
HL	25.8	21.3	25.3	28.1	25.7	27.7	24.7	26.7	26.8
HW	17.0	13.7	16.5	18.1	16.1	17.3	16.1	17.6	17.5
HD	10.0	8.2	9.8	10.3	9.2	10.3	9.6	10.4	10.0
SL	10.9	9.4	10.0	11.4	10.2	11.1	10.4	10.3	10.6
ED	6.1	5.1	5.9	6.6	6.3	6.8	5.5	6.0	6.7
EO**	3.7x1.3	3.0x1.0	3.5x1.0	3.9x1.6	3.5x1.1	3.5x1.1	3.1x0.8	4.2x1.0	3.5x0.8
AGL	36	28	36	40	34	38	33	38	41
Forelimb	31	27	32	34	30	33	28	30	34
Hindlimb	44	36	43	44	40	44	40	44	49
Supralab	14-14	14-14	14-14	14-14	14-15	12-14	14-14	13-14	—
Infralab	12-11	10-10	12-11	11-11	12-11	11-10	11-11	11-11	—
Sdlm I	9-9	9-9	9-9	9-9	8-9	9-9	10-9	10-9	8-8
Sdlm II	12-11	10-11	11-13	11-12	11-11	12-11	12-11	11-11	11-10
Sdlm III	13-13	12-14	15-15	14-13	14-15	14-14	13-13	14-14	14-13
Sdlm IV	14-14	12-13	15-15	14-13	14-14	14-15	14-14	15-14	13-13
Sdlm V	12-12	11-11	12-12	11-11	12-12	11-11	12-12	12-12	11-11
Sdlp I	10-9	9-9	9-9	8-9	10-9	9-9	9-9	9-10	8-7
Sdlp II	12-12	12-13	13-13	12-12	13-12	12-12	13-12	12-12	11-11
Sdlp III	16-14	14-15	15-15	15-14	16-16	14-15	15-15	15-16	15-16
Sdlp IV	17-17	16-16	16-18	16-17	16-17	15-15	16-17	18-16	17-16
Sdlp V	18-17	17-17	18-18	15-17	16-17	15-16	16-16	17-17	16-15

*Missing part or regenerated.

**height x length

ters. There is no evident sexual dimorphism other than that typically associated with the pygal portion of the tail in geckos. Sexual dichromatism is not apparent.

Three of the Bemaraha paratypes have two internasals (postrostral) scales between the prenasals instead of one, as in the holotype. All but two of the 32 Namoroka paratypes have a single internasal scale; the two exceptional individuals have no internasals.

Hatchlings and adults differ markedly in dorsolateral coloration of the body. The pattern of color change with age is paralleled by other species of *Paroedura*, notably *Paroedura bastardi* and *P. picta*. The change is from a distinctly white banded pattern in a dark, nearly black, matrix in hatchlings to one of obscured banding or dorsal blotching in older (larger) individuals. A hatchling paratype (UMMZ 221997), 31 mm SVL, has a light brown head, light brown limbs, and tail (upper surfaces), and a nearly black (dark purple brown) body with three vivid, white, even-edged transverse bands continuous with the white ventral coloration. The first white band is over the shoulder, the second is much wider and is positioned at midbody, and the third, which is narrow like the shoulder band, is over the hindlimbs. The venter is grayish white. The three white bands of juveniles are still clearly evident, but less vivid in small adults. The bands have changed to light gray, are edged in dark brown, and have darker, brown, irregular markings within them. The light border of the cranium is more distinct in larger specimens, and the tail is more irregularly banded.

Distribution. *Paroedura tanjaka* is found only in Bemaraha and Namoroka Reserves in west-central Madagascar (Fig 3).

Etymology. The specific name “*tanjaka*” (tawn zaka) is a Mala-

gasy word meaning “strength,” and is used as an unlatinized specific epithet.

Remarks. *Paroedura tanjaka* differs from other members of the *sanctijohannis*-Group as follows. It lacks the spiny vertebral ridge of *P. gracilis* and the spiny tail and white head spots and white transverse bands of *P. masobe*. It is more robust and has shorter limbs than *P. homalorhina*. The slender hindlimbs of *P. homalorhina* reach forward to the back of the head, whereas they fall short of the axilla in *P. tanjaka*. *Paroedura tanjaka* has small dorsal tubercles not arranged into regular rows, in contrast to *P. sanctijohannis*, *P. stumpffi*, *P. karstophila*, and *P. vazimba*, all of which have the larger dorsal tubercles disposed into longitudinal rows; and it is much larger (up to 102 mm SVL) than all of them. *Paroedura tanjaka* is larger than *P. oviceps* (maximum SVL = 68 mm) and differs from it in coloration. The dorsal ground color of *P. tanjaka* is light tannish brown compared to darker brown in *P. oviceps*. The head of *P. oviceps* does not differ markedly in coloration from the neck and body (brown with irregular darker markings), whereas the cranium of *P. tanjaka* is clearly demarcated as a squarish, immaculate light brown or tannish shelf. The snout of *P. tanjaka* is also often immaculately tannish.

Superficially, *Paroedura tanjaka* resembles *P. bastardi* and may have been confused with this species.

Paroedura tanjaka has been found only at relatively low elevations (100-300 m) in dry deciduous forest habitats associated with karst topography. All individuals were collected while they were active at night (20:00-22:30 hr). Most were found on the bases of tsingy cliffs from 1.0 to 4.0 m above ground. At Bemaraha, some individuals were collected on branches and tree

trunks 0.5 to 2.5 m above ground. One specimen (UMMZ 224231) was found during the day, in a cave, 30 m from the entrance. Another (UMMZ 221997) was taken from the stomach of a snake (*Lycodras gaimardi*, UMMZ 222438).

Paroedura vahiny n. sp.

Figures 9 and 10

Holotype. UMMZ 224236 (RAN 51463), mature female, collected 27 January 1996 at Dabara Forest, 20°22.446'S, 44°50.854'E, 150 m elevation, Mahabe Fivondronana, Toliara Province, Madagascar by A. P. Raselimanana, C. J. Raxworthy, and Angelin and Angeluc Razafimaintysoa.

Paratypes. None.

Other specimens. MNHN 1984-420 (2001/L), 23 January 1969, "15 km sud (?) Manja." Manja is a town lying about 130 km SSW of the type locality of this species, Manja Fivondronana, Toliara Province, Madagascar. This specimen, discovered in the Paris Museum after the holotype was described, fits the description of *Paroedura vahiny* in every detail.

Identification. A small *Paroedura* (42 mm snout-vent length); nostril excluded from contact with rostral scale by prenasal scale; digits nearly cylindrical, slightly dorsoventrally flattened; terminal pads small, barely wider than digits; head scales small, tuberculate, multicarinate, homogeneous, except few enlarged scales on side of head behind eyes; dorsolateral neck and body scales with scattered enlarged, multicarinate tubercles separated by 2-6 much smaller tubercles; all remaining scales (except subdigitals and those of palms and soles) small, regionally uniform in size, tuberculate, largely non-overlapping, and multicarinate; head uniform brown dorsolaterally, except supralabials, infralabials and rostral, which are boldly spotted with white; dorsolateral neck, body, upper surfaces of limbs, nearly uniform brown, except four very faint M- or W-shaped dorsal crossbands along neck and back; tail dark brown with few lighter, dorsal crossbands anteriorly and more numerous, smaller white crossbands ventrally; chin, throat, and lower jaw region conspicuously marked with large, often circular, white patches separated with narrow brown borders; ventral surfaces of neck, body, and limbs dirty white (white with numerous, nearly microscopic, brown spots). Distinguished from all other *Paroedura* by presence of multicarinate scales on ventral surfaces.

Description of holotype. Well-preserved, tail complete, original (Fig. 9). Small slit on left side of posterior abdomen. Left ovary with developing white ova, right side with one white, nearly round (5.8 x 4.2 mm), shelled, oviductal egg.

Measurements (mm); snout-vent length 42; tail length 34; head length 12.7; head width 8.2; snout length 4.8; horizontal eye diameter 3.2; ear opening 1.0 x 0.5; axilla-groin length 18.0; forelimb length 13.2; hindlimb length 18.5.

Counts: supralabials (left, right) 12-12; infralabials 10-11; subdigital lamellae, manus, I-V (left, right) 6-6, 9-9, 10-10, 10-10, 8-8; pes 6-6, 8-8, 12-11, 11-12, 10-11.

Head ovate, much wider than neck, narrower than body; cranium flat dorsally; snout short, 1.5 times longer than horizontal eye diameter, sloping sharply downward in front of eyes; distinct canthal ridges, canthal bridge concave near eyes, flat near nostrils; pupil vertical, borders crenate; ear small, vertical; body moderate build, slightly depressed; limbs

moderate, forelimb reaches barely past eye to loreal region; hindlimb laid forward fails to reach axilla by 5 mm; fingers and toes short, subcylindrical, tips barely expanded, small claws between pair of tiny terminal, pilose pads, each pad rhombic with rounded corners, about 0.4 mm across; tail short, 0.81 times snout-vent length, constricted at rounded base, swollen and slightly laterally compressed in midsection, tapering abruptly to short, sharply pointed terminal portion.

Rostral scale rectangular, bordered dorsolaterally by smooth prenasal, middorsally by three small keeled tubercles between the prenasals; nostril bordered anteriorly by prenasal, ventrally by two, small, flat, smooth scales, posteriorly by one flat, smooth postnasal, above by two, small, multicarinate tubercles; dorsolateral head scales nearly uniformly small, tuberculate, multicarinate; few enlarged tubercles on side of cranium behind eyes; skin on top of cranium co-ossified with underlying bone; supraocular and superciliary scales multicarinate; mental smooth, triangular, slightly narrower at lip than rostral, two smooth postmentals, roughly hexagonal, partially separated anteriorly by apex of mental, partially separated posteriorly by first small chin scale, contacting first infralabial and small, smooth chin shield laterally; dorsolateral scales of neck and body heterogeneous, with scattered, enlarged, approximately trihedral, multicarinate tubercles among much smaller multicarinate tubercles of similar shape; each enlarged dorsolateral tubercle separated by 2-6 smaller tubercles; remaining scales, except subdigitals and those on palms and soles, multicarinate and regionally homogeneous (no enlarged spines or tubercles among smaller scales), regionally varying from small, juxtaposed to larger, flatter, and slightly overlapping posteriorly (distally on limbs); scales of palms and soles raised, rounded, smooth; subdigital scales smooth, rounded, generally arrayed in double row, penultimate subdigital pair flattened, enlarged, resting at base of small terminal, pilose pads.

Color, after 18 months in preservative: dorsolateral surfaces generally dark brown, head uniformly so, neck with very faint, light dorsal patch, body with three, light, M- or W-shaped dorsal crossbands, first behind forelimbs very faint, second in front of hindlimbs gray and prominent, third over hindlimbs faint; lower sides of body with scattered, small, white spots usually confined to a single scale; upper surfaces of limbs dark brown with few small white spots; dorsal surface of fingers and toes dark brown with few white spots; tail dark brown with two broad, lighter gray crossbands anteriorly and dorsolaterally, more frequent, narrower, white crossbands and spots on ventral surface; pupil black; anterodorsal eyelash scales white; supralabials, mental, and infralabials with white spots; chin, anterior throat, and lower jaw area conspicuously marked with large, often circular white areas outlined with dark brown pigmentation; ventral surfaces of neck, body, and limbs whitish with tiny dark brown spots; subdigital scales, palms, and soles dark brown. The color in preservative has hardly changed from the color in life.

Etymology. The specific name "*vahiny*" (vuh he nee), a Malagasy word suggesting a newcomer or stranger, refers to the "new one" among the *Paroedura* species.

Distribution. Known only from the type locality and near Manja in west-central Madagascar.

Habitat. The holotype was collected at 22:00, 7 cm above ground on a plant stem in deciduous forest.

Remarks. *Paroedura vahiny* is likely to be confused only with *P.*

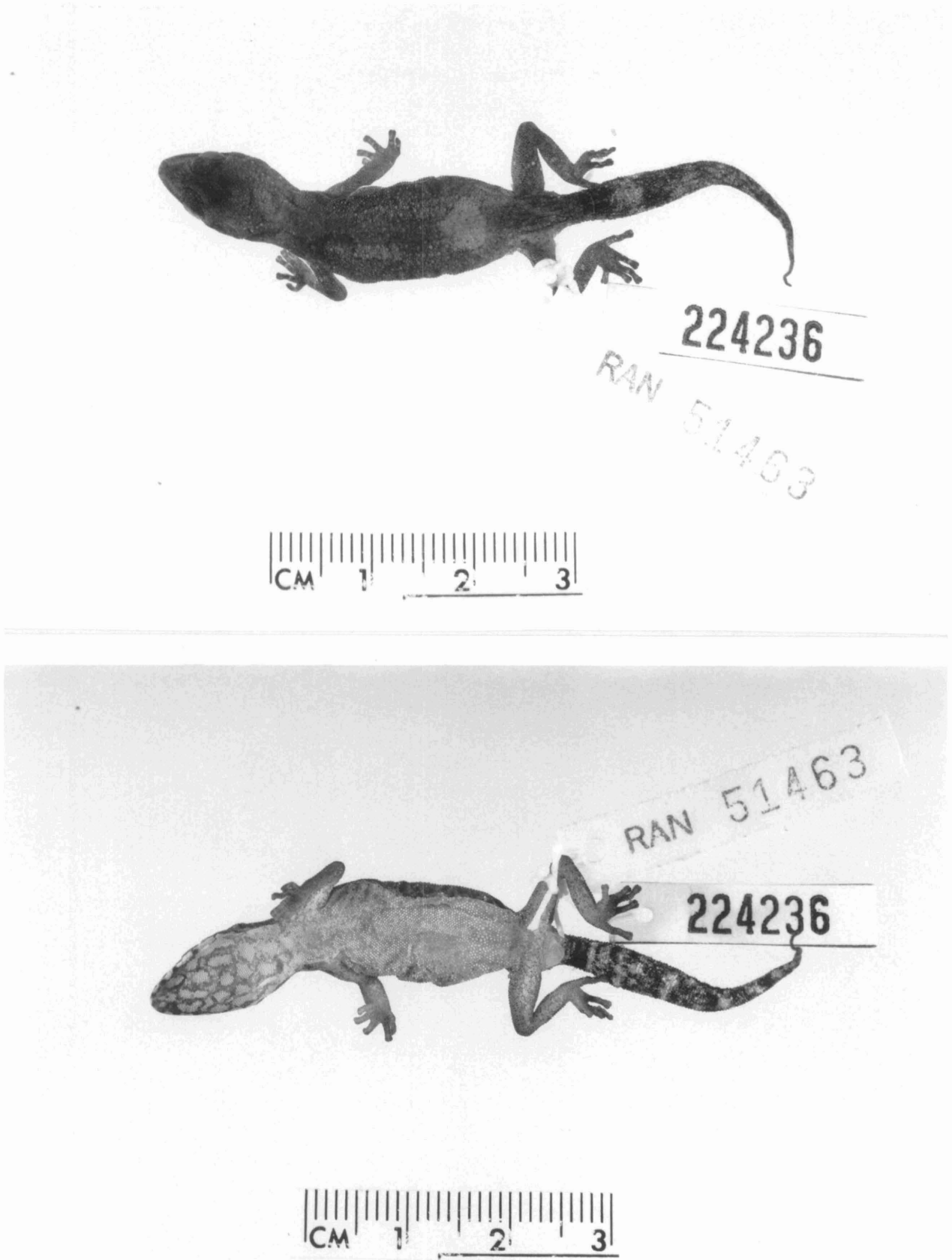


Figure 9. Holotype (224236; RAN 51463) of *Paroedura vahiny*.

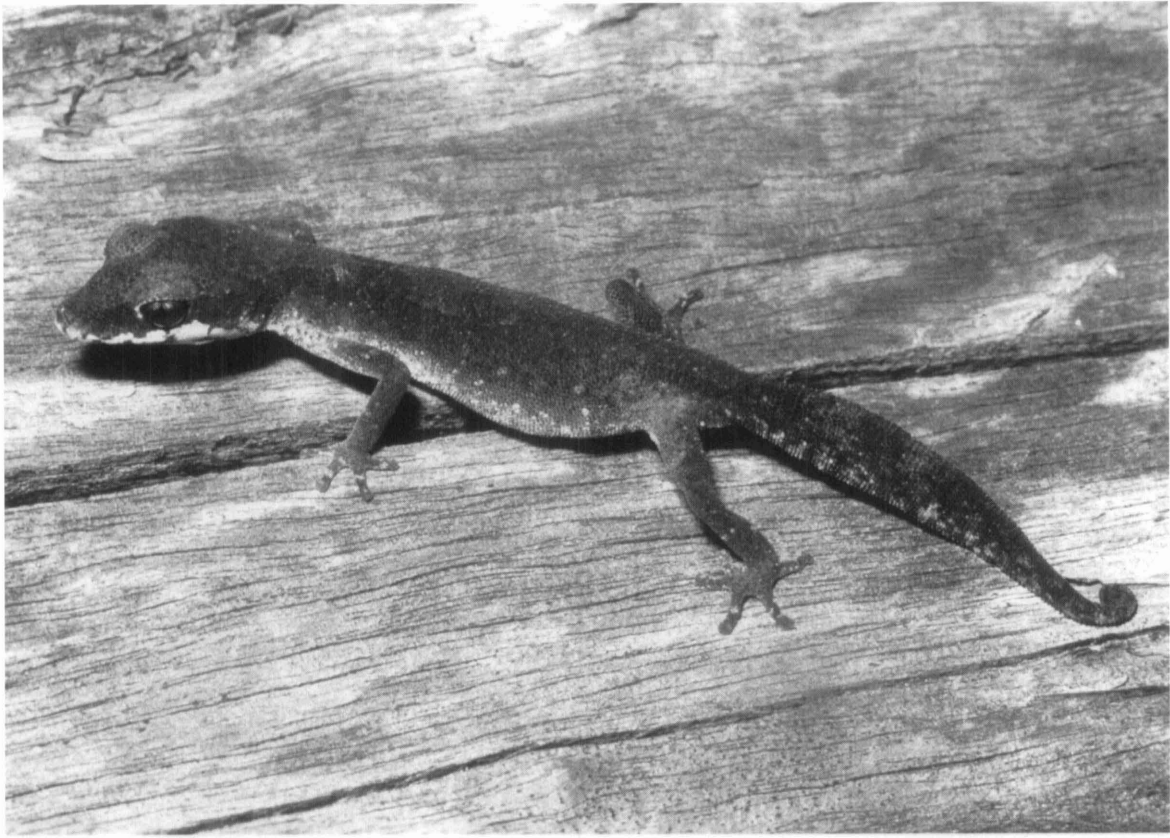


Figure 10. Holotype of *Paroedura vahiny* (upper) in life compared to living *Paroedura androyensis* (lower) from southeastern Madagascar. The smoother skin of *P. vahiny*, resulting from smaller more uniform dorsal scales, is apparent.

androyensis, which is similar in size, shape, digital morphology, and coloration. However, *P. vahiny* has a much smoother appearance because of having smaller scales on the head and body (Fig. 10), smaller enlarged tubercles on the neck and body, and smaller, homogeneous tail scales. The enlarged dorsolateral tubercles on the neck and body of *P. androyensis* are arranged roughly in longitudinal rows, whereas those of *P. vahiny* are randomly scattered. Both male and female *P. androyensis* have successive transverse rings of enlarged spines along the tail, one ring at the anterior margin of each tail whorl, separated by 2-4 (usually 3) rows of much smaller scales. These rings of spines are not present on regenerated tails of *P. androyensis*. The tail of the single known specimen of *P. vahiny* appears to be original, and it lacks rings of spines, which is consistent with having smaller, more homogeneous scales on other parts of the body. The postmental scales of *P. vahiny* are much longer than wide and are bordered posteriorly by the small, granular chin scales; whereas in *P. androyensis*, the postmentals are nearly as wide as long and are bordered posteriorly by at least one enlarged chin scale, often centrally placed. *Paroedura vahiny* has multicarinate ventral scales (smooth in *P. androyensis*), a uniformly dark colored head dorsolaterally (dorsum of head lighter than side of head in *P. androyensis*), and a less boldly marked dorsum (Fig. 10).

Paroedura androyensis and *P. vahiny* are the only species of the genus with multicarinate scales. The keeling of the scales is more strongly expressed in *P. vahiny*. Generally, there are three types of multicarinate scales in these two species. Firstly, the larger, nearly trihedral, dorsal tubercles have a large, longitudinal, central keel on a ridge with several smaller, secondary keels of variable length extending from the base of the scale up toward the central keel on all sides of the central keel. Often the enlarged dorsal tubercles of *P. androyensis* have only slightly roughened surfaces around the central keel rather than distinct secondary keels, and the strength of expression of secondary keels varies between individuals in this species. Secondly, the smaller, nearly granular scales lack a primary central keel, are conical rather than trihedral in shape, and have several small, irregular keels extending up the slope of the cone on all sides. Thirdly, the flatter scales, for example on the posterior abdomen and distal undersurface of the limbs of *P. vahiny*, usually have three, nearly parallel, longitudinal keels. Multicarinate scales is a seemingly derived character state and strongly suggests that *P. androyensis* and *P. vahiny* are sister-species. Keeling on the ventral scales is a further derived state found only in *P. vahiny* among *Paroedura* species.

***Paroedura vazimba* n. sp.**

Figures 11 and 12

Holotype. UMMZ 210515 (RAN 49568), adult female, collected 13 April 1995, at Botanical Garden B, Ampijoroa Forest Station, 16°19'S, 46°49'E, 90 m elevation, Marovoay Fivondronana, Mahajanga Province, Madagascar by Angelin and Angeluc Razafimanantsoa.

Paratypes. UMMZ 210516-8 (RAN 49658, 49731-2), adult females, collected 9-18 April 1995 at type locality by C. J. Raxworthy and Angelin and Angeluc Razafimanantsoa; UMMZ 210519 (RAN 49747), adult female, collected 19 April 1995 at Ampijoroa Forestry Station, Vavaran, Marovoay River, 16°17'S, 46°54'E, 90

m elevation, Marovoay Fivondronana, Mahajanga Province, Madagascar by C. J. Raxworthy and Angelin and Angeluc Razafimanantsoa; UMMZ 216551-8 (RAN 51924-6, 51957-60, 54008), 17-19 February 1996, Antsaravy River, Bora Reserve, 14°51.047'S, 48°13.582'E, 100 m elevation, Antsohihy Fivondronana, Mahajanga Province, Madagascar, C. J. Raxworthy and Angelin and Angeluc Razafimanantsoa.

Other specimens. None.

Identification. A small *Paroedura* (maximum snout-vent length 49 mm); rostral with dorsolateral processes that contact nostrils; first supralabial in contact with nostril; supraocular and superciliary scales keeled; dorsal trihedral tubercles moderate size, arranged in poorly defined rows, each tubercle separated from others by 1-3 smaller scales; body somewhat dorsoventrally flattened, no vertebral crest or ridge with double row of closely spaced tubercles; limbs and digits relatively short; forelimb laid forward extends to loreal region or nostril, never extending anterior of snout tip; double row of weak subdigital lamellae; fewer than 12 lamellae beneath 4th digit of manus, fewer than 15 below the 4th digit of pes; grayish brown dorsum with four broad W- or M-shaped dark transverse bands, first on neck, fourth above hindlimbs; light patch between first and second dark dorsal transverse bands squarish, confined to dorsum, without lateral extensions to insertions of forelimbs (Fig. 12); no dark mask from nostril to back of head.

Description of holotype. (Fig. 11), well preserved, no damage, a small slit posterolaterally on venter.

Measurements and counts in Table 6. Head only slightly wider than neck, slightly narrower than body, 1.5 times longer than wide. Skull flat behind orbits. Snout nearly same length as postorbital section of skull, sloping sharply downward anteriorly, shallow depression between distinct canthal ridges in front of orbits. Eyes directed slightly anteriorly, horizontal diameter 0.63 times snout length. Ear opening small, nearly vertical slit, not visible from above. Fore- and hindlimbs relatively short, appressed forelimb barely reaches nostril, appressed hindlimb falls short of axilla by about one toe length. Fingers and toes moderately long, third finger longest, only slightly longer than second and fourth; third toe longest. Tips of fingers and toes slightly expanded with an enlarged pair of terminal lamellae below each terminal phalanx, no separate claw-bearing segment. Claws small, curved down between terminal lamellae, do not extend beyond tips of digits. Tail complete, original, 0.87 times snout-vent length, postpygal portion slightly laterally compressed anteriorly (4.2 mm wide, 4.5 mm deep), round posteriorly, tapering abruptly then gradually to a fine point.

Nostrils in contact with rostral, first supralabial, two supranasals, and four postnasals. Supranasals adjacent to rostral separated by single granular scale. Rostral rectangular, much wider than tall, with pair of small dorsolateral processes touching nostrils. Supraocular and superciliary scales keeled. First supralabial tallest. Supra- and infralabials smooth (not tuberculate) throughout. Mental triangular, narrower than rostral, excluded from contact with first supralabial. Postmentals paired, hexagonal, longer than wide, in contact with each other medially, anteriorly with mental and first infralabials, laterally with an elongate chin shield, posteriorly with a large central chin shield, and posterolaterally with a smaller chin shield.

Skin on top of cranium co-ossified with underlying bones.

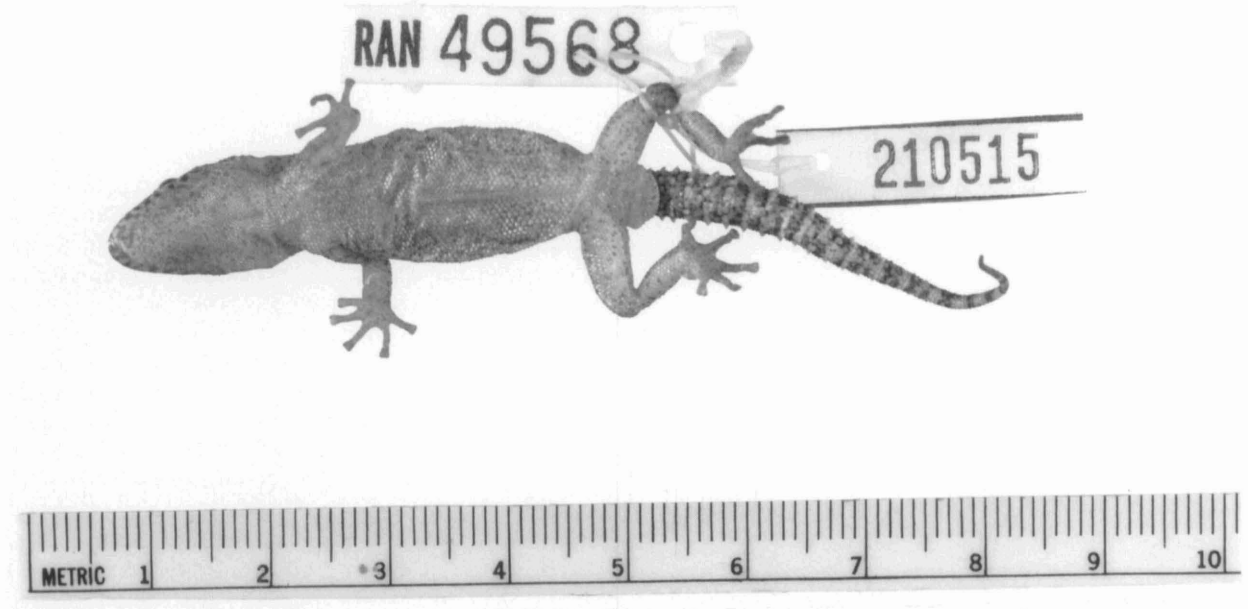
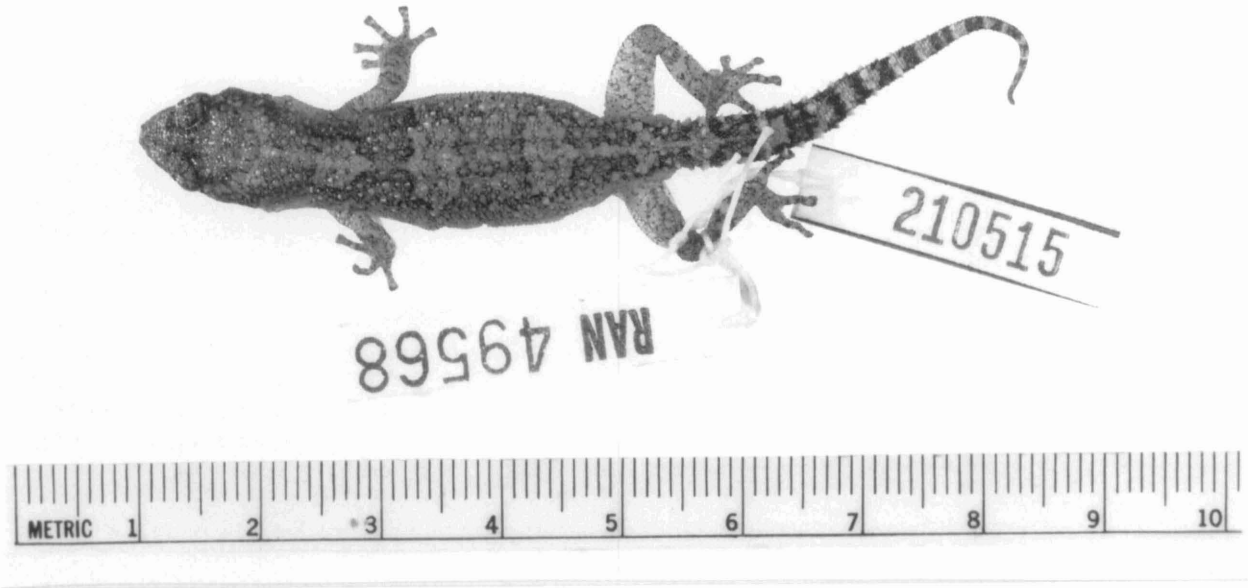


Figure 11. Holotype (UMMZ 210515; RAN 49568) of *Paroedura vazimba*.

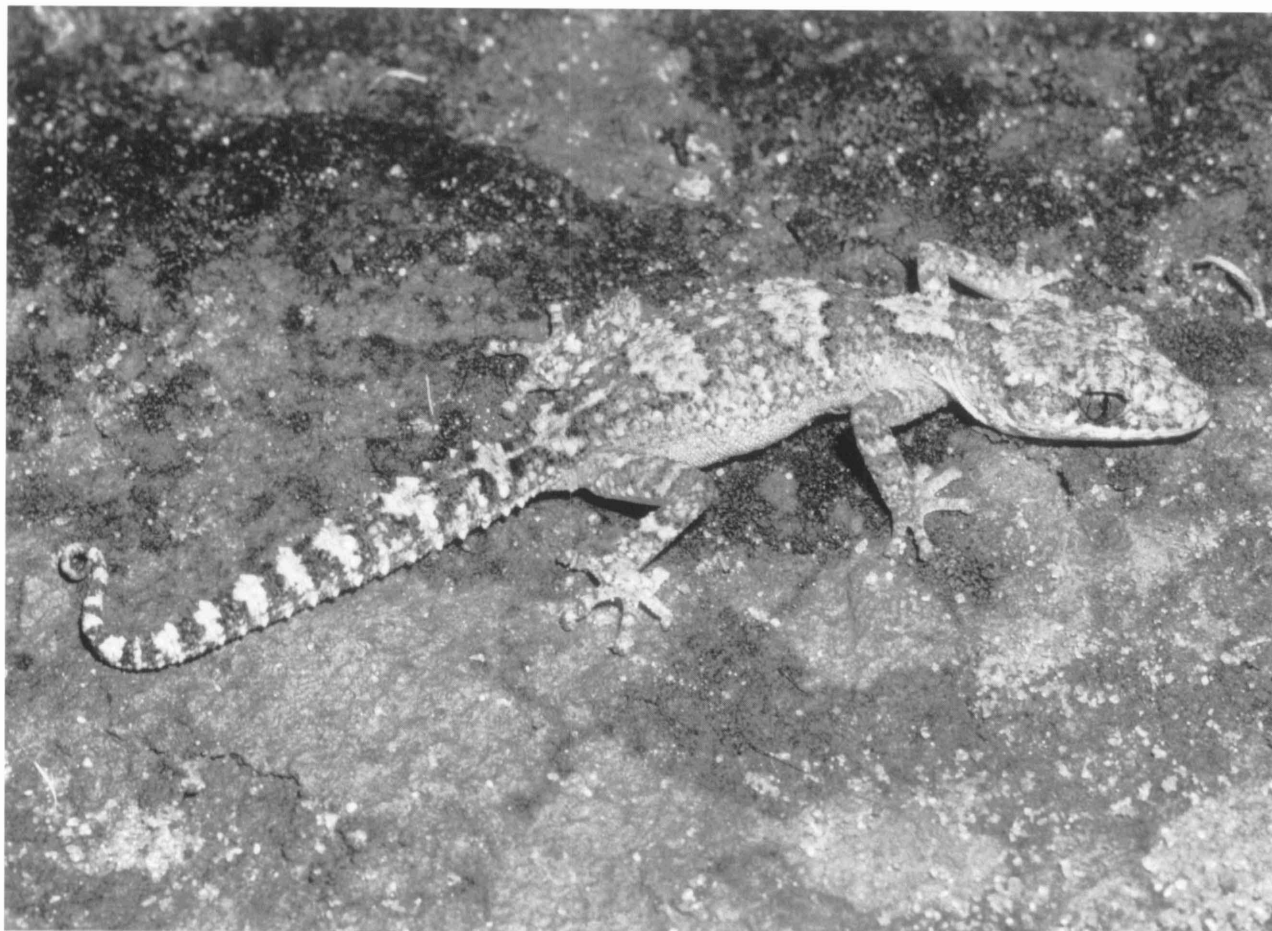


Figure 12. *Paroedura vazimba* in life from type locality. Note that the first light colored dorsal mark (above the forelimbs) does not extend down to the area of the forelimb insertion. Compare this color pattern to that of *P. karstophila* (Fig. 5).

Dorsolateral scales heterogeneous; tubercles on back of head, neck, body, and upper surfaces of limbs separated by 1-3 smaller scales; largely trihedral tubercles on body in about 12 poorly defined longitudinal rows. Tops of hands, feet, and digits with imbricate scales, lacking tubercles. Dorsolateral scales of postpygal tail with 21 transverse rows of tubercles decreasing from 6 to 2 tubercles per row posteriorly, rows of tubercles separated by about 3 rings of smaller imbricate scales, last 12 mm of tail without tubercles. Ventral scales homogeneous. Chin and throat scales granular, slightly separated; chest and belly scales flat, slightly separated or juxtaposed, larger in umbilical region. Undersurface of limbs and tail with small, slightly imbricate scales. Palms and soles with granular juxtaposed scales. Underside of digits with double row of lamellae, pair of pilose terminal pads on each digit, each pad about 0.5 mm wide.

Color (after 48 months in alcohol): Top and sides of head light brown with irregular darker markings, especially above the orbits; supra- and infralabials white with dark brown spots; dorsum of neck and body with four broad, dark, transverse bands with irregular borders (M- or W-shaped), the first just behind the head, the second just behind the shoulders, third at midbody, fourth over groin; dorsal surfaces of limbs gray with irregular lighter and darker markings; tail with alternating dark brown and white bands dorsolaterally, the white bands covering the transverse rows of tubercles where they occur proximally. Ven-

tral surfaces of head, neck, body, and limbs white with numerous tiny brown spots especially dense laterally on ventral surfaces of body and lateral regions of underside of head; ventral surface of tail banded, but less distinctly so than dorsolateral surfaces. The color has faded only slightly in preservative; the pattern is unchanged.

Variation. Morphometric and meristic variation among the types is summarized in Table 6. Some paratypes have a slightly darker brown dorsal ground color than the holotype. In two specimens, the darker dorsal bands of the body are divided at midline by a thin vertebral white line; in UMMZ 210517, these lines join to form a thin, light, vertebral stripe. The apparently regenerated tail of UMMZ 210519 is without bands, instead it is dark brown with light gray mottling, darker dorsally; there are no transverse rows of enlarged tubercles as on the original tail of the holotype.

The eight paratypes (UMMZ 216551-8) from Bora Reserve, 220 km NNE of the type locality, are similar in size (28-48 mm snout-vent length) and morphometric characteristics to the type series, but differ in coloration. The dorsolateral pattern is the same, but more faintly expressed, and difficult to discern in a few individuals, which are nearly unicolor. Generally, the Bora specimens have a lighter ground color, with fewer brown spots, especially ventrolaterally. A juvenile (UMMZ 216555), not listed in Table 6, measures 29 mm SVL. Despite its small size, it is very

Table 6. Morphometric and meristic variation among types of *Paroedura vazimba*. Measurements in mm.

UMMZ	210515 holo	210516 para	210517 para	210518 para	210519 para	216551 para	216552 para	216553 para	216554 para	216556 para	216557 para
Sex	female	female	female	female	female	male	female	female	female	female	female
Maturity	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature
SVL	45	39	43	47	49	42	39	47	47	46	46
TL	39	—	—	—	28*	13*	42*	37*	—	50	46
HL	14.2	14.0	14.1	15.6	16.1	14.2	13.0	15.1	15.8	14.9	15.2
HW	9.3	7.5	9.0	9.6	10.3	9.0	8.0	9.5	9.2	9.3	8.9
HD	6.4	5.0	5.8	5.9	5.9	6.0	5.3	5.9	6.1	5.9	5.5
SL	5.4	—	5.6	6.1	5.7	5.7	5.2	6.1	6.2	5.9	5.9
ED	3.4	—	3.1	4.4	3.5	3.6	3.3	3.9	4.1	3.9	3.7
EO**	1.5x0.4	1.1x0.2	1.0x0.2	1.2x0.3	1.1x0.3	1.2x0.1	1.0x0.6	1.1x0.6	1.2x0.3	1.2x0.6	0.9x0.5
AGL	20	17	20	22	22	20	16	21	22	21	21
Forelimb	15	14	16	16	16	15	14	15	17	17	15
Hindlimb	21	18	18	21	19	21	19	23	23	24	22
Supralab	16-16	17-16	15-16	15-15	17-16	13-14	15-17	16-16	16-17	16-17	18-19
Infralab	11-13	11-12	11-11	10-10	12-10	11-11	13-13	12-11	12-11	11-10	12-13
Sdlm I	7-7	8-8	7-7	7-7	7-7	6-6	6-7	8-8	7-7	7-7	7-7
Sdlm II	9-9	9-9	9-9	10-9	9-9	8-8	8-9	9-8	8-8	8-8	8-8
Sdlm III	9-10	11-11	10-9	10-9	11-9	9-9	10-10	10-10	9-9	10-10	10-
Sdlm IV	10-10	11-10	11-11	10-10	10-10	9-9	11-11	11-10	10-10	11-	10-10
Sdlm V	8-8	8-9	8-9	8-8	9-9	7-8	8-8	9-8	9-8	8-8	8-8
SdIp I	7-7	7-8	7-7	7-7	7-7	6-6	7-7	7-7	6-7	6-6	6-7
SdIp II	9-10	10-9	10-9	9-9	9-9	8-7	9-8	9-9	10-8	9-9	-8
SdIp III	12-12	13-12	12-11	12-12	12-12	11-11	11-11	11-12	11-11	11-10	11-10
SdIp IV	13-13	12-12	13-12	14-14	13-13	11-11	11-11	12-13	11-12	11-12	12-11
SdIp V	13-12	13-13	13-12	13-13	13-13	11-11	12-11	12-14	12-12	12-12	12-12

*Missing part or regenerated.

**height x length

similar in coloration to the adults. This is in contrast to the general ontogenetic pattern in *Paroedura* in which the juveniles are more vividly marked than adults.

Etymology. The name "*vazimba*" (pronounced "vuh zim buh") is a Malagasy word referring to small, mystical, and mythological people of the forest, and is used as an unlatinized specific epithet in reference to the small size and forest habitat of this species.

Distribution. Known only from the type locality near Ampijoroa Forest Station and Bora Reserve in northwestern Madagascar. See Fig. 3.

Remarks. *Paroedura vazimba* differs from *P. androyensis*, *bastardi*, *P. maingoka*, *P. picta*, and *P. vahiny* in having nostrils in contact with the rostral (excluded from contact by the interposition of a supranasal (=prenasal) in the latter four species). *Paroedura gracilis*, *P. homalorhina*, *P. masobe*, *P. oviceps*, and *P. tanjaka* are much larger and have irregularly placed dorsal tubercles on the body rather than arranged into longitudinal rows as in *P. vazimba*. *Paroedura sanctijohannis* and *P. stumpffi* are also much larger than *P. vazimba* and differ further as follows. *Paroedura sanctijohannis* has three granular scales between the supranasals (fide Dixon and Kroll, 1974); *P. vazimba* has only one. *Paroedura stumpffi* has more prominent dorsal tubercles and is much more boldly marked dorsally and generally darker ventrally than *P. vazimba*. The color differences are as follows. *Paroedura stumpffi* has prominent dark stripes from the nostrils to the ears; these stripes are absent or only faintly expressed in *P. vazimba*. There is great contrast between the dorsal dark transverse bands and the lighter intervening ground color in *P. stumpffi* (less contrast in *P.*

vazimba), and *P. stumpffi* almost invariably has a light vertebral stripe running through both the dark and lighter bands on the dorsum. *Paroedura vazimba* has no light vertebral stripe. *Paroedura vazimba* most closely resembles *P. karstophila*, but differs as follows.

Table 7. Analysis of covariance of four morphometric characters of *Paroedura karstophila* and *P. vazimba*. The means are adjusted to size (covariate = SVL). F-tests indicate homogeneity of slopes between species for all four characters. Scheffé tests for differences in adjusted means between species are all highly significant at $p < 0.001$.

	Adjusted means	F-tests (p) equal slopes	Scheffé (p) difference	r ²
Snout length		0.227	0.000	
<i>P. karstophila</i> (n=34)	6.58			0.669 ^a
<i>P. vazimba</i> (n=10)	5.92			0.507 ^c
Eye diameter		0.581	0.000	
<i>P. karstophila</i> (n=34)	4.18			0.288 ^b
<i>P. vazimba</i> (n=10)	3.77			0.319 ^b
Forelimb length		0.462	0.000	
<i>P. karstophila</i> (n=34)	18.39			0.082 ^c
<i>P. vazimba</i> (n=11)	15.71			0.487 ^b
Hindlimb length		0.823	0.000	
<i>P. karstophila</i> (n=34)	25.47			0.325 ^a
<i>P. vazimba</i> (n=11)	21.36			0.311 ^c

^ap<0.001^bp<0.01^cp<0.05

Paroedura vazimba has smaller eyes and a shorter, more steeply descending snout than *P. karstophila*. The diameter of the eye is less than the distance between the eye and the ear opening in *P. vazimba*; whereas the eye diameter is equal to or greater than the distance between the eye and ear in *P. karstophila*. The light ground color on the neck separating the first two dark, dorsal, transverse bands is confined to the dorsum of the neck in *P. vazimba*, whereas it invariably extends ventrally and slightly forward to a point near the insertion of the forelimbs in *P. karstophila*. There are also statistical differences between *P. vazimba* and *P. karstophila* in morphometric characteristics. *Paroedura vazimba* has a shorter snout, smaller eyes, and shorter fore- and hindlimbs, compared to *P. karstophila* (Table 7).

Paroedura vazimba and *P. karstophila* are probably sister species. *P. vazimba* occurs in northwestern deciduous forests lacking karst habitat, and they are most often found above ground on tree trunks and stems. *Paroedura karstophila* is known only from the karst regions of northwestern Madagascar, and has been found only on tsingy rock associated with open canopy, deciduous forests.

Although much smaller, both *Paroedura vazimba* and *P. karstophila* are both similar in scalation and coloration to *P. stumpffi* and *P. sanctijohannis*. The latter two species are also likely to prove to be sister-species. *Paroedura stumpffi* is found on Nosy Be and in the nearby forests of Montagne d'Ambre, areas which are geographically relatively close to the Comoro Islands where *P. sanctijohannis* is restricted. The latter form may prove to be just an isolated geographic race of *P. stumpffi*. Together these four species or lineages (*P. karstophila/vazimba* and *P. sanctijohannis/stumpffi*) are predicted to form a monophyletic unit within *Paroedura*, which is characteristic of the northwestern regions of Madagascar.

Paroedura vazimba is also superficially similar to *P. androyensis* of southwestern Madagascar. The two are similar in size, form, and habitat, and may occupy similar ecological niches in their respective regions.

Specimens of *Paroedura vazimba* were collected during the daytime from under bark on trees and at night when they were active on tree trunks 0.5-1.5 m above ground. One of the paratypes (UMMZ 210518) is heavily parasitized with large nematodes under the skin of the venter and in the coelom. This is the only female with seemingly inactive ovaries, which may result from severe parasitism.

Checklist of *Paroedura* Günther, 1879, Species

A. *picta*-Group

1. *Paroedura androyensis* (Grandidier), 1867
2. *Paroedura bastardi* (Mocquard), 1900
3. *Paroedura maingoka* Nussbaum and Raxworthy, 2000
4. *Paroedura picta* (W. Peters), 1854
5. *Paroedura vahiny* Nussbaum and Raxworthy, 2000

B. *sanctijohannis*-Group

6. *Paroedura gracilis* (Boulenger), 1896
7. *Paroedura homalorhina* (Angel), 1936
8. *Paroedura masobe* Nussbaum and Raxworthy 1994
9. *Paroedura oviceps* (Boettger), 1881
10. *Paroedura karstophila* Nussbaum and Raxworthy, 2000
11. *Paroedura sanctijohannis* Günther, 1879 (type species)
12. *Paroedura stumpffi* (Boettger), 1879
13. *Paroedura tanjaka* Nussbaum and Raxworthy, 2000
14. *Paroedura vazimba* Nussbaum and Raxworthy, 2000

Key to *Paroedura* Species

- 1a. Nostrils separated from rostral scale by interposition of supranasal (prenasal) scale (*picta*-Group) 2
- 1b. Nostrils in contact with dorsolateral processes of rostral scale (*sanctijohannis*-Group) 6
- 2a. Scales multicarinate, at least those on upper surfaces of body; small size, not exceeding 47 mm SVL; toes short with small terminal pads, tips not or barely expanded; bold dark brown and white markings (streaks, marbling, circular white patches) on lips, chin and throat 3
- 2b. Scales unicarinate; large size, adults often much longer than 47 mm SVL; toes long, may or may not have expanded terminal pads; no bold brown and white markings on lips, chin, and throat (weakly expressed light and dark markings may be present on labial scales and angles of jaws, but chin and throat immaculate) 4
- 3a. Ventral scales of body acarinate; dorsal tubercles moderately large, easily visible to naked eye, especially in larger individuals (moderately rough-skinned) *Paroedura androyensis*
- 3b. Ventral scales of body multicarinate; dorsal tubercles small, not readily distinguishable from surrounding scales with naked eye (smooth-skinned) *Paroedura vahiny*
- 4a. Dorsal tubercles prominent (rough-skinned), juxtaposed, arranged into longitudinal rows; toe tips expanded *Paroedura bastardi*
- 4b. Dorsal tubercles not prominent (relatively smooth skinned), not juxtaposed, separated by 2-4 smaller tuberculate or flat scales, not arranged into obvious longitudinal rows; toe tips expanded or not 5
- 5a. Terminal pads of digits small, tips of digits not expanded; dorsal tubercles separated entirely by small, flat, smooth scales; transverse white bands on neck and body not vertical, angled anteroventrally across sides *Paroedura picta*
- 5b. Terminal pads of digits large, tips of digits greatly expanded; dorsal tubercles separated by small, flat, scales and a few smaller tubercles; transverse white bands on neck and body vertical *Paroedura maingoka*
- 6a. Dorsal tubercles moderately to strongly expressed, (relatively rough-skinned), regularly disposed into longitudinal rows 7
- 6b. Dorsal tubercles small (smooth-skinned), not regularly disposed into longitudinal rows 10
- 7a. Dorsal tubercles tetrahedral; large, adults, up to 72 mm SVL 8
- 7b. Dorsal tubercles trihedral; small, adults up to 55 mm SVL 9
- 8a. Dorsal tubercles prominent, arranged into regular longitudinal rows; four large, prominent, light-colored, dorsolateral bands with dark edges on neck and body (the fourth over the hindlimbs); thin, light-colored vertebral stripe usually present; dark eye mask normally present, extending from nostrils across eye to occiput *Paroedura stumpffi*
- 8b. Dorsal tubercles less prominent, arranged into irregular longitudinal rows; dorsum brownish with four faint, light-colored dorsal bands without dark edges on neck and body; no light-colored vertebral stripe; no dark eye mask *Paroedura sanctijohannis*
- 9a. Light dorsal neck band narrow, extends ventrally and slightly anteriorly on each side to a point near insertion of forelimbs; eyes large, horizontal diameter equal to or nearly equal to distance between eye and ear opening *Paroedura karstophila*

- 9b. Light dorsal neck band wide, squarish or shield-shaped, confined dorsally, not extending ventrally to forelimb insertion; eyes small, horizontal diameter less than distance between eye and ear *Paroedura vazimba*
- 10a. Long slender limbs, appressed hindlimb reaches occiput, appressed forelimb extends beyond tip of snout; eyes large, horizontal diameter greater than distance between posterior border of eye and posterior border of ear opening; snout elongate and flattened, spatula-like; 20 or more subdigital lamellae on fourth toe; ground color of head, neck, and body generally light, usually with poorly defined darker crossbands or irregular darker markings; original tails boldly banded *Paroedura homalorhina*
- 10b. Moderate limb length, appressed hindlimb does not reach beyond axilla; appressed forelimb usually extends to loreal region or maximally to nostril (*P. gracilis* is exceptional; forelimb may exceed tip of snout in this species); eye variable in size, horizontal diameter not greater than distance between posterior edge of eye and anterior edge of ear opening, usually less than distance to anterior edge of ear opening; snout not elongate and flattened; fewer than 20 subdigital lamellae on fourth toe (rarely 20 in *P. tanjaka*); ground color of head, neck, and body generally darker 11
- 11a. Pattern of white spots on dark purplish brown ground color of head, neck, body, and upper surfaces of limbs (absent from tail); white spots especially dense on head, usually confined to single large tubercle; body with 3-4 light, transverse bands; original tail with four light bands; eyes dark, nearly black, directed strongly forward; original tail laterally compressed, with 2-3 rings of spines just posterior to basal constriction, usually within first light-colored tail band; double row of dorsal spines on original tails; three parallel rows of subdigital lamellae; large, up to 107 mm SVL *Paroedura masobe*
- 11b. No pattern of white spots on dark purplish ground color; eyes not remarkably dark and directed strongly forward; original tails without double row of dorsal spines; fewer than three rows of subdigital lamellae (usually two) 12
- 12a. Raised vertebral ridge on body bearing double row of enlarged, alternating tubercles; forelimbs long, extending forward beyond tip of snout; dark brown ground color with irregular darker brown markings on either side of vertebral ridge; vertebral ridge usually light colored; often with two additional, irregular, paravertebral light stripes on body; head coloration not markedly different from coloration of body and neck; venter nearly as dark as dorsum *Paroedura gracilis*
- 12b. No raised vertebral ridge on body bearing double row of enlarged, alternating tubercles; forelimbs shorter, not reaching beyond nostrils when appressed; no light-colored vertebral stripe; ventral ground much lighter than dorsal ground color 13
- 13a. Large and robust, up to 102 mm SVL; upper surfaces of neck, body, tail, and limbs of adults light gray with irregular, coarse, brown markings; tail gray, banded with darker brown; cranial shelf immaculate tannish, clearly demarcated in coloration from neck and body; snout also often immaculate tannish; hatchlings and juveniles vividly banded *Paroedura tanjaka*
- 13b. Smaller, up to 68 mm SVL; dorsal surfaces brown with darker brown markings; neck and body with four, irregular, M- or W-shaped, dark brown, dorsal bands, often broken up into brown spots; upper surfaces of limbs brown with irregular darker brown markings; original tails with alternating dark gray and dark brown bands; head brown dorsolaterally with irregular dark brown markings, not distinctly different in coloration from neck and body *Paroedura oviceps*

DISCUSSION

The number of described species of *Paroedura* has nearly doubled (from 8 to 14 species) since 1994. As a result of these discoveries, *Paroedura* is becoming recognized as an important component of the terrestrial vertebrate fauna of Madagascar. Because of its newly discovered diversity and its broad distribution in a variety of habitats, *Paroedura* has the potential to reveal historical distributional patterns within Madagascar. This potential depends on detailed cladistic analyses within the genus using appropriate outgroups.

The relationships within the *Paroedura* have not been explored cladistically, and the relationships of *Paroedura* to other genera are poorly understood. Bauer's (1990) cladistic analysis of Afro-Madagascan genera of geckos, based on morphological characters, placed *Paroedura* in a terminal trichotomy with two other Madagascan endemics, *Ebenavia* and *Uroplatus*. This trichotomy was estimated to be the sister-group to a polytomy of five additional gekkonid genera (*Ailuronyx*, *Geckolepis*, *Homopholis*, *Lygodactylus*, *Urocotyledon*) from Africa, Madagascar, and other islands of the western Indian Ocean. These results led Bauer (1990) to hypothesize that most of the western Indian Ocean gekkonid fauna evolved as a single unit.

Kluge and Nussbaum (1995) also studied the cladistic relationships of the gekkonid genera of Africa and the western Indian Ocean with results somewhat at variance with those of Bauer (1990). Kluge and Nussbaum (1995) showed that with the addition of genera and characters, Bauer's inferred history of the Afro-Madagascan gekkonid radiation becomes more complex with the suggestion of repeated dispersals between Africa, Madagascar, and other islands of the western Indian Ocean. In addition, Kluge and Nussbaum (1995) found that the available data are inadequate to formulate a robust (stable) phylogenetic tree for the genera of geckos that occur in Africa, Madagascar, and islands of the western Indian Ocean. Although *Paroedura* may prove to be part of a monophyletic radiation of Afro-Madagascan geckos, this remains to be demonstrated.

The two informally named groups of *Paroedura* species, the *sanctijohannis*- and *picta*-Groups, may or may not prove to be monophyletic. However, it is noteworthy that the newly discovered species described in this paper support the biogeographic pattern previously defined by these two groups. The two new members of the *picta*-Group, *P. maingoka* and *P. vahiny*, occur in drier southwestern Madagascar where the other species of this group occur; and the three new members of the *sanctijohannis*-Group, *P. karstophila*, *P. tanjaka*, and *P. vazimba*, occur in wetter parts of west-central and northwestern Madagascar, closer to the geographic range of the other members of this group. The recognition that *P. guibae* is synonymous with *P. bastardi* removes what would have been a biogeographic anomaly in regard to this pattern. *Paroedura guibae* was misidentified as a member of the northern group occurring in southern Madagascar.

The five new species described in this paper are restricted to rather specialized, relatively dry habitats in western Madagascar. Three of the five species are known only from karst habitats, and none is known from more than two localities. The restricted distributions of these species are, however, not necessarily reasons for concern about their survival. In general, the biota of western Madagascar is poorly known, and all five species may prove to have a much broader distribution than is currently known.

Paroedura maingoka is probably restricted to the limestone habitats of the Mahafaly Plateau of southeastern Madagascar. The fauna and flora of the Mahafaly Plateau is recorded from only a few surveys along the readily accessible, coastal limestone cliffs that mark the southwestern boundary of this extensive limestone plateau. The interior of the plateau is virtually unknown, but recent discoveries along its edge suggest that the plateau may harbor a locally endemic fauna and flora. These discoveries include *P. maingoka*; the gekkonid *Ebenavia maintimainty* (Nussbaum and Raxworthy, 1998); and the striped mongoose, *Galidictis grandidiensis* (Wozencraft, 1986).

Paroedura karstophila is known only from two isolated karst massifs, Namoroka and Ankarana. The dry deciduous forests of Namoroka and Ankarana are separated by the Sambirano rainforests, which currently pose a dispersal barrier to relatively arid-adapted species like *P. karstophila*. Other arid-adapted herpetofaunal species, such as *Furcifer oustaleti*, *Heteroliodon* n. sp. (Nussbaum and Raxworthy, in press), *Leioheterodon modesta*, *Ophurus cuvieri*, and *Zonosaurus laticaudatus* are also restricted to opposite sides of the Sambirano. This distributional pattern suggests that xeric corridors once spanned the Sambirano region. *Paroedura karstophila* may yet be found in the limestone regions of the largely unknown Kelifely Plateau to the southwest of Namoroka. It seems unlikely, however, that it will be found further south in the Bemaraha karsts, as Bemaraha is relatively well surveyed.

Paroedura tanjaka is currently recorded only from the two limestone regions of Bemaraha and Namoroka, a distributional pattern known for other lizards, notably the new scincid species *Mabuya tandrefana* (Nussbaum et al., 1999). The region between Bemaraha and Namoroka is not well known, and *P. tanjaka*, *M. tandrefana*, and other species with similar disjunct distributional patterns may eventually be found in this gap. The calcareous Kelifely Plateau between Bemaraha and Namoroka is a likely place to search for undiscovered populations of *P. tanjaka*. It is unclear whether *P. tanjaka* is dependent on limestone habitats. At both Bemaraha and Namoroka, it was found on trees as well as tsingy, suggesting that it could occur in deciduous forests outside of limestone regions.

Paroedura vahiny is the only one of the five new species that does not occur within a protected reserve. This, in addition to its apparent rarity (two known specimens) and restricted distribution, suggest *P. vahiny* may be the most vulnerable of the new species of *Paroedura*. The holotype was found in restricted deciduous forest. The habitat of the other specimen (MNHN 1984 420) was not noted, but the locality lies in a region of degraded, dry deciduous forest. Neither locality is associated with limestone country rock, nor any other specialized habitat. Therefore, speculation about the biogeographic relationships of this species is precluded until further information is acquired.

Paroedura vazimba is the apparent sister-species of *P. karstophila*, but, unlike the latter, it is unknown from limestone habitats. Instead, it seems to be restricted to the dry deciduous forests near Ankarafantsika and Bora Reserves. Its survival seems assured, at least for now, by its inclusion in reserves. It seems likely that it will be found in other deciduous forests near and between Ankarafantsika and Bora.

Paroedura has proven to be far more speciose and diverse in niche breadth than previous literature suggested. Additional fieldwork is needed to refine the distributional relationships of

the *Paroedura* species, and undoubtedly new species will be discovered. Understanding the evolution of this genus and its biogeographic revelations await detailed cladistic analyses.

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