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A NEW *LEPIDODACTYLUS* (SQUAMATA: GEKKONIDAE) FROM VANUATU

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ABSTRACT: We describe a new gekkonid species, *Lepidodactylus vanuatuensis*, from Vanuatu, Melanesia. This species most closely resembles *L. guppyi* and *L. gardineri*, and belongs to Brown and Parker's (1977) Group II based on having entire terminal scansors on all digits and two or three divided or deeply notched subterminal scansors on digits II–V. However, it differs from these species in having the following combination of character states: only 99–114 scales around the midbody, relatively weak dilation of digits, and slight to moderate webbing of toes III and IV. The new species also differs from *L. guppyi* in mtDNA nucleotide sequences of cytochrome-*b* gene. A dichotomous key is provided for the Group II species from the Pacific.

Key words: Reptilia; Gekkonidae; *Lepidodactylus vanuatuensis* new species; Vanuatu; Melanesia; Taxonomy; mtDNA

THE genus *Lepidodactylus* Fitzinger is a group of small geckos and, except for the widely ranging parthenogenetic/bisexual *L. lugubris* complex (including *L. moestus*: Ota et al., 1995; Radtkey et al., 1995), each species has a relatively small distribution limited to a few islands in Southeast Asia and Oceania (Bauer and Henle, 1994; Brown and Alcala, 1978; Brown and Parker, 1977; Ota et al., 1995). Brown and Parker (1977) and Brown and Alcala (1978) originally recognized 18 species classified into three well diagnosed, but informal, phenetic groups (Groups I, II, and III). Subsequent systematic studies have raised the number of species to 26 (e.g., Brown et al., 1992; Ota and Crombie, 1989; Ota et al., 1995). Additional insular populations, most likely representing undescribed species, remain unstudied (Brown and Parker, 1977; Ineich, 1992, unpublished data; Radtkey et al., 1995).

During recent fieldwork in Vanuatu, Melanesia, a series of bisexual *Lepidodactylus* was collected from Espíritu Santo and Efate (Fig. 1). These specimens, as well as four previously collected from Vanuatu and deposited in AMNH, FMNH and MNHN, differ from *L. lugubris*, the only known Vanuatuan representative of the genus (Bauer, 1988; Medway and Marshall, 1975; Zug, 1991). They also differ from all other species outside Vanuatu. Thus, we describe a new species on the basis of these specimens.

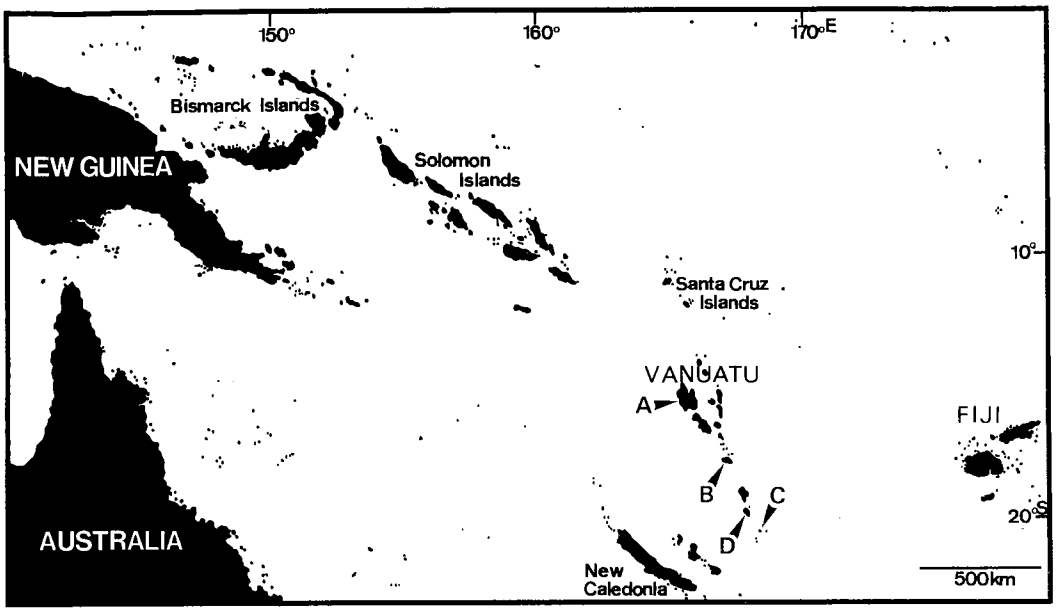

FIG. 1.—Map of Melanesia showing distribution of *Lepidodactylus vanuatuensis*. (A) Espíritu Santo Island; (B) Efate Island; (C) Anatom Island; (D) Tanna Island.

MATERIALS AND METHODS

We examined 18 specimens from Vanuatu (eight from Espíritu Santo Island, seven from Efate Island, one from Anatom Island, and two lacking specific locality data) after preservation in 70% ethanol. Measurements were taken to the nearest 0.1 mm with dial calipers or microscope micrometer. Each specimen was sexed on the basis of the presence (male) or absence (female) of preanal and femoral pores. The following individuals were considered as adults: males having distinct swelling in the cloacal region; females having vitellogenic ovarian follicles (discriminated by their yellow color in preservative), oviductal eggs, and, or, enlarged flaccid oviducts.

The Vanuatu specimens possess the characteristics of Brown and Parker's (1977) Group II (i.e., undivided terminal scansors on all digits; deep notch or division in two or three subterminal scansors on digits II–V; non-depression of tail); therefore, we compared them with the six currently recognized Group-II species (Brown and Parker, 1977; Ota et al., 1995). We derived data from the literature for *Lepidodactylus shebae*; other species were compared by examination of specimens (Appendix I).

Mitochondrial DNA nucleotide sequences of cytochrome-*b* gene were obtained by direct sequencing of asymmetric polymerase chain reaction (PCR) products (993 base pairs) following Radtkey et al. (1995). Sequences for the new species (from USNM 323268) and *L. aureolineatus* (from T. J. Case's personal collection No. 1683) were reported in Radtkey et al. (1995), who referred the former as "*L. guppyi* from Vanuatu", and are available from GENBANK. Unpublished sequence data for *L. guppyi* (from a tail sent by M. McCoy) are used for comparisons, and also are available from GENBANK. The nucleotide distances were obtained as percentages of nucleotide substitutions uncorrected for multiple substitutions.

Terminology for descriptions of morphological characters follows that of Ota et al. (1995) and Ota and Hikida (1989). Spellings for island names are those of Motteler (1986). Museum codes are those suggested by Leviton et al. (1985).

Lepidodactylus ***vanuatuensis*** sp. nov.

Lepidodactylus guppyi: Radtkey et al., 1995:146.

Holotype.—USNM 334189, an adult male from approximately 10 km NE of Palikulo Point Peninsula, Luganville, Espíritu Santo Island, Vanuatu, collected by G. R. and P. B. Zug on 15 December 1993.

Paratypes.—CAS 196053, an adult male from near Independence Park, Port Vila, Efate Island, Vanuatu, collected by D. T. Bolger and R. N. Fisher on 6 December 1988; USNM 323264, an adult female from approximately 14 km W of Devil's Point, Port Vila, collected by G. R. Zug on 15 February 1993; USNM 323265 and 323266, an adult female and a juvenile from the same locality as that for the former, collected by G. R. Zug and R. N. Fisher on 17 February 1993; USNM 323267–268, two adult females from the same locality, collected by G. R. Zug and R. N. Fisher on 18 February 1993; USNM 334163, an adult male from approximately 13 km E of Devil's Point, Port Vila, collected by G. R. and P. B. Zug on 20 December 1993; AMNH 71033, an adult male from Espíritu Santo Island, collected in 1944 (detailed locality, collector and date unknown); USNM 334184–186, one juvenile and two adult females, localities and collectors same as those for the holotype, collected on 14 December 1993; USNM 334187, an adult male from approximately 6.5 km E of Million Dollar Point, Luganville, collected by G. R. and P. B. Zug on 15 December 1993; USNM 334188 and 334190, an adult male and a juvenile, sampling data same as those for the holotype; FMNH 69612, a juvenile from Anatom Island, Vanuatu, collected by Marshall Laird on 25 February 1953; AMNH 65374, an adult male from Vanuatu (detailed sampling data unknown); MNHN 1986.632, an adult female from Vanuatu (detailed locality unknown), collected by N. L. H. Krause in January 1986.

Diagnosis.—A small species (Fig. 2) with snout–vent length (SVL) ranging 35.1—40.3 ($\bar{x}$ = 37.8) mm for five adult males, 38.6—47.4 ($\bar{x}$ = 44.3) mm for seven adult females. This species is assigned to Brown and Parker's (1977) Group II by having entire terminal scansors on all digits, two or three divided or deeply notched subterminal scansors on digits II–V, and subcylindrical tail.

FIG. 2.—*Lepidodactylus vanuatuensis*, an adult female paratype from Efate (USNM 323267); SVL = 38.6 mm.

Six species (*L. gardineri*, *L. guppyi*, *L. novaeguineae*, *L. paurolepis*, *L. pulcher*, and *L. shebae*) are known for Group II (Brown and Parker, 1977; Ota et al., 1995). Of these, *L. novaeguineae*, *L. paurolepis*, *L. pulcher*, and *L. shebae* differ from *L. vanuatuensis* in having smaller numbers of enlarged, pore-bearing preanal and femoral scales (16–20, 31–34, 18–20, and 30–34, versus 36–41, respectively) (Bauer and Henle, 1994; Brown and Parker, 1977; Ota et al., 1995; this study). Also, *L. paurolepis* differs from *L. vanuatuensis* in lacking a cloacal spur. *Lepidodactylus pulcher* differs from *L. vanuatuensis*, as well as from most other species belonging to Group II, in having more scansors on toe IV (17–19: Ota et al., 1995; this study; versus 10–12 in *L. vanuatuensis*). The unique type of *L. shebae* differs from *L. vanuatuensis* in possessing fewer lower labials (nine: Brown and Parker, 1977; versus 10–11 in *L. vanuatuensis*).

Lepidodactylus vanuatuensis shares these as well as many other characters with *L. gardineri* and *L. guppyi*. However, it differs from *L. gardineri* in being smaller (adult SVL: 35.1–47.4 mm, $\bar{x}$ = 41.9 mm: Table 1; versus 48.0–53.4 mm, $\bar{x}$ = 50.4 mm in *L. gardineri*), and having fewer scansors on finger IV (FIVS: 10–13, $\bar{x}$ =

TABLE 1.—Variation in morphometric characters of adult types of *Lepidodactylus vanuatuensis* (means, followed by ranges in parentheses). See text for abbreviations.

Characters	Males (n = 5)	Females (n = 7)
SVL (mm)	37.8 (35.1–40.3)	44.3 (38.6–47.4)
HL/SVL (%)	25.9 (25.1–26.4)	23.9 (23.0–24.9)
HW/HL (%)	69.0 (66.0–72.7)	71.0 (68.0–74.8)
SEL/HL (%)	41.7 (39.6–44.3)	42.8 (40.9–44.9)
EL/HL (%)	24.0 (21.7–25.5)	25.6 (23.6–27.1)
EEL/HL (%)	32.4 (31.1–33.7)	33.7 (31.3–35.8)
ERL/HL (%)	10.3 (9.4–11.4)	8.7 (6.5–9.6)
IND/HL (%)	17.1 (16.0–18.3)	17.7 (15.0–19.8)
IOD/HL (%)	45.9 (43.6–47.2)	44.3 (40.8–47.3)
SFL/SVL (%)	38.5 (35.9–40.0)	36.8 (34.2–39.8)
AGL/SVL (%)	51.0 (50.1–51.7)	50.3 (46.8–51.8)
TIVW/TIVL (%)	28.4 (24.4–31.4)	28.8 (25.5–31.3)
TD/TW (%)	91.0 (80.7–95.5)	83.4 (79.4–89.3)

TABLE 2.—Variation in meristic characters of types of *Lepidodactylus vanuatuensis* (means, followed by ranges in parentheses). See text for abbreviations.

Characters	Males (n = 6)	Females (n = 8)
UL	11.2 (10–12)	10.8 (10–12)
LL	10.4 (10–11)	10.8 (10–11)
IOS	36.6 (35–38)	35.6 (35–37)
MSR	104.0 (99–110)	111.7 (108–114)
FIS	9.4 (9–10)	8.5 (8–9)
FIIIS	11.0 (10–13)	11.3 (10–12)
FIVS	11.6 (10–13)	11.8 (10–13)
TIS	10.0 (9–11)	9.6 (8–11)
TIIIS	12.6 (11–14)	12.0 (10–14)
TIVS	11.0 (10–12)	10.6 (10–12)
PFP*	38.8 (36–41)	—

* Counted only for adult males (n = 5).

11.7: Table 2; versus 14–16, $\bar{x}$ = 15.4 in *L. gardineri*). In preservative, the chin of *L. gardineri* is dark bluish gray, whereas this area is creamy-white in *L. vanuatuensis*.

Externally, *Lepidodactylus vanuatuensis* seems most closely to resemble *L. guppyi*, from which it differs in having fewer rows of scales around midbody (MSR: 99–114, $\bar{x}$ = 108.9: Table 2; versus 117–138, $\bar{x}$ = 126.9 in *L. guppyi*). Range of MSR in these species are bridged by that in *L. gardineri* (108–122, $\bar{x}$ = 115.9). *Lepidodactylus vanuatuensis* and *L. guppyi* also can be distinguished by the degree of digital dilation; scansor-bearing phalanges are more dilated in *L. guppyi* (and *L. gardineri*) than in *L. vanuatuensis* (Fig. 3)—i.e., the maximum breadth of toe IV is as great as, or greater than, one-third of the length of its dilated portion in *L. guppyi* (and *L. gardineri*), whereas it is <⅓ in *L. vanuatuensis*.

Description of holotype (measurements in mm).—SVL 40.3; head length (HL) 10.6; head width (HW) 7.0; snout–eye length (SEL) 4.2; eye length (EL) 2.3; eye–ear length (EEL) 3.3; ear opening length (ERL) 1.0; internasal distance (IND) 1.7; interorbital distance (IOD) 5.0; snout–forelimb length (SFL) 16.0; toe IV width (TIVW) 1.4; toe IV length (TIVL) 4.6; axilla–groin length (AGL) 20.2; tail length (TL) 34.0; tail width (TW) 3.1; tail depth (TD) 2.5.

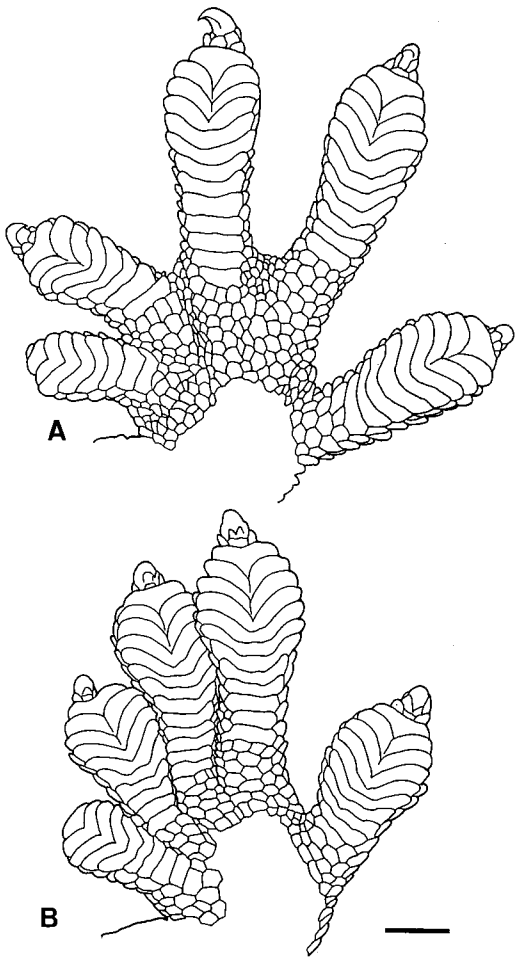

FIG. 3.—Ventral views of left feet of (A) *Lepidodactylus vanuatuensis* (holotype) and (B) *L. guppyi* (CAS 191256, from Guadalcanal Island of the Solomons). Scale bar = 1 mm.

Snout tapered, rounded at tip; rostral entering nostril, height about half its width; nostril surrounded by two supranasals, rostral, first upper labial, and one distinctly enlarged scale posteriorly; anterior supranasals separated by three scales that border the rostral; 10 upper labials (UL), the eighth and ninth centered below orbit, the tenth smallest, about three times as large as surrounding scales; mental pentagonal, as large as adjacent labials; anterior chin shields about half as large as mental, size of chin shields gradually reducing posteriorly; gular scales slightly convex and mostly small, but those adjacent to lower labials slightly enlarged; 10 lower labials (LL); scales on snout slightly larger than those on dorsal and lateral surfaces of remaining part of head and body; 36 scales between midpoints of upper margins of orbits (IOS).

Body not depressed; 102 rows of scales around midbody (MSR); dorsal and lateral scales granular, without enlarged tubercles; ventral scales almost flat, cycloid, larger than dorsal scales; limbs well developed; scales on limbs somewhat convex, slightly larger than dorsal body scales; those on midventral surface of shank flattened, cycloid, as large as or slightly larger than ventral scales on body; subdigital scansors 8-9, 8-9, 11-10, 12-12, and 9-9 on left–right fingers I (FIS), II, III (FIIIS), IV (FIVS) and V, 8-9, 9-9, 13-13, 11-11 and 9-9 on left–right toes I (TIS), II, III (TIIIS), IV (TIVS) and V, respectively; scansors covering distal two-thirds on toe IV; all digits except the first clawed; distal, compressed, claw-bearing phalanges arising from anterior margin of dilated part, extending only a short distance beyond; breadth of inderdigital webb between toes III and IV about one-sixth of length of the latter; preanal and femoral pores (PFP) 39, forming a continuous series, almost reaching distal portion of thigh; scales adjacent to pore bearing ones in preanal region slightly larger than others; in femoral region, scales just posterior to pore-bearing series as large as preceding scales, slightly larger than following scales.

Proximal three-quarters of tail original, distal one-fourth regenerated, subcylindrical, lateral margins without spines or flanges of skin; base of tail somewhat swollen, with two slightly, but clearly enlarged, convex scales forming cloacal spur on each side; scales on tail annulated, dorsals as large as those on anterior margin of thigh and distinctly larger than dorsal body scales, subcaudal scales slightly larger than dorsal caudal scales; scales on original portion relatively cycloid, those on regenerated portion more squarish.

Radiographs of the holotype and nine paratypes show: interclavicle dagger-shaped, lacking lateral projections; 26 presacral vertebrae; phalangeal formula of hand 2-3-4-5-3, of foot 2-3-4-5-4.

Color of holotype in preservative.—Dorsal ground color of head, body, and limbs light grayish tan; parietal region of head darker; two indistinct, large dark brown markings on dorsolateral part of neck on each side, followed by dorsolateral region of body slightly darker than ground color; dorsal ground color of original portion of tail pale yellowish tan, with four broad transverse dark brown bands; regenerated portion of tail dark gray dorsally and ventrally; ventral ground color of head, body, limbs and original portion of tail creamy-white; scansors dark brownish gray except for those on digit I; numerous dark dots on lower labials, and ventral surfaces of thigh and unregenerated portion of tail.

Color in life (based on color photographs of three paratypes from dorsolateral angle).—Dorsal ground color varying from light creamy-gray to rusty-tan, slightly darker on head, lighter on tail; two specimens with more or less distinct, light-margined dark brown bar between orbit and jaw angle, and with cloud-shaped dark brown marking on each side of neck, followed by six such markings forming a longitudinal row in dorsolateral region of body; in the other specimen, postorbital region and dorsolateral regions of neck and body almost uniformly light reddish brown, lacking dark markings; several broad transverse dark brown bands on tail.

Variation.—Morphometric and meristic variation in the type series of *Lepidodactylus vanuatuensis* are summarized in Ta-

bles 1 and 2, respectively. In preservative, the dorsal ground color is more brownish or yellowish tan in a few specimens than in the holotype. One paratype (USNM 323267) has an indistinct W-shaped dark marking in occipital region and six indistinct, broad, transverse dark brown bands on dorsum of body. Some paratypes have the posterior extension of the dorsolateral row of dark brown spots (evident only in nuchal region in holotype and other paratypes) throughout the body on each side. They also show another row of dark brown spots on the flank.

Distribution.—Known only from Espíritu Santo, Efate, and Anatom islands, Vanuatu, Melanesia. Judging from photographs provided by A. H. Whitaker, the geckos that he found on Tanna Island (Fig. 1D) (Anonymous, 1996:16) seem to belong to *Lepidodactylus vanuatuensis*. This record, however, requires verification on the basis of specimens. *Lepidodactylus vanuatuensis* probably occurs on all main islands of the archipelago.

Ecological notes.—All CAS and USNM specimens of *Lepidodactylus vanuatuensis* came from human-disturbed habitats. CAS 196053 was collected with a series of *L. lugubris* at night from the wall of one of the government buildings in Port Vila, Efate. Other specimens from Efate were found (at night, 1830–2100 h) on *Casuarina* and other trees on the grounds of World War II command buildings immediately adjacent to a marine cove. Most occurred on an ornamental evergreen fruit tree and were foraging/gleaning on the outside foliage. The specimens from Espíritu Santo were collected in beachside scrub within hollow branches or beneath loose bark usually by day. Several specimens were beneath the bark of living *Casuarina*.

On Espíritu Santo Island, three clutches of eggs were found beneath loose bark of a living *Casuarina* (0.70 m dbh) approximately 1.5 m above the base of the tree on 14 December 1993. The eggs are brittle-shelled and adhesive. Two clutches, each consisting of two eggs, had already hatched; the empty egg shells were 9.4 × 6.8 mm and 10.0 × 6.3 mm, and 9.3 × 6.5 mm and 9.5 × 6.6 mm. The other clutch contained a single egg (9.5 × 6.2 mm); it hatched on 17 December (1500–1530 h), producing a hatchling 18.4 mm long with a tail 15.3 mm long (USNM 334190).

Etymology.—The specific name *vanuatuensis* refers to Vanuatu, the nation to which this species appears to be endemic.

Key to the Species of Group-II *Lepidodactylus* from the Pacific Region

1. Less than 35 enlarged scales in preanal-femoral region 2
   Thirty-five or more enlarged scales in preanal-femoral region 5
2. More than 16 scansors on toe IV ..... *L. pulcher*
   Sixteen or fewer scansors on toe IV ... 3
3. Less than 25 enlarged scales in preanal—femoral region ..... *L. novaeguineae*
   More than 25 enlarged scales in preanal—femoral region 4
4. More than 120 scales around midbody (Brown and Parker, 1977) ... *L. shebae*
   Less than 110 scales around midbody .. .. *L. paurolepis*
5. Digits poorly dilated, maximum breadth of toe IV <⅓ of length of its dilated portion ..... *L. vanuatuensis*
   Digits moderately dilated, maximum breadth of toe IV as great as or >⅓ of length of its dilated portion 6
6. Chin creamy-white; webbing between toes III and IV extending to basal ⅕–¼ of digits ..... *L. guppyi*
   Chin dark bluish-gray; webbing between toes III and IV extending to only less than basal ⅙ of digits ..... *L. gardineri*

Discussion

The percent differences in cytochrome-*b* sequences between *Lepidodactylus vanuatuensis*, and *L. guppyi* from the Solomons and *L. aureolineatus* from the Philippines are 6.6 and 25.4 based on all substitutions (both transitions and transversions), 2.7 and 11.4 based on only transversions, respectively. Between *L. guppyi* and *L. aureolineatus*, those distances are 24.1 and 11.2, respectively. The distance between *L. vanuatuensis* and *L. guppyi* is consistent with each of these taxa representing independent evolutionary units and, therefore, separate species, al-

though the distance data alone should not be regarded as direct evidence for the recognition of species (Frost and Hillis, 1990). An overall distance of 6.6% (2.7% for transversions alone) is less than those typically observed between species within *Lepidodactylus* (e.g., 24.1% between *L. guppyi* and *L. aureolineatus*: see above), but it is an order of magnitude larger than that observed between the distributional extremes of the widely distributed populations of *L. moestus* (0.60%: Radtkey et al., 1995). Furthermore, the distance between *L. vanuatuensis* and *L. guppyi* is similar to cytochrome-*b* gene distances between recently diverged species in the gekkonid genus *Phelsuma* [e.g., 8.9–10.4% (3.0–3.1% for transversions alone) between *P. sundbergi* and *P. astriata*: Radtkey, 1996] and the xantusiid genus *Xantusia* [e.g., 13.0% (2.3% for transversions alone) between *X. vigilis* and *X. riversiana*: Hedges et al., 1991].

Several previous authors demonstrated that the herpetofauna of Vanuatu is less diverse than those of neighboring Melanesian island groups. Moreover, most Vanuatuan taxa have conspecific or closely related populations in the Solomon Islands (e.g., Bauer, 1988; Donnellan and Moritz, 1995; Medway and Marshall, 1975; Zug and Moon, 1995). Thus, it is assumed that most Vanuatuan reptiles are derived primarily from populations in the Solomons via overwater dispersal, and upon arrival, the colonists may or may not have differentiated rapidly (Bauer, 1988; Brown, 1991; Gibbons, 1985). *Perochirus guentheri*, an endemic gekkonid species distantly isolated from other congeneric species, may be an exception to this typical biogeographic pattern for Vanuatuan lizards [Bauer, 1988: but see Pregill (1993) for data suggesting a different view]. The small degree of differentiation of *L. vanuatuensis* from *L. guppyi* and the occurrence of the latter species in the Solomons suggest that *L. vanuatuensis*, like many other Vanuatuan lizards such as *Gekko vittatus* and several species of *Emoia* (Brown, 1991), may represent a relatively recent colonization from the Solomons. This hypothesis needs verifications by detailed phylogenetic analyses.

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APPENDIX I

Comparative Specimens Examined

Lepidodactylus gardineri, Fiji: USNM 268142, 268144–148, 268151, 268153–155, 268158, 268160–161, 268167.

Lepidodactylus guppyi, Solomon Is.: CAS 139650, 191256, MCZ 65862, 67122, 67124, 67126, 74517–519, 135433–434, 139418, USNM 120877–878, 313866.

Lepidodactylus novaeguineae, New Guinea: CAS-SU 11028–029.

Lepidodactylus paurolepis, Belau: USNM 284400, 284402–403.

Lepidodactylus pulcher, Admiralty Is.: CAS 139832.