

## A new gecko (Reptilia: Squamata: Genus *Lepidodactylus*) from Tuvalu, South-central Pacific

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*Abstract.*—A Group II *Lepidodactylus* was discovered during a recent biodiversity survey of Tuvalu. These geckos uniquely share a heavily pigmented oral cavity with the Rotuman *L. gardineri* and also are most similar to *L. gardineri* in scalation, size, and body proportions; however, differences in the pubic patch of enlarged scales and the thickness of the head support speciation of the Tuvaluan population. This population is described and characterized.

Two families of lizards are widespread and common colonizers of the islands of Oceania. The skinks (Scincidae) are diurnal and predominantly terrestrial lizards; the geckos are nocturnal and mainly arboreal ones. The origins and dates of these lizards' colonization of Oceania remain debatable, although recent man-assisted colonization seems unquestionably the mode of dispersal for a few species, e.g., moth skink (*Lipinia noctua*; Austin 1999) and house gecko (*Hemidactylus frenatus*; Case et al. 1994).

For other taxa, such as the geckos of the genus *Lepidodactylus*, dispersal throughout western Oceania likely occurred in the distant past and well before human colonization of this area, because several endemic species occur irregularly from Rotuma, Viti Levu, 'Eua and westward. These species (*L. gardineri*, *L. manni*, *L. euaensis*, respectively, and others) are morphologically well differentiated and largely forest residents, thereby suggesting long periods of isolation. The interrelationships of these three taxa to one another and to congeners of the more western island groups are unresolved. Phenetically, *Lepidodactylus* consists of three species groups (Brown & Parker 1977). Group III (*L. lugubris* and relatives)

consists of bisexual and unisexual species and populations, and one or more Group III species occur on almost every island in Oceania. Group III members are considered to be the most derived taxa of *Lepidodactylus* (Ota et al. 1995), and their current distribution likely derives from natural and human-assisted dispersal. The other two phenetic groups, Group I (*L. pumilis* and allies) and Group II (*L. guppyi* and allies) are less specialized in morphology and are irregularly distributed among the islands west of and including the Tongan arc. *L. manni* (Fiji) and *L. euaensis* (Tonga) are members of Group I that is characterized by undivided digital lamellae, and *L. gardineri* (Rotuma) is a Group II species, characterized by a few subterminal divided lamellae.

It was, thus, surprising when a recent biotic survey in Tuvalu discovered another Group II *Lepidodactylus*. Individuals of this *Lepidodactylus* appear similar to *Lepidodactylus gardineri*; however, some subtle differences suggest that the Tuvaluan population represents a more ancient dispersal than a man-assisted one and that this population's isolation has resulted in speciation. We recommend that the Tuvaluan population be known as:



Fig. 1. The holotype of *Lepidodactylus tepukapili*, USNM 531712.

*Lepidodactylus tepukapili*, new species

Fig. 1

*Holotype*.—USNM 531712, an adult male from Fuakea [Fuagea] ( $8^{\circ}34'S$ ,  $179^{\circ}04'E$ ), Funafuti Atoll, Tuvalu, collected by Dick Watling on 4 September 1998.

*Paratypes*.—USNM 531713-16, a juvenile male, an adult female and two adult males, respectively, from Tepuka ( $8^{\circ}28'S$ ,  $179^{\circ}05'E$ ), Funafuti Atoll, Tuvalu, collected by Dick Watling on 3 September 1998.

*Diagnosis*.—*Lepidodactylus tepukapili* is a Group II species with the division or deep notching of two or three of the subterminal digital lamellae of second through fifth digits of the fore- and hindfeet. It differs from other Group II members: by the possession of a continuous row of 36 or more femoral-precloacal pores in adult males, 35 or less in *L. novaeguineae*, *L. paurolepis*, *L. pulcher*, and *L. shebae*; by moderately dilated digital pads of fore- and hindfeet, only slightly dilated in *L. vanuatuensis*; by a bluish gray chin and throat, creamy white in *L. guppyi*; and by a larger pubic or pre-cloacal patch of enlarged scales (median 18 vs. 13.5; Table 3) and a flatter head (median HeadL/SVL 103 vs. 123%; Table 2) in *L. gardineri*.

*Etymology*.—The specific name *tepuka-*

*pili* derives from the Tuvaluan language and is used as a noun in apposition. Pili refers to any small lizard, (either gecko or skink), and Tepuka is the island on which the first specimens were discovered. Puka of tepuka is the root word for two culturally important trees on the island, i.e., pukavai, *Pisonia grandis*, and pukavaka, *Hernandia nymphaeifolia*.

*Description of the holotype*.—Snout-vent length 50.3 mm; head length 11.5; head width 7.6; head height 5.4; snout-eye length 4.6; naris-eye length 3.6; orbit diameter 3.2; eye-ear length 3.0; snout width 1.9; interorbital width 3.6; snout-forelimb length 17.0; trunk length 20.9; crus length 6.0; tail length 37 (regenerate). All measurement here and subsequently are in millimeters. Mensural and scalation characters defined in appendix.

Snout tapered, rounded at tip; rostral entering nares, width about 2.5 times height; nares bordered by five scales, three nasals, one rostral, and first supralabial; five scales touching rostral between left and right nares; 35 interorbital scales; ten left and nine right supralabials; eight left and nine right infralabials; mental scale distinct, its anterior width equals midline length; six postmental and seven chin scales.

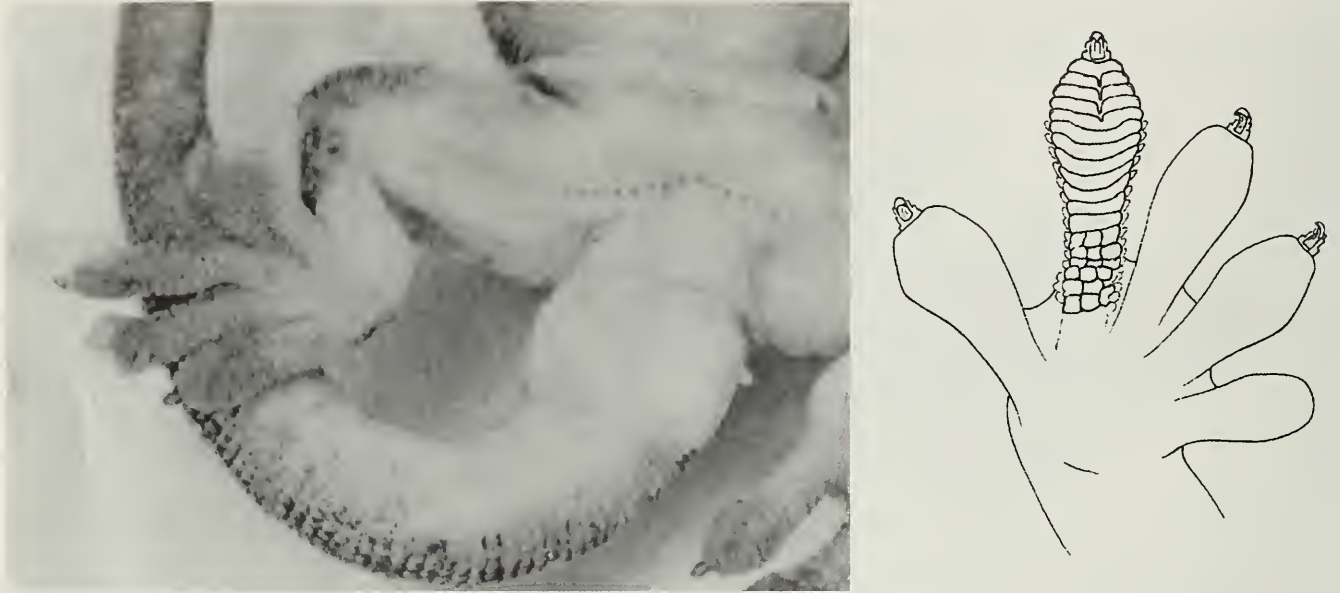


Fig. 2. Ventral view of the posterior trunk and limbs (left) and right hindfoot (right) of the holotype of *Lepidodactylus tepukapili*, USNM 531712.

Body slightly depressed; 118 rows of scales around midbody; dorsal and lateral scales granular, without enlarged tubercles, and in juxtaposition; ventral scales almost flat, cycloid, 2–3 times larger than dorsal scales; limbs well developed; subdigital lamellae 16/16 and 11/12 on left/right sides of on digits IV of fore- and hindfoot (Fig. 2), respectively; digital lamellae ventrally covering nearly all of forefoot digits and I–II digits of hindfoot, about  $\frac{3}{4}$  of digits III–V of hindfoot; all digits of fore- and hindfoot clawed except the first; ultimate claw-bearing and penultimate phalanges of fore and hind digits raised above pad although only claw free and extending over distal edge of pad; fore- and hindfoot webbing modest ( $\leq 1/5$  digit length); precloacal and femoral pore rows continuous with 38 excreting pores, reaching about  $\frac{3}{4}$  length of thigh; scales adjacent to pore bearing ones enlarged, usually in two rows anterior to pore row and posteriorly forming pubic patch of enlarged scales (Fig. 2).

Posterior third of tail recently regenerate and likely regenerated from hemipenial sheath distally; tail subcylindrical throughout length, gradually tapering to a blunt tip; lateral margins without spines or skin flanges; scales on tail annulate, cycloid, larger

ventrally than dorsally, and subcaudal scales about 1.5 times belly scales; base of tail distinctly swollen by hemipenes; single large, blunt cloacal spur on each side.

*Color of holotype.*—In preservation, dorsal ground color of head, body, limbs, and tail brown with faint and discontinuous mottling of darker brown; ventrally, chin to anterior throat dusky, thereafter white with slight ventrolateral dark flecking on belly, ventrally tail white except for dusky on recently regenerate portion. When first found, the gecko was a rich chocolate brown dorsally with lighter brown patches or mottling on the sides; the venter from chin onto tail was a bright dark yellow. Scales around eye and along upper lip were light, and interior of the mouth and tongue were black. The brighter coloration faded within an hour to a grayish brown dorsally and laterally, and a less intense yellow venter.

*Variation.*—The two adult male paratypes (USNM 531715–716) are distinctly smaller (43.5, 43.1 mm SVL, respectively) than the holotype but not greatly different from the adult female paratype (USNM 531714, 41.1 mm). There appear to be no proportional differences either between the smaller males and holotype or the female. The small sample size prevents any test of

size dimorphism between adult females and males. The absence of dimorphism also appears to be the situation for most aspects of scalation. Comparing the scalation of the holotype with the four paratypes yield the following: Ros, width usually  $2.5\times$  height; RosC, absent in all; NaRos, no contact in all; NaInf, no contact in all; CircNa, invariant 3; SnS, 5 scales in holotype and either 4 or 5 in paratypes; IntorbS, 35 and 29–34; Suplab, 9 and 7–9; Inflab, 9 and 8–9; Men, width equals height in all; PosMen, 6 and 7–10; Chin, 7 and 8–14; Midb, 118 and 100–113; CloacS, 1 and 1–2; Subcaud, width  $1.5\times$  height and  $1.0\text{--}2.0\times$ ; ForefL, 16 and 14–15; HindfL, 12 and 12–15; LamNF, invariant 2; LamNL, invariant 4<sup>th</sup>; PoreRS, 43 and 37–42; Web, invariant basal  $\frac{1}{4}$ <sup>th</sup>; PreclP, 17 and 12–18; for the males PreclPor, 38 and 39–40. These scalation traits show little variation within the Tuvalu sample.

Color notes for the individual *L. tepukapili* are not available and likely would display no greater variation among individuals than within an individual as an individual's coloration shifted owing to physiological and psychological state. In preservation, the paratypes share the dorsal ground color with the holotype, although the dark brown mottling is more extensive on all paratypes, and the mottling largely dominates the dorsal coloration of USNM 531714 and 531716. Similarly the paratypes share the holotype's ventral coloration with more ventrolateral flecking from the neck to the hindlimbs; their chins and throats are dusky but somewhat lighter than the holotype's.

*Distribution.*—*L. tepukapili* is known presently from two islands, Tepuka and Fuakea, in the Funafuti Atoll, Tuvalu. Limited searches on the main atoll island of Fonafale did not reveal any specimens.

*Natural history.*—McLean and Hosking (1992) described the habitats of Funafuti Atoll, and Tepuka's vegetation is almost entirely a 'Coconut and Broadleaf Woodland.' This mixed forest results from gardening

and regeneration, which create a medium density coconut woodland harboring stands and scattered individuals of broadleaf trees, such as the wide ranging *Pisonia*, *Cordia*, *Calophyllum*, *Guettarda*, *Hernandia*, *Morinda*, *Hibiscus*, *Terminalia*, and *Thespesia*. Of these, *Pisonia* and *Hernandia* are the most common species. The understory includes *Ficus* and *Pipturus* scrub, and a groundcover of ferns, e.g., *Asplenium* and *Nephrolepis*. The smaller motu of Fuakea contains only a few coconuts in a similar mixture of broadleaf trees as on Tepuka.

*L. tepukapili* was found under loose bark and in crevices, at one and two metres from the ground on the trunks of living trees, specifically *Calophyllum inophyllum* and coconut. Search time was limited by other bioinventory task, and we believe that *L. tepukapili* probably occurs in a larger variety of microhabitats and tree types.

#### Comparison to Other Group II Members

As noted in the Introduction, the three species groups of *Lepidodactylus* are phenetically delimited. No study has tested the monophyly of these groups or, for that matter, tested the monophyly of the taxon *Lepidodactylus* (Kluge [1968] provided a set of diagnostic traits for this genus but did not address monophyly.). These two tasks are beyond the goals of our study; however, we wish to examine briefly the phylogenetic relationships of *L. tepukapili*.

Our assessment of relationships assumes the monophyly of the *guppyi* complex (=Group II *Lepidodactylus*). Tables 1 and 2 provide a summary of select mensural and scalation characteristics of this complex. Only three species (*gardineri*, *guppyi*, *vanuatuensis*) are represent by reasonable, yet statistically inadequate, samples of adult specimens. Sexual dimorphism is a common attribute among geckos. All members of the *guppyi* complex show this dimorphism in the presence of secreting precloacal-femoral pores in adult males and their absence in adult females. Otherwise there

Table 1.—Summary of selected mensural traits of adults of Group II *Lepidodactylus* species. Abbreviations are defined in section I of Appendix. Medians and ranges are presented for adults; SVL is in millimeters, proportions in percent; and sample size is in parentheses below specific name, females and males, respectively.

Taxon	SVL		Head/SVL	HeadW/SVL	OrbD/HeadL	Intorb/HeadL	TrunkL/SVL	CrusL/TrunkL
	Female	Male						
<i>gardineri</i>	49.7	49.7	23	11	30	32	44	27
(4, 5)	47.5–50.0	43.1–50.1	22–24	9–12	29–31	29–36	44–46	24–33
<i>guppyi</i>	45.6	40.5	24	10	30	36	48	24
(3, 4)	37.3–54.4	36.1–47.9	22–24	8–11	28–35	31–37	45–51	22–28
<i>intermedius</i> <sup>1</sup>	—	39.0	—	—	—	—	—	—
(2, 1)	?–42							
<i>lombocensis</i> <sup>2</sup>	38.0	37.5	—	—	—	—	—	—
(1, 1)								
<i>novaeguineae</i>	38.2	38.6	24	10	32	32	48	24
(5, 2)	35.8–39.0	38.3–38.9	23–25	8–12	30–33	29–36	44–51	21–24
<i>paurolepis</i>	—	37.7	23	9	29	31	46	25
(0, 3)		37.4–38.4	22–23	9–10	28–33	29–33	46–48	25–26
<i>pulcher</i>	—	39.0	25	11	33	29	45	27
(0, 1)								
<i>shebae</i> <sup>3</sup>	36.0	—	25	17	30	—	—	—
(1, 0)								
<i>tepukapili</i>	41.1	43.5	24	12	31	32	43	29
(1, 3)		43.1–50.3	23–25	11–12	28–33	30–33	42–49	26–29
<i>vanuatuensis</i>	44.2	35.3	24	10	30	31	47	24
(6, 4)	40.0–46.5	33.0–39.2	22–25	8–12	27–34	29–33	44–50	21–28

Data from literature: <sup>1</sup> Darevsky 1964; <sup>2</sup> Mertens 1929; <sup>3</sup> Brown & Tanner 1949.

is little commonality in the traits displaying statistically significant (Student's *t* test,  $p < 0.05$ ) sexual dimorphism among these three samples. Only one other character, ForefL displays sexual dimorphism in *L. guppyi*, five characters (Suplab, CloacS, HeadL/SVL, HeadW/SVL, OrbD/HeadL) in *L. gardineri*, and seven characters (SVL, TrunkL, HeadW, EyeEar, SnW, Inflab, HeadL/SVL) in *L. vanuatuensis*. The sample sizes are simply too small to decide whether these dimorphic differences are real or a sampling bias. We provide body size differences for both males and females

in Table 1, but otherwise the data are medians and ranges for all adult specimens (Tables 1, 2).

In overall size, *L. gardineri* averages larger than any other *guppyi* member (Table 1) and appears to have equal-sized females and males. *L. guppyi* and *L. tepukapili* are the next largest geckos of this group; females average larger in *L. guppyi* and possibly the reverse in *L. tepukapili*, but the small samples argue for caution for such an interpretation. Caution is re-enforced by the *L. vanuatuensis* sample with females nearly as large as female *L. guppyi* yet with males

Table 2.—Comparison of the relative head dimension of adult *Lepidodactylus gardineri* and *L. tepukapili*. Abbreviations are defined in section I of Appendix. Medians and ranges are presented for adults; proportions in percent; and sample sizes are same as in Table 1.

Taxon	HeadL/SVL	HeadH/SVL	HeadH/HeadL	EyeEar/HeadL	NeckL/HeadL
<i>gardineri</i>	23	103	45	34	157
	22–24	98–116	44–49	31–36	150–165
<i>tepukapili</i>	24	123	50	30	148
	22–25	107–126	47–53	26–35	138–154

Table 3.—Summary of selected scalation traits of adult Group II *Lepidodactylus*. Abbreviations are defined in section I of Appendix. Median and ranges of the traits are presented when known; all values are for females and males, except males only for CloacS and PoreRS; sample sizes are same as in Table 1.

Taxon	IntorbS	Suplab	Midbody	CloacS	PoreRS	PreclPore	PreclP	ForefL	HindfL	LamNL	Web
<i>gardineri</i>	33	9	111	3	39	38	18	15	12	4	1
	31–35	8–10	103–118	2–3	46–41	38–41	13–22	12–16	12–17	3–4	1–1
<i>guppyi</i>	35	9	115	2	42	41.5	14	13	10	3	2
	33–37	8–11	110–133	0–4	39–44	33–43	12–15	11–15	9–12	2–4	1–2
<i>intermedius</i> <sup>1</sup>	—	10–11	—	—	—	24	—	9–10	10–12	—	1
		(10) <sup>3</sup>	(121) <sup>3</sup>	(2) <sup>3</sup>					(8) <sup>3</sup>		
<i>lombocensis</i> <sup>21</sup>	—	9–10	—	—	—	20	—	10–11	12–14	—	—
		(11) <sup>3</sup>	(110–112) <sup>3</sup>	(1–2) <sup>3</sup>							(1) <sup>3</sup>
<i>novaeaguineae</i>	35	9	118	2	18	16	16	12	11	2	2
	32–39	8–10	108–125	2–2	15–19	13–19	14–19	10–12	10–13	2–3	2–3
<i>paurolepis</i>	32	10	100	1	31	26	12	14	13	3	2
	31–32	10–11	99–110	1–2	30–33	25–29	11–13	11–14	12–16	3–3	1–1
<i>pulcher</i>	39	10	143	1	13	13	14	16	20	1	1
<i>shebae</i> <sup>4</sup>	—	10	—	—	—	—	—	—	11	2–3	2
						(30 or 32) <sup>3</sup>					
<i>tepukapili</i>	33	8.5	110	2	41.5	39	13.5	14.5	12	4	1
	29–35	7–9	105–118	1–2	37–45	38–40	12–17	14–16	12–13	4–4	1–1
<i>vanuatuensis</i>	33	9.5	100	1	40	26	13.5	12.5	11.5	3	1
	31–35	9–10	91–118	1–2	30–43	10–40	8–21	10–14	10–14	2–4	1–2

Data from literature: <sup>1</sup> Darevsky 1964; <sup>2</sup> Mertens 1929; <sup>3</sup> Ota et al. 2000; <sup>4</sup> Brown & Tanner 1949.

averaging smaller than all other *guppyi* group males or females (Table 1).

The standard head proportion traits (Table 1) of *Lepidodactylus* systematics show little difference among *guppyi* members; however, the shorter relative trunk length (TrunkL/SVL) and the longer relative crus length (CrusL/TrunkL) differentiate *L. gardineri* and *L. tepukapili* from the other *guppyi* members. Although these latter two species appear quite similar, several aspects of head shape (Table 2) are different. *L. tepukapili* has a thicker head relative to both body (HeadH/SVL) and head length (HeadH/HeadL) than does *L. gardineri*. This difference appears associated with a somewhat shorter head (EyeEar/HeadL, NeckL/HeadL; Table 2) in *L. tepukapili*. These proportional differences in head shape are not evident to the authors' eyes.

Discriminant function analyses (stepwise, backward entry) of male and female morphometric data show a strong differentiation of *L. gardineri* and *L. tepukapili* in multivariate space (Fig. 3). In the female

analysis, none of the thirteen characters were eliminated in the final step, and classification attained 100% for the five taxa. For males, the final step retained six characters (SnEye, SnForel, SnW, NarEye, OrbD, CrusL) and attained 100% classification for all taxa except *L. guppyi* and *L. vanuatuensis* (75% each). Neither the relative positioning of the taxa clusters nor the classification accuracy should be weighed too heavily in interpretation of relationships owing to the small sample sizes of all taxa. We note only that these data offer confirmation to our interpretation of speciation of the Tuvalu population.

*L. gardineri* and *L. tepukapili* are similar in scalation (Table 3) with the exception of the pubic patch of enlarged scales, which is larger and has more scales in *L. gardineri*. In this trait, *L. gardineri* differs from all other Group II members; all other members are similar with the exception of *L. novaeaguineae* and its intermediate-sized patch. Our impression is that *L. gardineri* and *L. tepukapili* are more similar to one another

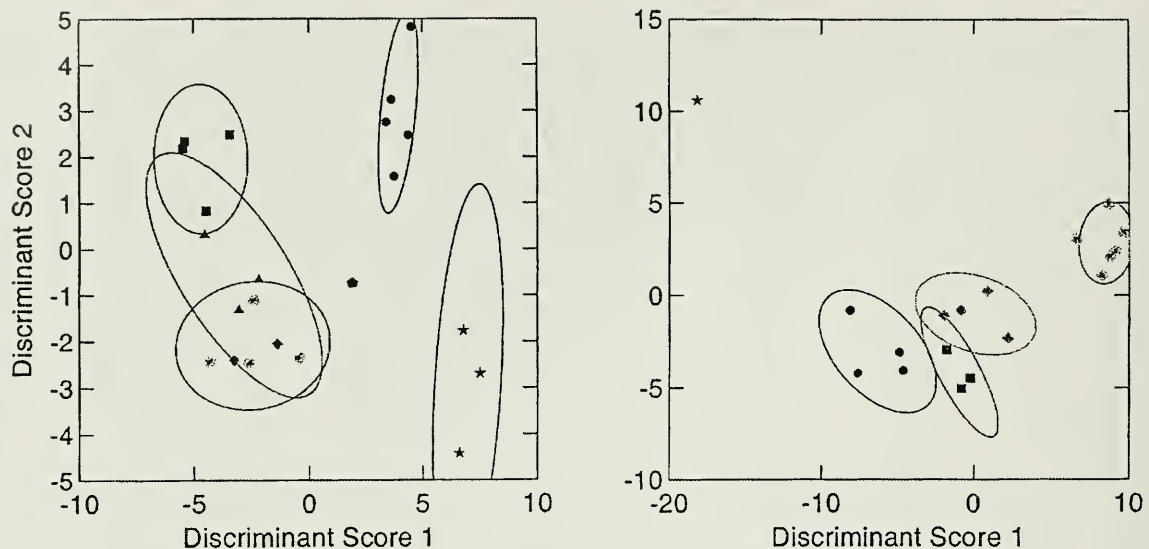


Fig. 3. Discriminant functional analyses of morphometric characters of Group II *Lepidodactylus*, males (left) and females (right). Each ellipse defines the 60% confidence limit. Species symbols are: *gardineri*, circle; *guppyi*, square; *novaeaguineae*, diamond (no confidence ellipse shown for males); *paurolepis*, triangle; *pulcher*, pentagon (no confidence ellipse); *tepukapili*, star; *vanuatuensis*, star burst.

than either is to any other *guppyi* member. This similarity and the uniquely shared intense melanism of the oral cavity indicate that these two taxa share a common ancestor. They also presently represent the deepest penetration of Oceania by the Group II species. Their discovery in Tuvalu and the persistence of large tracts of forest in Samoa suggest that one of these taxa or a close relative probably occurs there also.

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#### Literature Cited

- Austin, C. C. 1999. Lizards took express train to Polynesia.—*Nature* 397:113–114.
- Brown, W. C., & F. Parker. 1977. Lizards of the genus *Lepidodactylus* (Gekkonidae) from the Indo-Australian Archipelago and the islands of the Pacific, with descriptions of new species.—*Proceedings of the California Academy of Sciences*, 4<sup>th</sup> ser. 41:253–265.
- , & V. M. Tanner. 1949. Discovery of the genus *Pseudogekko* with description of a new species from the Solomon Islands.—*The Great Basin Naturalist* 9:41–45.
- Case, T. J., D. T. Bolger, & K. Petren. 1994. Invasions and competitive displacement among house geckos in the tropical Pacific.—*Ecology* 75: 464–477.
- Darevsky, I. S. 1964. Two new species of gekkonid lizards from the Komodo island [sic] in Lesser Sundas Archipelago.—*Zoologischer Anzeiger* 173:169–174.
- Kluge, A. G. 1967. Systematics, phylogeny, and zoo-

- geography of the lizard genus *Diplodactylus* Gray (Gekkonidae).—Australian Journal of Zoology 15:1007–1108, plates 1–19.
- . 1968. Phylogenetic relationships of the gekkonid lizard genera *Lepidodactylus* Fitzinger, *Hemiphyllodactylus* Bleeker, and *Pseudogekko* Taylor.—Philippine Journal of Science [1966] 95:331–352.
- , & M. J. Eckardt. 1969. *Hemidactylus garnottii* Duméril and Bibron, a triploid all-female species of gekkonid lizard.—Copeia 1969(4):651–664.
- Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985(3):802–832.
- McLean, R. F., & P. L. Hosking. 1992. Tuvalu Land Resources Survey—Island Report No. 7 Funafuti. Prepared for the FAO/UNDP by the Dept. of Geography, Auckland University, New Zealand.
- Mertens, R. 1929. Zwei neue Haftzeher aus dem Indo-Australischen Archipel (Rept.).—Senckenbergiana 11:237–241.
- Ota, H., R. I. S. Darevsky, I. Ineich, & S. Yamashiro. 2000. Reevaluation of the taxonomic status of two *Lepidodactylus* species (Squamata: Gekkonidae) from the Lesser Sunda Archipelago, Indonesia.—Copeia 2002(4):1109–1113.
- , R. N. Fisher, I. Ineich, & T. J. Case. 1995. Geckos of the genus *Lepidodactylus* (Squamata: Reptilia) in Micronesia: description of a new species and reevaluation of the status of *Gecko moestus* Peters, 1867.—Copeia 1995:183–195.
- , & T. Hikida. 1988. A new species of *Lepidodactylus* (Sauria: Gekkonidae) from Sabah.—Copeia 1988:616–621.
- Zug, G. R. 1998. Australian populations of the *Nactus pelagicus* complex (Reptilia: Gekkonidae).—Memoirs of the Queensland Museum 42: 613–626.

## Appendix

### I. Characters and analysis

Kluge (1967) defined a basic set of measurement and scale counts for geckos and subsequently (Kluge and Eckardt 1969) added additional characters and redefined some of the earlier ones. These characters and their definitions have been largely adopted by other herpetologists (e.g., Ota and Hikida 1989). We use a subset of these characters and their definitions. Each character and its abbreviation follow; we include a definition only where we record the character differently than the preceding researchers. Abbreviations follow Zug (1998) for ease of recognition. All characters reported for the right side.

*Mensural characters.*—Crus length: **CrusL**—Length of tibia from knee to heel. Eye-ear length: **EyeEar**. Head height: **HeadH**—Dorsoventral distance from the top of head to the underside of the jaw at the transverse plane intersecting the angle of jaws. Head length: **HeadL**. Head width: **HeadW**—Straight-line distance from left to right outer edge of jaw angles; this distance does not measure the jaw musculature broadening of the head. Interorbital width: **Interorb**—Transverse distance between the anterodorsal corners of left and right orbits. Nares-eye length: **NarEye**. Orbit diameter: **OrbD**—Eye diameter or length of other authors, although they measure anteroposterior axis length of orbit. Snout-eye length: **SnEye**. Snout-forelimb length: **SnForel**. Snout-vent length: **SVL**. Snout width: **SnW**—Internasal distance of other authors. Trunk length: **TrunkL**—Body length or axilla-groin length of others; distance between the posterior edge of the forelimb insertion (axilla) to the anterior edge of the hindlimb insertion (inguen).

*Meristic characters.*—Circumnasal scales: **CircNa**—Number of scales abutting naris, exclusive of rostral and first infralabial. Chin (secondary postmentals) scales: **Chin**—Number of scales transected by straight line from left to right 3<sup>rd</sup>-4<sup>th</sup> infralabial sutures. Cloacal spurs: **CloacS**. Femoral pores: **FemPor**—Number of pores perforating scales and secreting. Forefoot lamellae (scansors): **ForefL**—Number of 4<sup>th</sup> digit lamellae; lamella is wider than deep and contacts the marginal scales; fragmented proximal scales are excluded. Hindfoot lamellae (scansors): **HindfL**—As for ForefL. Infralabials: **Inflab**. Interorbital scales: **IntorbS**. Lamellar notching, first: **LamNF**—The number of the first lamella divided or deeply notched on 4<sup>th</sup> digit of hindfoot counting from terminal or ultimate lamella. Lamellar notching, last: **LamNL**—The last divided or notched lamellae, as in LamNF. Mental size: **Men**—Width to height proportion; scored as for Ros. Midbody scale rows: **Midb**. Naris-infralabial contact: **NaInf**—Naris abuts or separated from first infralabial. Naris-rostral contact: **NaRos**—Naris abuts or separated from rostral by scale. Precloacal and femoral pore-scales in contact: **PoreC**—Precloacal and femoral scales bearing pores, separate or continuous. Pore row scales: **PoreRS**—Number of enlarged scales in the precloacal-femoral pore-scale row, whether or not the scales contain pores. Postmental (primary) scales: **PosMen**—Number of scales touching mental and infralabials from left to right 3<sup>rd</sup>-4<sup>th</sup> infralabial sutures. Precloacal (preanal) pores: **PrecIPor**—As for FemPor. Precloacal scale patch: **PrecIP**—Number of scales as large or larger than the scales bearing precloacal pores and slightly larger than surrounding scales. Rostral size: **Ros**—Width to height proportion: 1, W = H; 1.5, W 1.5 times H; etc. in 0.5 intervals. Rostral cleft (crease): **RosC**—Absence or presence of midline cleft or crease. Snout scales: **SnS**—Number of scales between left and right nares and touching rostral. Sub-



caudal scales: **Subcaud**—Size of the median subcaudal scales relative to the dorsal caudal scales; score as for Ros. Supralabials: **Suplab**. Webbing: **Web**—Relative amount of webbing, four states: 0, none between the 2<sup>nd</sup> and 3<sup>rd</sup> digit of hindfoot; 1, slight, basal  $\frac{1}{4}$  of 2<sup>nd</sup> digit's length; 2, moderate,  $\frac{1}{4}$  to  $\frac{1}{3}$ ; 3, strong, more than  $\frac{1}{3}$ .

*Sex and maturity*.—Examination of the gonads revealed sex and maturity. Females were considered mature when they possessed vitellogenic follicles, typically >1.5 mm diameter, oviducal eggs, or stretched oviducts; males when the testes and epididymides were enlarged, supplemented by the presence of secreting precloacal or femoral pores.

*Comments on characters*.—Several researchers have attempted to quantify digit shape and length, as well as other traits. Although we support quantification because it permits statistical analysis and presumably removes a degree of bias or subjectivity, many voucher specimens are not carefully prepared resulting in bent or folded specimens or parts thereof. Thus, we believe that quantification of some characters implies a degree of accuracy, which does not exist. Our selection of mensural characters emphasizes those possessing termini ending on bone and along axes that have rigorous bony struts reducing compression or bending. SnForel and TrunkL, for example, are two useful measurements

but also two that can have significant variation resulting from poor preparation.

## II. Specimens examined

Museum abbreviations follow Leviton et al. (1985).

*Lepidodactylus gardineri* Boulenger 1897 [type-locality: "Rotuma, north of the Fiji Islands"]. Rotuma: USNM 268142, 268145, 268147–48, 268151, 268153–54, 268156, 268161, 268169.

*Lepidodactylus guppyi* Boulenger 1884 ["Faro Island"]. Solomon Islands: CAS 139650, 156114; UMMZ 99966; USNM 120346, 120877–079, 313866.

*Lepidodactylus novaeguineae* Brown & Parker 1977 ["Lake Sentani area, West Irian"]. Papua New Guinea: CAS 11028–029, 12182, 89684; UMMZ 122450; USNM 112824–27, 119248.

*Lepidodactylus paurolepis* Ota, Fisher, Ineich & Case 1995 ["Ngerukewid Group (7°11'N, 134°16'E), Belau islands"]. Palau: USNM 284400, 284402–403.

*Lepidodactylus pulcher* Boulenger 1885 ["Admiralty Islands"]. Papua New Guinea: CAS 139832.

*Lepidodactylus tepukapili* new species. Tuvalu: USNM 531712–716.

*Lepidodactylus vanuatuensis* Ota, Fisher, Ineich, Case, Radtkey & Zug 1998 ["... Espíritu Santo Island ..."]. Vanuatu: USNM 323264–268, 334163, 334184–189.