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LIZARDS OF THE GENUS *LEPIDODACTYLUS* (GEKKONIDAE) FROM
THE INDO-AUSTRALIAN ARCHIPELAGO AND THE ISLANDS OF
THE PACIFIC, WITH DESCRIPTIONS OF NEW SPECIES

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ABSTRACT: An annotated list and a key to species of the genus *Lepidodactylus* recorded from the Indo-Australian Archipelago are presented; four new species (*L. magnus*, *L. mutahi*, *L. novaeguineae*, and *L. orientales*) from New Guinea and the Solomon Islands are described. The relationships and distribution of the species are discussed.

INTRODUCTION

While revising Philippine species of the genus *Lepidodactylus*, one of us (Brown) examined samples, including types of extra-Philippine species. In the course of these comparisons, it became evident that the Indo-Australian species of *Lepidodactylus*, with the exception of the *lugubris-woodfordi* complex, comprise two groups distinct from the species in the Philippines. Also recent extensive collections from New Guinea and the Solomons include previously undescribed species. It seems most appropriate to present these results in a report separate from our monograph, currently in preparation, on the gekkonid lizards of the Philippines.

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TABLE I. Counts, measurements and pertinent ratios for species of *Lepidodactylus*.

Species (No. of Specimens used)	Snout-Vent Length at Maturity	No. of Pores (♂)	No. of 4th Toe Scansors	No. of 1st Toe Scansors	No. of Divided Scansors on 4th Toe	Terminal Scansor Entire or Divided	Webbing Between 3rd & 4th Toes	No. of Upper Labials	Ratios			
									Eye Diameter	Head Breadth		Hind Limb Length
										Snout Length	Snout-Vent Length	
Group I												
<i>L. listeri</i> (4)	40.8-46 (2 ♂)	11-14	11-13	8-10	0	entire	base+	10-12	74-84%	20-22%	83-89%	
<i>L. magnus</i> (20)	50-71 (15 ♂)	38-49	10-13	10-12	0	entire	1/5±	10-12	80-88%	17-20%	74-84%	
<i>L. manni</i> (7)	38.6-42.7 (2 ♂)	12-13	9-12	8-10	0	entire	base+	9-12	79-88%	20-22%	72-87%	
<i>L. nutahi</i> (15)	37.2-56 (16 ♂)	27-34	10-11	8-10	0	entire	1/4±	11-12	79-90%	17-20%	73-84%	
<i>L. oorti</i> (3)	53.7-57 (2 ♂)	28-29	13-14	9-10	0	entire	base+	10-12	67-72%	20-21%	73-80%	
<i>L. orientalis</i>	37± (1 ♂)	19 (1)	10-11	8-9	0	entire	base-1/6	10-11	69-86%	18-19%	67-78%	
<i>L. pumilus</i> (18)	38.4-45.0 (4 ♂)	31-40*	11-12	8-9	0	entire	1/6-1/2	10-12	81-94%	14-16%	59-67%	
Group II												
<i>L. gardeneri</i> (1)	45.3 (1 ♂)	—	12	11	2-3	entire	base+	11	75±%	17±%	71±%	
<i>L. guppyi</i> (20)	37.5-48.2 (10 ♂)	39-51	11-13	8-10	2-4	entire	1/4±	11-13	78-88%	16-19%	67-77%	
<i>L. novaequinae</i> (15)	36.7-41.2 (7 ♂)	11-18	11-16	8-11	1-3	entire	1/4-1/3	9-12	85-97%	16-20%	65-77%	
<i>L. pulcher</i> (3)	54± (1 ♂)	16	17-19	10-13	2-3	entire	1/4-1/3	10-12	70-85%	18-19%	81-85%	
<i>L. shebae</i> (1)	36.2 (1 ♂)	32	11	—	2	entire	1/5	10	78±%	16-17%	—	
Group III												
<i>L. lugubris</i> (20)	37.3-48 (10 ♂)	19-26 (5)	11-15	9-11	3-4	divided	1/6±-1/4	10-12	75-85%	17-22%	74-87%	

* In separate preanal series (10-14) and femoral series (10-14).

examining pertinent material. CAS and CAS-SU refer to collections at the California Academy of Sciences. I am also deeply indebted to my colleagues Dr. Alan E. Leviton and Mr. Robert C. Drewes for their assistance and suggestions. Illustrations were prepared by L. Meszoly of the Museum of Comparative Zoology, Harvard University, and W. Zawojski of Stanford University. This study is part of the Philippines-Pacific Islands research project under the auspices of National Science Foundation Grant GB-41947.

SYSTEMATIC SECTION

The available keys to *Lepidodactylus*, such as those of Taylor (1922) and de Rooij (1915) have not proven satisfactory to the non-specialists. For this reason, we have combined a more or less typical key to species-groups with diagnoses of species which should prove more useful.

DIAGNOSTIC KEY TO SPECIES OF *LEPIDODACTYLUS*
OCCURRING IN THE INDO-AUSTRALIAN
ARCHIPELAGO AND ISLANDS OF THE PACIFIC
(See Table 1 for additional data on species.)

- 1a. A relatively small species, adults usually less than 50 mm snout-vent length; terminal and 2-4 subterminal scansors on all digits but first divided (Fig. 1a); range of fourth toe scansors 11-15, covering distal 3/4 to 4/5 of toe; tail usually moderately flattened, with lateral fringe evident (rarely subcylindrical); usually parthenogenetic; males, when present in populations, with about 20-30 preanal and femoral pores
..... *L. woodfordi-lugubris* complex
- 1b. Terminal scansor on all digits entire or slightly notched (Fig. 1b); subterminal scansors entire or a few distal ones divided; tail subcylindrical without lateral fringe..... 2
- 2a. One or more (usually 2-4) subterminal scansors divided medially (Figs. 1b and 1d) 3
- 2b. All scansors entire, or at most, with only shallow median notches (Figs. 1c and 1e) 6
- 3a. Enlarged scales of pore-series and pores limited to preanal region or including only 1 or 2 scales on proximal part of thigh; no greatly enlarged scales on rest of thigh; usually 20 or fewer preanal pores in males 4
- 3b. Enlarged scales of pore-series not limited to preanal region, at least one or more rows of scales on thigh distinctly enlarged although they may be separated from preanal series; 25 or more preanal and femoral pores in males 5
- 4a. An intermediate-sized species, adults about 40-55 mm snout-vent length; 16-19 fourth toe scansors, covering toe to base (Fig. 1d); 11-13 first toe scansors; 1/4 to 1/3 webbed between third and fourth toes; 18-20 enlarged scales in preanal pore-series, bearing 16 pores for one male; brown blotches on head and nape (sharply outlined for Wild Island specimens), length of hind limb more than 80% of axilla-groin distance *L. pulcher*
- 4b. A small species, adults about 36-45 mm snout-vent length; 11-16 fourth toe scansors, covering approximately distal 3/4 of toe; 8-11 first toe scansors; 1/6 to 1/4 webbed between third and fourth toes; 16 to 20 enlarged scales in preanal pore-series, bearing 12-19 pores for males; length of hind limb about 65 to 75% of axilla-groin distance; blotches on head and nape not sharply outlined
..... *L. novaeguineae* new species
- 5a. A relatively small species, 45± snout-vent length (one available adult); 12 fourth toe scansors, covering distal 3/4 of toe; 11 first toe scansors; webbed only at base between third and fourth toes; the unique holotype, female, with about 38-39 enlarged preanal and femoral scales in position of pore-series, covering basal 3/4 plus of thigh
..... *L. gardeneri*
- 5b. A small to moderate-sized species, adults usually less than 50 mm in snout-vent length; 11-13 fourth toe scansors, covering distal 2/3 to 3/4 of toe (Fig. 1b); 8-10 first toe scansors; about 1/4 to 1/3 webbed between third and fourth toes; 40-52 enlarged preanal and femoral scales in position of pore-series, continuous and extending almost to distal end of thigh; bearing 39-52 pores (sample of 9 males) *L. guppyi*
- 5c. A relatively small species, about 36 mm snout-vent length for known adult speci-

- men; digits moderately dilated; $11 \pm$ fourth toe scansors, 2 subterminal ones divided; toes $\frac{1}{5}$ to $\frac{1}{4}$ webbed; unique holotype (a male) with about 34 enlarged preanal and femoral scales in the position of the pore-series, continuous, bearing 32 pores *L. shebae*
- 6a. Adult size relatively small; enlarged scales of pore-series and pores limited to the preanal region or with only 2 or 3 on proximal part of thigh; usually 20 or fewer preanal pores in males; webbed at base to $\frac{1}{6}$ between 3rd and 4th toes 7
- 6b. Adult size variable; 26–50 or more enlarged preanal and femoral pore scales in the position of the pore-series, in either a continuous series or separate preanal and femoral series; 25 or more preanal and femoral pores in a continuous or separate series in males 9
- 7a. Small to moderate-sized species, adults usually less than 50 mm snout-vent length; digits relatively broadly dilated; 9–12 undivided fourth toe scansors, covering distal $\frac{3}{4}$ of toe; 8–10 first toe scansors; webbed at base or to $\frac{1}{6}$ between third and fourth toes; usually 18 or fewer scales in position of pore-series, limited to preanal region or with only one or two such scales on base of thigh; bearing 15 or fewer preanal pores in males; (see note under Discussion) ... 8
- 7b. A relatively small species, 37 to 43 mm snout-vent length (3 adults); digits long and relatively slender; 10–12 undivided fourth toe scansors, covering approximately distal $\frac{2}{3}$ of toe; 20–24 enlarged scales in pore-series, confined to the preanal region or only a few on base of thigh; bearing 19 preanal pores (sample of one male)
..... *L. orientalis* new species
- 8a. Limited to Fiji Islands in central Pacific Ocean *L. manni*
- 8b. Limited to Christmas Island in Indian Ocean *L. listeri*
- 9a. Usually $\frac{1}{4}$ or more webbed between third and fourth toes; usually 12 or fewer scansors beneath the fourth toe 10
- 9b. Usually only $\frac{1}{5}$ or less webbed between third and fourth toes; usually more than 12 scansors beneath the fourth toe 11
- 10a. A relatively small species, 34 to 48 mm snout-vent length (12 adults); digits relatively short and broadly dilated; 11–13 entire fourth toe scansors, covering the distal $\frac{1}{2}$ to $\frac{2}{3}$ of the toe (Fig. 1e); $\frac{1}{3}$ to $\frac{1}{2}$ webbed between third and fourth toes; 12–15 enlarged scales in preanal pore-series, separated by several scales (7 to 12 in samples) from moderately enlarged femoral series; bearing 11–14 preanal pores separated from femoral series of 10 to 14 in males; length of hind limb about 59 to 70% of axilla-groin distance *L. pumilus*
- 10b. A moderately large species, adults from about 40 to 55 mm snout-vent length; digits moderately dilated; 10 or 11 entire fourth toe scansors, covering approximately the distal $\frac{2}{3}$ of toe; about $\frac{1}{4}$ webbed between third and fourth toes; 28–36 enlarged preanal and femoral pore scales, extending almost to distal end of thigh; bearing a continuous series of 27–34 pores in males; length of hind limb usually more than 70% of axilla-groin distance *L. mutahi* new species
- 11a. A relatively large species, 53 to 57 mm snout-vent length (3 adults); digits moderately dilated; 12–14 entire fourth toe scansors; 9 or 10 first toe scansors; webbed at base only between third and fourth toes; 32–36 enlarged preanal and femoral pore scales in continuous series, extending over proximal $\frac{2}{3}$ of thigh; bearing 28–30 pores in males *L. oorti*
- 11b. A large species, adult males measure 50 to 71 mm snout-vent length; 12–15 entire fourth toe scansors (Fig. 1c); 10–12 first toe scansors, $\frac{1}{6}$ to $\frac{1}{5}$ webbed between third and fourth toes; 40–50 enlarged preanal and femoral pore scales in a continuous series, extending almost to distal end of thigh; bearing 38 to 49 pores in males *L. magnus* new species

LEPIDODACTYLUS SPECIES OF THE
INDO-AUSTRALIAN ARCHIPELAGO AND ISLANDS OF THE PACIFIC

***Lepidodactylus gardeneri* Boulenger**

Lepidodactylus gardeneri BOULENGER, 1897:306 (type-locality: Rotuma Island, Polynesia; type in BMNH).

MATERIAL EXAMINED.—BMNH 1946.8.22.35 (holotype).

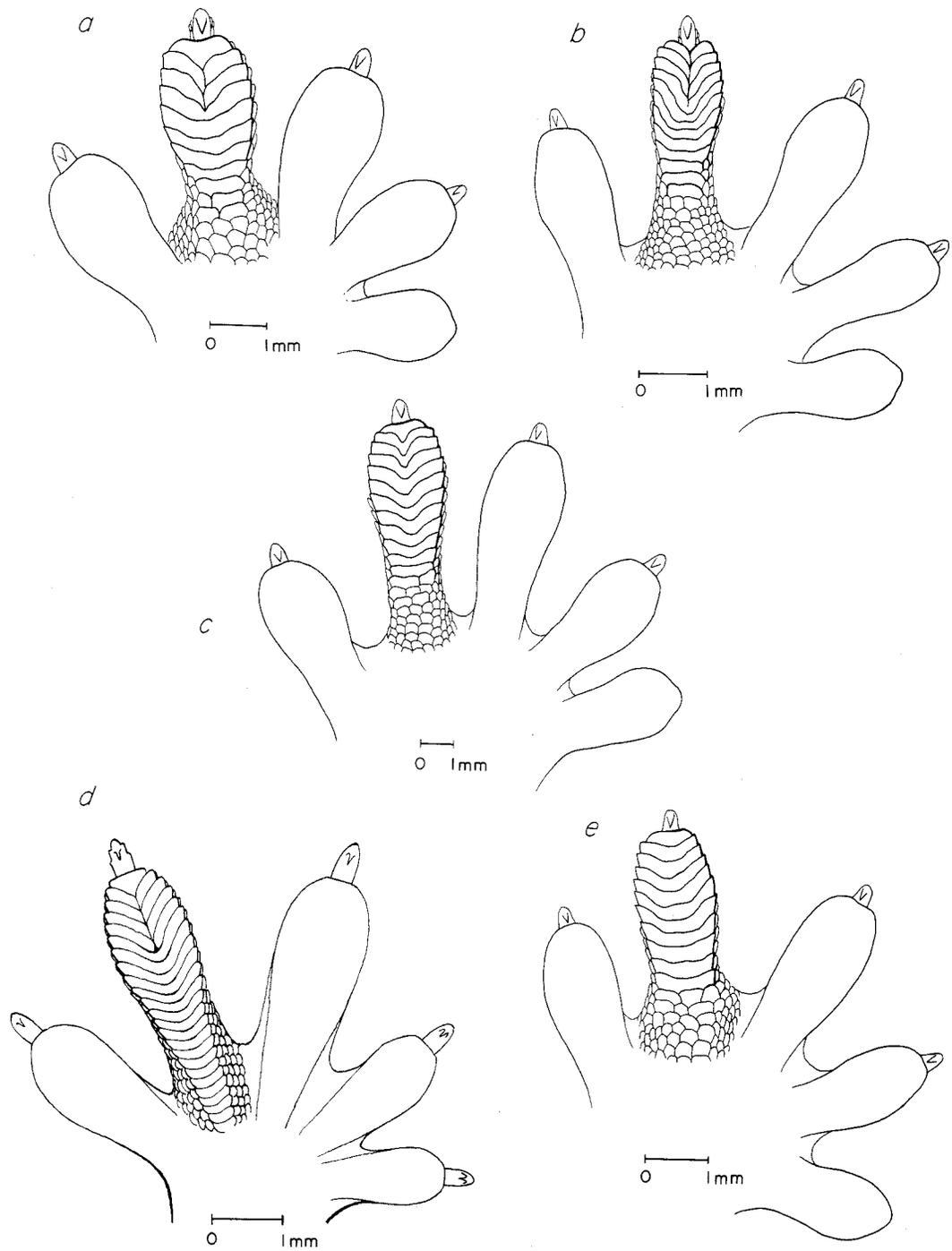


FIGURE 1. Inferior view of foot of five species of *Lepidodactylus*: (a) *L. lugubris*; (b) *L. guppyi*; (c) *L. magnus*; (d) *L. pulcher*; (e) *L. pumilus*.

RANGE.—The known range is the type-locality, Rotuma Island.

Lepidodactylus guppyi Boulenger

Lepidodactylus guppyi BOULENGER, 1884:210 (type-locality: Faro Island, Solomon Islands; holotype in BMNH).

MATERIAL EXAMINED.—BMNH 84.3.2.54 (holotype); 1972.223-4, 1973.218; CAS 139650; MCZ 65862, 67122, 67124, 67126, 74517-19, 75904 ab, 75905, 115559, and 115563-65.

RANGE.—This species has been recorded from Bougainville, Buka, Faro, Guadalcanar, Kolombangara, Malaita, Puruata, Savo, Sterling, and Tulagi Islands in the Solomons. Hediger (1934:490) also lists *L. guppyi* as occurring in New Britain.

Lepidodactylus listeri (Boulenger)

Gecko listeri BOULENGER, 1888:535 (type-locality: Christmas Island, Indian Ocean; syntypes in BMNH).

Lepidodactylus listeri KLUGE, 1967:9

MATERIAL EXAMINED.—BMNH 1946.8.25.91 (holotype), 1905.6.24.16-17, 1909.3.4.7; MCZ 143838; CAS 16861.

RANGE.—This species is known only from Christmas Island in the Indian Ocean.

Lepidodactylus lugubris (Duméril and Bibron)

Platyedactylus lugubris DUMÉRIL AND BIBRON, 1836:304 (type-locality: Otaïti (= Tahiti) Island, Polynesia; holotype in MNHN).

Peropus neglectus GIRARD, 1858:197 (syn. fide M. A. Smith 1935; type-locality: Rio de Janeiro, Brazil; holotype lost).

Hemidactylus meijeri BLEEKER, 1859:47 (syn. fide M. A. Smith 1935; type-locality: Bintang, Rhio-Archipel fide M. A. Smith; holotype in BMNH).

Gecko moestus PETERS, 1867:13 (syn. fide M. A. Smith 1935; type-locality: Palau Islands; holotype in Berlin Museum).

Gymnodactylus caudeloti BAVAY, 1869:13 (syn. fide M. A. Smith 1935; type-locality: New Caledonia; repository data not available).

Peripia mysorensis MEYER, 1874:129 (syn. fide M. A. Smith 1935; type-locality: Mysore (= Biak Island); holotype in Berlin Museum).

Peripia ornata MCLEAY, 1878:98 (syn. fide Kluge 1963; type-locality: Port Moresby, New Guinea; type lost).

Lepidodactylus divergens TAYLOR, 1918:242 (syn. fide M. A. Smith 1935; type-locality: Great Govenen Island, Sulu Islands, Philippines; type lost).

MATERIAL EXAMINED.—MNHN 5323a-b (syntypes); AMNH 65484-87, 66223, 69628, 41867, 41875-77, 41880-87; CAS 50274-96, 60613-18, 62485-86, 72031; CAS-SU 9159-60, 9173, 9175-76, 9178, 9189, 12164-66, 12176-81, 18047-56, one hundred plus uncatalogued; DASF 10297-99, 11462, 11853-60; FMNH 44504, 73377 (paratype, *L. divergens*); MCZ 16403, 19646, 27936, 33518, 48625-31, 49496-97, 69499, 69501a-b, 26087-88 (paratypes, *L. divergens*), 85747-50, 26091-93, 135431-32, 137648-50, 140981; USNM 28239, 68044-46, 68048, 68866, 70736, 119195, 121387, 121398.

RANGE.—This species has a wide distribution in the tropics, extending from India, Sri Lanka (Ceylon) and nearby islands through southeast Asia, Philippines, Indo-Australian Archipelago, northern Australia, islands of the tropical Pacific, and western Mexico and Central America.

Lepidodactylus magnus, new species

Holotype: MCZ 101504, an adult male, collected by J. Higginbotham in the Kol Jim Valley Highlands, Papua New Guinea, 28 Mar. 1967.

Paratypes: Central mountain area of New Guinea between about longitude 142° and 146° E, Lufa area: MCZ 96907-19; Karimui area: MCZ 101505-07, 101509; Nondiri area: MCZ 91602-06, AMNH 98513-14; Yandime area: MCZ 91585-88, AMNH 98512; Orumba area: MCZ 91589; Yangamugl area: MCZ 91597; Chauve area: MCZ 91598-99; Elmagale area: MCZ 91601, CAS 139656; Huon Peninsula: MCZ 54246; Kundiawa area: 109242; Irumbafoie area: MCZ 91591-96, BMNH 1974.4217, AMNH 95209-13; Kaironk Valley: UPNG 3405-17, CAS 139654-55, FMNH 197933, CM 59037, MNHN A833, USNM 198147; Gono: AMNH 92527-43 + 18 uncatalogued, CAS 139830; Kassam: AMNH 92653; Lalang: AMNH 95655; Rugli: AMNH 105880-92; Kwi Valley: MCZ 91597.

DIAGNOSIS.—A large *Lepidodactylus*, snout-vent length about 50 to 70 mm for adults; digits long, moderately dilated, *Gekko*-like; distal two thirds or more of ventral surface bearing undivided scancers, though one to four subterminal ones may occasionally exhibit shallow notches; 12 to 13 scancers beneath fourth toe; 10 to 12 beneath first toe; toes webbed at base between first and second toes and about one-fourth between third and fourth toes; adult males with about 40 to 50 preanal and femoral pores, femoral series extending from base to near the distal end of thigh; sometimes disrupted within femoral series or between preanal and femoral series by one or a few scales; tail subcylindrical, without lateral flange or spines.

DESCRIPTION.—A large *Lepidodactylus*, snout-vent length 50 to 70+ mm in 12 mature males (one 43-mm male immature), 55 to 67 mm in 10 mature females, and 24.5 to 25.9 mm (about 25 to 27 mm before preservation) in four hatchlings; moderately depressed, neither strongly robust nor slender in appearance; snout slightly tapered, rounded, length 38 to 41+% of length of head; internasal distance 46 to 49% of snout length; head breadth 72 to 80% of head length and 17 to 20% of snout-vent length; diameter of eye about 80 to 88% of snout length; rostral about 1-½ times as broad as long, somewhat longer between supranasals than at lateral mar-

gins; nostril surrounded by rostral, first upper labial, supranasal and two enlarged scales dorso-posteriorly; supranasals separated by two or three scales (most frequently three) bordering rostral; 9 to 12 upper labials, eighth to tenth beneath median plane of eye; 9 to 10 lower labials, anterior ones as large as triangular mental; first row of scales behind mental gives appearance of four short chin shields followed by two to three rows of slightly enlarged scales; scales on snout larger than those on dorsal and lateral surfaces of body, which are covered by small, relatively uniform granular scales, enlarged tubercles lacking; limbs moderately developed, length of extended hind limb (in preserved condition) 75 to 84% of axilla-groin distance; toes webbed at base between first and second and as much as $\frac{1}{4}$ between third and fourth; digits moderately dilated throughout their length (*Gekko*-like); breadth of fourth toe about 35 to 42% of its length to base of web; 10 to 13 (most frequently 12) entire scansors under fourth toe, covering approximately distal $\frac{2}{3}$ to $\frac{3}{4}$ of toe (Fig. 1c); 10 to 12 scansors under first toe; all digits but first finger and toe clawed; compressed, clawed phalanges free only at end of dilated part, extending short distance beyond; a series of about 50 enlarged scales in position of preanal and femoral pore-series, bearing 40 to 51 pores in mature males, preanal series forming a broad, rounded arch and femoral series extending almost to distal end of thigh; (femoral series often exhibits some breaks of one to three or four scales without pores); pore-series followed by several rows of enlarged scales in preanal region but only by a single row on thighs before meeting smaller, more granular scales of posterior surface; tail appears subcylindrical, depth just posterior to basal swollen area 74 to 90% of its breadth at same point, and tail breadth 53 to 62% of head breadth; lateral margin without flange of skin or spines; scales on ventral surface of tail larger than on dorsal surface, squarish or at times fused to form quadrangular platelike scales (see also Table 1).

Color. *In preservative*: dorsum and upper lateral surfaces grayish tan or brown, varying from relatively uniform or with a few dark lines or blotches along dorsolateral area to a pattern of five or six diffuse, wide, irregularly margined, transverse bands between nape and base of tail; venter rather uniformly light to heavily flecked with brown. *In life*: neck, body, and tail varying

from pale grayish brown through dark gray-brown to brown; neck and body pattern often with shallow W-shaped bars; tail with pale blotches having distinct anterior border, fading posteriorly into darker ground color to next pale blotch; a pale stripe from ear to axilla and usually from posterior corner of eye to ear; often a pair of dark stripes dorsolaterally on neck and usually a very distinct dark vertebral stripe on base of tail, reaching only to first or second pale blotch; frequently with pale spots around ear, and some specimens with pale spots on dorsum and in a line midlateral surface.

Measurements (in mm) of holotype: snout-vent length 70.7; axilla-groin distance about 34.5; hind limb length 27; length of head 16.7; breadth of head 13.8; snout length 6.7; diameter of eye 5.7; internasal distance 3.2; interorbital distance 3.3; tail breadth at base 7.3; tail depth at base 6.1.

ECOLOGICAL NOTES.—The localities listed for the holotype and paratypes are in the central mountains at elevations between about 1000 and 2000 meters. One of us (Parker) and Professor J. I. Menzies have observed the species in crevices of limestone cliffs, among dead leaves, particularly of *Pandanus* and banana trees, and occasionally in houses, especially those built of bush material. These are resting sites during the day. The species is active at night. Pairs of eggs were found in a vertical fissure in a limestone cliff at Irumbafoie. Two large eggs were also present in the oviducts of several gravid females.

Lepidodactylus manni Schmidt

Lepidodactylus manni SCHMIDT, 1923:51 (type-locality: Suene, Viti Levu, Fiji Islands; holotype in MCZ).

MATERIAL EXAMINED.—MCZ 16880 (holotype), AMNH 81746-51.

RANGE.—This species is known only from the Fiji Islands.

Lepidodactylus mutahi, new species

Holotype: MCZ 127844, an adult male, collected by Fred Parker in Mutahi area, Bougainville Island, Solomon Islands, 17 May 1966.

Paratypes: Bougainville Island, same locality as holotype: MCZ 118317-118321; Tinputz area: MCZ 118316; Kieta area: MCZ 64152, 69216; Kunua area: MCZ 75863-75866, 75869, 77590-77593, BMNH 1974.4218, UPNG 5192; Torokina area: USNM 120875-76, 120880, 120882, CAS 139657.

DIAGNOSIS.—An intermediate-sized *Lepidodactylus*, snout-vent length 37 to 56 mm for

adults; digits moderately dilated (*Gekko*-like); scansors covering approximately distal $\frac{2}{3}$ of ventral surface of fourth toe; scansors undivided but often two to four subterminal ones with shallow notches; toes webbed about $\frac{1}{5}$ between the first and second and about $\frac{1}{4}+$ between third and fourth; adult males with 29 to 34 preanal and femoral pores in a continuous series, extending almost to distal end of thigh; tail subcylindrical without lateral fringe of skin or spines.

DESCRIPTION.—An intermediate-sized *Lepidodactylus*, snout-vent length 37 to 56 mm for 16 mature males, 43 to 50 mm for five mature females; habitus moderately depressed, moderately slender; snout tapered, tip broadly rounded, its length about 39 to 42% of head length; internasal distance 40 to 50% of snout length; breadth of head 67 to 75% of head length and 17 to 20% of snout-vent length; diameter of eye 79 to 90% of snout length; rostral much broader than long and usually with a mid-dorsal bulge between the supranasals; nostril surrounded by rostral, first upper labial, supranasal, and two enlarged scales dorso-posteriorly; supranasals usually separated by two or three scales (rarely one) which border rostral; 10 to 12 upper labials, usually ninth or tenth beneath center of the eye; 9 to 11 lower labials, anterior ones larger than triangular mental; latter followed by four, occasionally five, rows of enlarged scales in position of chin shields, anterior rows largest; scales on snout larger than those on dorsal and lateral surfaces of body which are covered by small, relatively uniform, granular scales; enlarged tubercles lacking; limbs moderately developed, length of extended hind limb (in preserved condition) 73 to 87% of axilla-groin distance; toes webbed, about $\frac{1}{5}$ between first and second, usually about $\frac{1}{4}$ between third and fourth; digits moderately dilated, long; greatest breadth of fourth toe about 37 to 41% of its length to base of web; 9 to 12 undivided scansors beneath fourth toe, covering about distal $\frac{2}{3}$ of toe; 11 to 14 under third toe and 8 to 10 under first toe (Table 1); all digits but first finger and toe clawed; compressed, clawed phalanges rising free at end of dilated part and extending for only short distance beyond; a series of 30 to 36 enlarged scales in position of pore-series; preanal series chevron-shaped, femoral series extending almost to distal end of thigh; a continuous series of 27 to 34 preanal and femoral pores in males; preanal series followed by several rows of en-

larged scales and preceded by two or three rows of slightly enlarged scales; femoral series forming an isolated enlarged row; tail subcylindrical, depth just posterior to basal swollen area 72 to 92% of breadth at same point, and breadth 44 to 51% of head breadth (one example greater than 50%); lateral margins of tail without flange of skin or spines; scales on ventral surface of tail somewhat larger than those on dorsal surface and somewhat squarish.

Measurements (in mm) of holotype: snout-vent length 55.2; axilla-groin distance 26.2; length of hind limb 19.8; head length 14.9; head breadth 9.8; snout length 5.6; diameter of orbit 4.2; tail breadth 5.0; tail depth 3.6; internostril distance 2.2.

Color. *In preservative:* dorsal ground color varies from gray-tan to brown, often with rather vague darker blemishes; venter uniformly light or with brown flecks which are most numerous laterally. *In life:* dorsum varies from pale yellow-brown to dark red-brown; often with a light stripe from eye to ear; usually orange patches on the tail; black blotches or bars which are evident on dorsum of many individuals appear in life to vary for any given individual and are assumed to change in response to some stimulus.

ECOLOGICAL NOTE.—Field observations for the Kunua area (by Parker) indicate the species is most abundant in *Pandanus* in permanent coastal swamps, but that it also occurs in banana trees and newly cleared garden areas.

RANGE.—Known at present only from Bougainville Island.

***Lepidodactylus novaeguineae*, new species**

Lepidodactylus pulcher (part), LOVERIDGE, 1948:334; (part) WERMUTH, 1965.

Holotype: CAS 89684, collected in Lake Sentani area, West Irian, by E. S. Herald, 1944.

Paratypes: West Irian: BMNH 1938.6.6.72, FMNH 43059-60; Hollandia area, West Irian: AMNH 66346; Finchaven area, Marobe District, Papua New Guinea; CAS-SU 11028-29, 12182, USNM 118824-25, 159826-27; Guisika area, Huon Peninsula, Papua New Guinea: USNM 119428, AMNH 66665, 66667, MCZ 49612; Mt. Nibo, Sepik District, Papua New Guinea: AMNH 100209-10.

DIAGNOSIS.—A moderate-sized *Lepidodactylus* distinguished by the following combination of characters: about 36 to 41 mm snout-vent length for 7 mature males; 11 to 14 scansors beneath the fourth toe, covering approximately the distal

$\frac{2}{3}$ of the toes; 8 to 11 beneath first toe (16 to 19 and 10 to 13, respectively, for *L. pulcher* with which species has been confused); tail subcylindrical without fringe or spines; terminal scissor on all digits entire; a few subterminal ones, one to three on fourth toe divided; enlarged scales in pore-series limited to preanal region, about 14 to 18 and bearing 12 to 18 pores in males; toes about $\frac{1}{4}$ to $\frac{1}{3}$ webbed.

DESCRIPTION.—A relatively small *Lepidodactylus*, snout-vent length about 36 to 44 mm in adults; habitus not strongly depressed; snout slightly tapered and broadly rounded, its length about 35 to 39% of head length; internasal distance 48 to 58% of snout length; breadth of head 67 to 81% of head length, and 16.5 to 21% of snout-vent length; diameter of eye 85 to 97% of snout length; rostral about twice as broad as long, quadrangular to slightly trapezoidal; nostril surrounded by rostral, first labial, supranasal and two enlarged scales dorso-posteriorly; supranasals usually separated by two scales which border the rostral; 9 to 12 upper labials, eighth or ninth beneath the center of the eye; 9 to 12 lower labials, the anterior ones larger than the triangular mental; four or five rows of somewhat enlarged scales, in same position as chin shields, anterior row or two most enlarged; scales on snout larger than those on dorsal and lateral surfaces of body, which are covered by relatively uniform granular scales; enlarged tubercles lacking; limbs moderately developed, length of extended hind limb (in preserved condition) 66 to 76% of axilla-groin distance; digits about $\frac{1}{6}$ to $\frac{1}{3}$ webbed, about $\frac{1}{6}$ between first and second toes, and $\frac{1}{4}$ to $\frac{1}{3}$ between third and fourth toes; digits rather broadly dilated, noticeably more so in distal half; breadth of fourth toe 37 to 40% of its length to the base of the web; terminal scissor on all digits entire; two or three subterminal scissors divided medially; 11 to 16 scissors beneath fourth toe, covering about the distal $\frac{2}{3}$; all digits but first finger and toe clawed, compressed, clawed phalanges rising free at end of dilated part and extending for only a short distance beyond; about 16 to 20 enlarged scales in position of pore-series, bearing 11 to 19 pores in mature males (sample of three), limited to preanal region or with one or two at base of thigh; tail subcylindrical, depth just posterior to basal swollen area about 75 to 85% of breadth at a corresponding point, and tail breadth about 47 to 58% of head breadth; lateral margin without

fringes or spines; scales on ventral surface of tail larger than those on dorsal surface and more or less squarish in shape (see also Table 1).

Color. *In preservative:* dorsal ground color rusty-tan to grayish, often with vague brownish markings; in some a little lighter in middorsal region and usually rather vague, reddish-brown flecks and markings on dorsal and dorso-lateral surfaces; or occasionally a *woodfordi*-like pattern of diffuse light and dark transverse bands; tail dorsally with a pattern of diffuse to fairly sharp, irregular, tan and reddish-brown cross bands.

Measurements (in mm) of holotype: snout-vent length 40.1; axilla-groin distance 20.1; length of hind limb 15.4; head length 10.1; head breadth 8.1; snout length 3.9; diameter of eye 3.3; tail breadth 4.5; tail depth 3.8; internasal distance 1.9.

ECOLOGICAL NOTE.—Loveridge (1948:334) notes that one of the Gusiko specimens was collected on the trunk of a coconut palm and the other beneath the bark of a dead tree.

RANGE.—Known from Hollandia area, West Irian to Huon Peninsula in northern Papua New Guinea.

Lepidodactylus oorti (Kopstein)

Gekko oorti KOPSTEIN, 1926:77 (type-locality: Teun and Seruna Islands, Banda Sea and Samlakk, Tanimbar Islands; syntypes in BMNH, Leiden Museum and MCZ).
Lepidodactylus oorti KLUGE, 1967:9.

MATERIAL EXAMINED.—BMNH 1946.8.25.9, MCZ 38970 and 39721 (3 syntypes).

RANGE.—The species is known only from the Banda and Tanimbar Islands in the East Indies.

Lepidodactylus orientalis, new species

Gekko pumilus BOULENGER, 1898:697 (not Boulenger, 1885a:473).

Holotype: BMNH, 1897-12-10-7, collected in the Port Moresby area, Central District, Papua New Guinea, by Dr. L. Loria.

Paratypes: Port Moresby area, Central District, Papua New Guinea: PNGM 10025, Konedobu, Central District, Papua New Guinea: MCZ 147357 and CAS 139833.

The holotype of this previously undescribed species was one of three referred by Boulenger (1898) to *G. pumilus*. We have not seen the other two of Dr. Loria's specimens, but we assume they are still in the museum at Genoa.

DIAGNOSIS.—A relatively small *Lepidodactylus* distinguished by the following combination

of characters: snout-vent length 37 to 43 mm for four adults; digits moderately dilated (*Gekko*-like); 10 to 11 scansors covering $\frac{1}{2}$ to nearly $\frac{2}{3}$ of ventral surface of fourth toe; scansors undivided, but two or three subterminal ones often with shallow notches; about $\frac{1}{6}$ webbed between third and fourth toes; adult males with a series of 19 plus or minus preanal pores; enlarged scales in pore-series not extending beyond one or two scales on the base of the thigh; tail subcylindrical without lateral fringe of skin or spines.

DESCRIPTION.—A relatively small *Lepidodactylus*, snout-vent length 37 to 43 mm in four adults; habitus moderately depressed, rather slender; snout tapered, tip broadly rounded, its length about 41 to 43% of head length; internasal distance about 50% of snout length; breadth of head 72 to 76% of head length and 18 to 19% snout-vent length; diameter of eye 69 to 86% of snout length; rostral broader than long, usually with a median, dorsal groove; nostril surrounded by rostral, first upper labial, supranasal, and two enlarged scales dorso-posteriorly; supranasals usually separated by two scales which border the rostral; 10 to 11 upper labials, usually the eighth or ninth beneath the center of eye; 9 or 10 lower labials, anterior ones larger than mental; latter followed by three or four rows of enlarged scales in position of chin shields; scales on snout larger than those on the dorsal and lateral surfaces of the body, which are covered by small, relatively uniform, granular scales; no enlarged tubercles; limbs moderately developed, length of extended hind limb (in preserved condition) 67 to 78% of axilla-groin distance; toes weakly webbed, at base to about $\frac{1}{6}$ between third and fourth toes; digits moderately dilated, long; greatest breadth of fourth toe about 40% of its length to the base of the web; 10 to 11 undivided scansors beneath the fourth toe; usually two or three subterminal ones slightly notched; scansors covering distal $\frac{3}{5}$ to $\frac{2}{3}$ of fourth toe; 8 or 9 undivided scansors beneath the first toe (Table 1); all digits but the first finger and toe clawed, the compressed, clawed phalanges rising free at the end of the dilated part, but extending only a short distance beyond; a series of about 20 to 24 enlarged scales in position of pore-series including only one or two scales on basal end of thigh, and bearing, for males (one example), 19 preanal scales in a continuous series; the series followed by several rows of enlarged scales between it and vent; tail subcylindrical, depth just posterior

to basal swellings 74 to 82% of breadth at same point, tail breadth 56 to 67% of head breadth; lateral margins of tail without flange of skin or spines; scales on ventral surface of tail larger than those on dorsal surface.

Color. *In preservative*: dorsal ground color grayish tan to tan, with two or three pairs of small- to moderate-sized, brown, dorsolateral spots in region of fore limbs; dorsum, tail and limbs marked by faint to relatively prominent, narrow, irregularly margined, brownish, transverse bands, separated by somewhat broader light areas.

Measurements (in mm) of holotype: snout-vent length 37.1; axilla-groin distance 19.5; length of hind limb 13.0; head length 9.1; head breadth 6.8; snout length 4.0; diameter of orbit 3.2; tail breadth 3.8; tail depth 3.1; internasal distance 2.1.

ECOLOGICAL NOTE.—We have no habitat data for this species.

RANGE.—Known only from Konedubo and Port Moresby, Central District, Papua New Guinea.

***Lepidodactylus pulcher* (Boulenger)**

Lepidodactylus pulcher BOULENGER, 1885b:166 (type-locality: Wild Island, Admiralty Islands; syntypes BMNH).

MATERIAL EXAMINED.—BMNH 1946.9.8.48–50 (syntypes); PNGM 10294, 10296, CAS 139832.

RANGE.—This species is known from Wild Island off the northwest coast of Manua Island, Admiralty Islands, and Plot and Lengendrowa islands on the southeast coast.

***Lepidodactylus pumilus* (Boulenger)**

Gekko pumilus BOULENGER, 1885a:473 (type-locality: Murray Island, Torres Straits; type in BMNH).
Lepidodactylus pumilus, KLUGE, 1967:9.

MATERIAL EXAMINED.—BMNH 1946.8.25.93 (holotype); MCZ 135353–55, 135364–66, 135529–30, 137568, 137586, 139420, 141048–49, 141366–68, AM 44233, PNGM 10293, CAS 139834.

RANGE.—This species is recorded from Murray and Hammond islands, Torres Straits, and Daru Island of southeast New Guinea, Western District, Papua New Guinea.

***Lepidodactylus shebae* (Brown and Tanner)**

Pseudogekko shebae BROWN AND TANNER, 1949:43 (type-locality: Lower Lunga River, Guadalcanar Island, Solomon Islands; type in the Museum, Brigham Young University).
Lepidodactylus shebae, KLUGE, 1967:9.

MATERIAL EXAMINED.—Brigham Young University 7002 (holotype).

RANGE.—This species is known from Guadalcanar, Solomon Islands.

Lepidodactylus woodfordi Boulenger

Lepidodactylus woodfordi BOULENGER, 1887:334 (type-locality: Faro Island, Solomon Islands; type in BMNH). (See Discussion.)

MATERIAL EXAMINED.—BMNH 1946.8.22.34.

RANGE.—This questionable species has been recorded from the Solomon Islands, New Guinea, Philippines, and islands of the Pacific Basin.

Lepidodactylus species

Very small samples (1 to 3 specimens) from the following populations have not been referred to any of the designated species because of some differences in characters studied. We have not assigned these to a species pending the availability of larger samples.

1. A unique specimen from Mount Riu on Sudest Island, Louisiade Archipelago, (AMNH 76766, female) is close to *L. orientalis* in most characters but the interdigital webbing is more extensive.
2. Two examples from the Adelbert Mountains in Madang District, Papua New Guinea, (AMNH 105087–88, male and female) appear most closely related to *L. magnus* based on the webbing and the shape of their digits but are most like *L. pumilus* in size and, possibly, in the pore pattern of males.
3. Two specimens, BMNH 1974.3027 from Waigue Island and an uncatalogued example from Jappen Island, both off the northwest New Guinea coast, are close to *L. novaeguineae* in most characters but appear larger.
4. Three specimens, MCZ 135433–34, 139418, mature males, from Ndrova Island, Admiralty Islands, are close to *L. guppyi* but are smaller (31.5 to about 38 mm snout-vent length) and have slightly fewer pores (34–36).

DISCUSSION

Kluge (1967) pointed out some of the similarities and differences among the related gekkonid genera *Gekko*, *Pseudogekko*, *Lepidodactylus*, and *Hemiphyllodactylus*. By

numerical weighting (as a method of quantifying a judgment as to the degree of advancement exhibited for eleven characters analyzed), he ranked *Pseudogekko*, *Lepidodactylus*, and *Hemiphyllodactylus* in that order of change from an assumed *Gekko*-like ancestor. Kluge's approach enabled him better to define the genera and, in so doing, it became necessary to reassign several species within these genera, including some from *Gekko* to *Lepidodactylus* (Kluge 1967:332).

Russell (1972) included *Gekko*, *Pseudogekko*, *Luperosaurus*, *Ptychozoon*, *Lepidodactylus*, *Hemiphyllodactylus*, *Gehyra*, and *Perochirus* in a related group, the *Gekko*-group of the subfamily Gekkoninae. Within the genus *Lepidodactylus*, he regarded the evidence from the foot structure as supporting the hypothesis of an evolutionary trend involving a distal shift and reduction in number of subdigital scansors, accompanied by a median division of some of the distal ones to form two rows. We believe the evidence also indicates that a more depressed habitus parallels this shift as evidenced by the flattened and broadened tail and limbs.

Based on these characters, we recognize three evolutionary lines within the genus. Species of Group I are characterized by numerous *Gekko*-like, undivided scansors on all digits. Members of Group II also have well developed scansors on almost all the undersurface of the digit, but a few subterminal scansors are divided. The tail in species of Group I and Group II is subcylindrical, without lateral flanges or spines. Species of Group III are characterized by a reduced number of scansors, with the terminal as well as a few subterminal scansors divided, and by being more depressed with flatter and broader tail. Three of the four new species of *Lepidodactylus* described here are members of the *pumilus-oorti* group (Group I) and one of the *guppyi-pulcher* group (Group II). Additional changes which are evident but more variable within these evolutionary lines involve breadth relative to length of dilated part of digit, the proportion of the toe covered by scansors, and the extent of webbing.

We accept Russell's (1972:56) hypothesis that evolutionary trends within the genus involve shifts from the basic combination of characters exhibited by some *Gekko*-like ancestor. Group I, which is thus the most primitive of the three groups, includes seven species (Table 1). If we

assume that the *Gekko*-like ancestor was as large as nearly all living members of the genus *Gekko*, *L. magnus* would be the most primitive member in size, with *L. oorti* next. *L. magnus* also has long, slender digits and small webs between the digits. Based on these features, *L. pumilus* is the most advanced member of the group. The species is small and has extensive interdigital webbing, shorter limbs and digits, and more broadly dilated digits. The difference in adult size between *L. magnus* and *L. pumilus* is also evidenced by hatchlings. Four hatchlings of *L. pumilus* (MCZ 141048-49 and 1135529-30) were 18.5-21.1 mm in snout-vent length, and four hatchlings of *L. magnus* (MCZ 98796-99) were 24.5-25.9 mm in snout-vent length.

The species of Group I occur in the islands of western Indonesia, New Guinea, and islands in the Torres Straits, the Solomons and Fijis in the Pacific, and Christmas Island in the Indian Ocean. *L. pumilus* of this group also is recorded from Hammond Island, offshore from Cape York, Australia, and may also occur in that region of Australia. It is also of some interest that the two species within this group which are most alike are *L. manni* (Fiji Islands in the Pacific) and *L. listeri* (Christmas Island in the Indian Ocean). Based on the small samples available, the two are so similar in the characters studied that they cannot be distinguished except as widely separated populations (see Key). The two populations may indeed be conspecific, but we have chosen not to synonymize them pending the availability of larger samples and field studies. It is also possible that recent human introduction accounts for one or the other of these populations.

Group II includes *L. guppyi*, *novaeguineae*, *pulcher*, *shebae*, and *gardeneri*—species with undivided terminal scansors on all digits, but with a varying number of subterminal ones divided. Within this group, *L. gardeneri* and *L. guppyi* comprise a closely related pair. The two differ most obviously in the extent of the development of interdigital webs (Table 1). *L. pulcher* and *L. novaeguineae* are another pair of related species which differ from each other in the number of scansors, the size of the eye relative to the snout length, and the length of the hind limbs relative to the axilla-groin distance (Table 1).

The species of Group II have a more restricted distribution. They are known from northern

New Guinea, the Solomons, Admiralties, Bismarks, and Rotuma Island north of the Fijis.

Group III includes those species which are most advanced with respect to digital structure in terms of Russell's hypothesis. Several distal scansors, including the terminal one, are divided, and scansors tend to be lost from the basal part of the digits and to be reduced in number. The tail is more depressed and is broader.

The species of Group III include four endemic to the Philippine Archipelago and the widely distributed *L. lugubris-woodfordi* complex. Populations in this complex range from islands of the Indian Ocean and India to the western shores of the New World. The populations in Central America and South America, however, are apparently the result of very recent transport by man. In the past, some samples from various populations throughout the range have been referred to *L. lugubris* by numerous authors, some have been described as distinct species only to be placed in synonymy by later authors, and still others from New Guinea, Philippines and other Pacific islands have been referred to *L. woodfordi*. Boulenger's (1887:334) brief description of *L. woodfordi*, based on a single specimen, was erroneously related to *L. guppyi* rather than *L. lugubris*. *L. woodfordi* and *L. lugubris* belong to the same evolutionary line and, in terms of characters used here, may possibly differ in color pattern and degree of flattening of the tail, but little else (Table 1). Adequate samples from numerous populations throughout the Pacific region must be carefully studied and compared to determine the variability between and within the populations before the usefulness of these characters and the validity of these two named species, or the possible existence of additional races or species, can be finally determined.

The distributional pattern of the four species which inhabit Papua New Guinea is also of interest because of the similarity in basic features with those seen in some of the Papuan species of the genus *Sphenomorphus* (Scincidae) such as *solomonis*, *nigrolineatus*, *cinereus*, and *brunneus* (Greer 1973; Greer and Parker 1974). *L. novaeguineae* and *S. solomonis* are recorded only from low to moderate elevations along the north coast; *L. magnus*, *S. brunneus*, and *S. cinereus* are known from the central mountains; and *L. orientalis* and *S. nigrolineatus* are known from the Central District on the south coast, east

of the Gulf of Papua. The fourth species of *Lepidodactylus*, *L. pumilus*, is found in the Western District, west of the Gulf of Papua, and on the islands in the Torres Strait.

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