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A NEW SPECIES OF FROG OF THE *ELEUTHERODACTYLUS LACRIMOSUS* ASSEMBLAGE (LEPTODACTYLIDAE) FROM THE WESTERN AMAZON BASIN, WITH COMMENTS ON THE UTILITY OF CANOPY SURVEYS IN LOWLAND RAINFOREST

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ABSTRACT: We describe a new species of *Eleutherodactylus* from the lowlands of the western Amazon Basin. The new species is referred to the *Eleutherodactylus unistrigatus* group, *lacrimosus* assemblage. It differs from other members of the group by having a dorsal olive-green coloration with an interorbital creamy yellow stripe that extends posterolaterally and reaches the level of the sacrum, and low ulnar and tarsal tubercles. The new species inhabits western Amazon tropical rainforests and has been found in arboreal bromeliads by day and on vegetation by night. We discuss the effect of lack of sampling in the forest canopy in our understanding of tropical amphibian communities. Based on work conducted at two localities in Ecuadorian Amazonia, we find that even limited sampling effort in the canopy can greatly improve efficiency of biological inventories.

Key words: Anura; Canopy sampling; Ecuador; *Eleutherodactylus aureolineatus*; *E. lacrimosus*; *E. unistrigatus*; Leptodactylidae; New species; Peru

THE GENUS *Eleutherodactylus* comprises 621 recognized species (Amphibiaweb, 2005) distributed in Central and South America, as well as the West Indies. The *Eleutherodactylus lacrimosus* assemblage is a phenetic subgroup of the larger *E. unistrigatus* group (sensu Lynch and Duellman, 1997) and currently contains 14 species: *Eleutherodactylus apiculatus* Lynch and Burrowes 1990 (but see Heyer and Hardy, 1991:444); *E. boulengeri* Lynch 1981; *E. brevifrons* Lynch 1981; *E. bromeliaceus* Lynch 1979; *E. dorsopictus* Rivero and Serna 1988 "1987"; *E. eremitus* Lynch 1980; *E. lacrimosus* (Jiménez de la Espada 1875); *E. mendax* Duellman 1978*a*; *E. olivaceus* Köhler, Morales, Lötters, Reichle, and Aparicio 1998; *E. petersorum* Lynch 1991; *E. prolixodiscus* Lynch 1978; *E. schultei* Duellman 1990; *E. tayrona* Lynch and Ruíz-Carranza 1985; and *E. zimmermanae* Heyer and Hardy 1991. Most members of this assemblage likely are bromeliad-dwelling and have a small body size (SVL in males, 14.5–26.6 mm; in females, 20.3–33.8 mm) and broad, flat, pointy heads.

The morphological resemblance among the species in the *Eleutherodactylus lacrimosus* assemblage has been explained as the result of convergent evolution in response to their microhabitat use (bromeliads; Lynch and Ruíz-Carranza, 1985), rather than as a result of common ancestry, although no formal test has been performed to distinguish between these two hypotheses. Until robust phylogenetic hypotheses are available, the *E. lacrimosus* assemblage is recognized only as a matter of convenience (Lynch and Ruíz-Carranza, 1985).

Recent collection efforts in the canopy of Amazon rainforest and examination of specimens previously identified as *Eleutherodactylus lacrimosus* revealed the presence of an

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undescribed species. Herein, we describe this new species and discuss the effect of sampling the forest canopy in our understanding of tropical amphibian communities.

Materials and Methods

The diagnosis and description of the new species follow those of Lynch and Duellman (1997). We examined alcohol-preserved specimens from the herpetological collections at Museo de Zoología of the Universidad Católica del Ecuador, Quito (QCAZ); Universidad San Francisco de Quito, Quito (DFCH-USFQ); Natural History Museum of The University of Kansas, Lawrence (KU); and The Natural History Collection at Texas A&M University – Texas Cooperative Wildlife Collection, College Station (TCWC). In addition to the type series of the new species, specimens examined are listed in Appendix I; one of us (WL) examined an additional specimen (CRG 931; adult female from Reserva Allpahuayo, 25 km S Iquitos) of the new species that currently forms part of a collection by Carlos Rivera G.

Morphological measurements were taken as described in Guayasamin (2004) and are: (1) snout–vent length (SVL); (2) tibia length; (3) foot length; (4) head length; (5) head width; (6) interorbital distance; (7) upper eyelid width; (8) internarial distance; (9) eye-to-nostril distance; (10) snout–eye distance; (11) eye diameter; (12) tympanum diameter; (13) eye-to-tympanum distance; (14) radioulna length; (15) hand length; (16) Finger-I length. Sexual maturity was determined by the presence of eggs or convoluted oviducts in females or by the presence of vocal slits in males. Color patterns in life were taken from field notes and color photographs.

At Yasuní Scientific Research Station of the Universidad Católica del Ecuador (YSRS), visual encounter surveys (mainly ground-level VES) have been carried out regularly since 1995, and sporadic canopy searches (especially in tank bromeliads) were carried out during one week in May 2002.

At Tiputini Biodiversity Station of the Universidad San Francisco de Quito (TBS), surveys (ground-level transect VES and quadrats) have been carried out since 1998; at this locality, canopy surveys were conducted within a 100 m-long system of canopy bridges, and annual bromeliad inspections were pern1.0983led (surveys of all bromeliads on three trees once per year). During the VES, most of the amphibians found were collected; thus, the number of specilens recorded was used as a

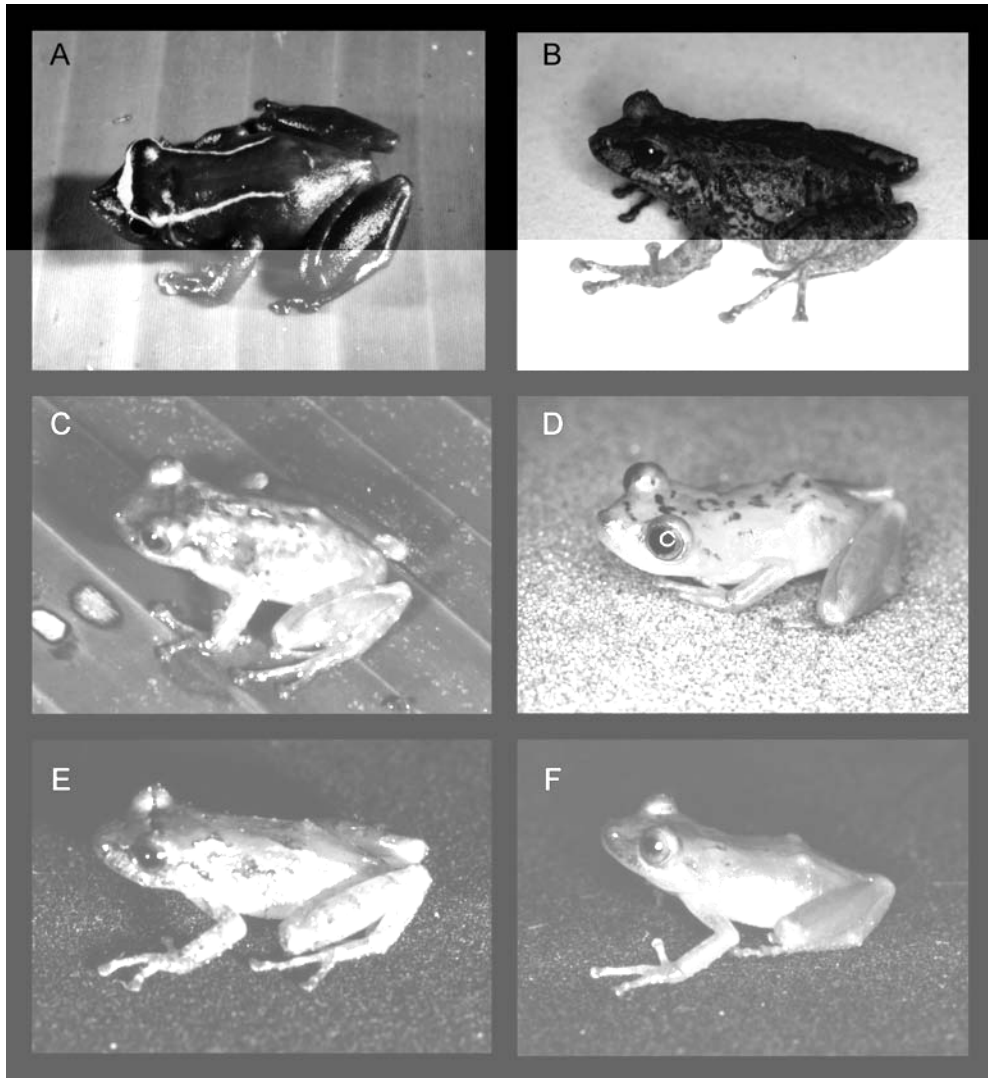

FIG. 1.—Species in the *Eleutherodactylus lacrimosus* assemblage. (A) *Eleutherodactylus aureolineatus*, QCAZ 19534, female, SVL 27.8 mm (photo by SRR); (B) *E. boulengeri* KU 169055, female, SVL 30.6 mm (William E. Duellman); (C) *E. eremitus*, KU 165884, male, SVL 19.7 mm (WED); (D) *E. lacrimosus*, KU 119513, female, SVL 24.5 mm (John D. Lynch); (E) *E. mendax*, KU 162290, SVL 19.6 mm (WED); (F) *Eleutherodactylus petersorum*, KU 165993, juvenile female, SVL 20.7 mm (WED). Color photographs are available at AmphibiaWeb (http://elib.cs.berkeley.edu/aw/).

SFM on 31 July 2004; and TCWC 90342, adult female collected by SFM on 08 Aug 2004; *Provincia de Sucumbíos:* Limoncocha (00° 24′ S, 76° 37′ W; altitude 220 m): KU 106967 (adult male) and 104623 (juvenile) collected by W. E. Duellman on 22 November 1966 and 16 August 1966, respectively; KU 123402, juvenile collected by M. L. Crump on 14 July 1968; Santa Cecilia (00° 03′ N, 76° 58′ W; altitude 340 m): KU 148902, 148906, adult males collected by M. L. Crump on 05 October 1971 and 25 February 1972, respectively. *Peru: Departamento de Loreto:* Explornapo Lodge, junction between Río Sucusari and Río Napo (03° 16′ S, 72° 54′ W): KU 220426, adult female collected by WL on 17 June 1992.

Diagnosis.—A member of the *Eleutherodactylus unistrigatus* group, *lacrimosus* assemblage

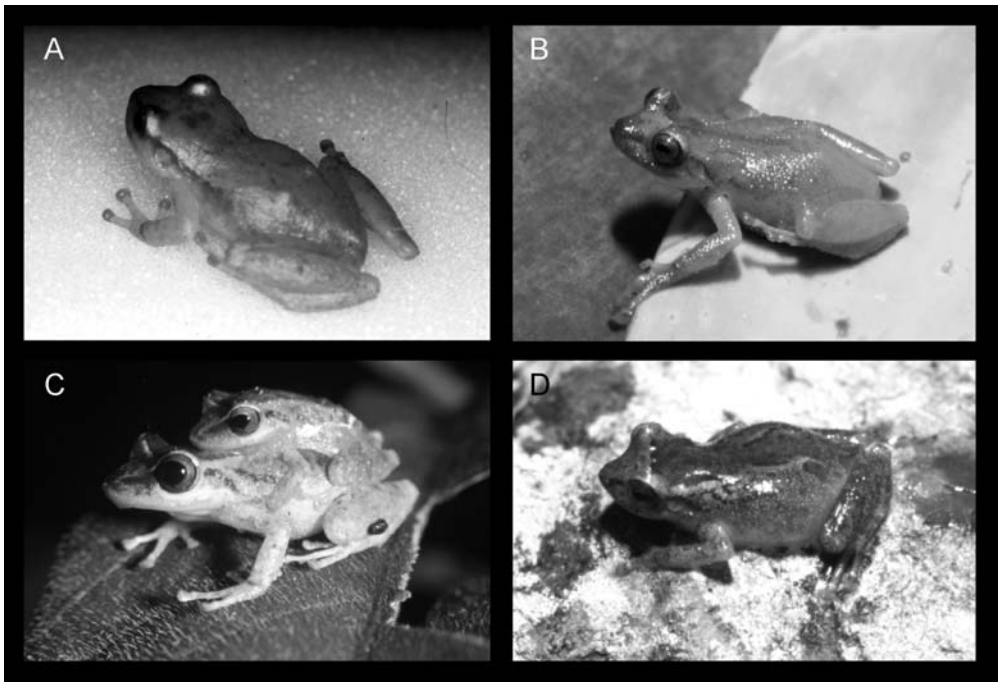

FIG. 2.—Species in the *Eleutherodactylus lacrimosus* assemblage. (A) *Eleutherodactylus prolixodiscus*, KU 132733, male, SVL 25.1 mm (photo by Stephan R. Edwards); (B) *E. schultei*, KU 212222, male, SVL 27.4 mm (William E. Duellman); (C) *E. zimmermanae*, amplectant pair, NMW 32112:2–3 (Walter Hödl); (D) *E. bromeliaceus*, KU 212214, male, SVL 22.5 mm (WED). Color photographs are available at AmphibiaWeb (http://elib.cs.berkeley.edu/aw/).

(as defined by Lynch and Duellman, 1980, 1997; Lynch and Ruíz-Carranza, 1985) having (1) skin texture of dorsum finely shagreen, that on the venter areolate (sensu Lynch and Duellman, 1997); discoidal fold low; dorsolateral folds absent; (2) tympanic membrane not differentiated in males and slightly evident in females; tympanic annulus evident, with supratympanic fold obscuring upper and posterodorsal edges, horizontal diameter of tympanum 31–39% of eye diameter; (3) snout subacuminate in dorsal view, protruding in profile; (4) upper eyelid lacking tubercles or with one small tubercle; cranial crests absent; (5) dentigerous process of the vomer triangular, each bearing 0–6 teeth; (6) males with vocal slits and median subgular vocal sac; white nuptial pads present; (7) first finger shorter than the second; Fingers III–IV bearing rounded discs about twice as wide as digits; (8) fingers with narrow lateral fringes; (9) antebrachial tubercle evident, ulnar tubercles low or absent; (10) tarsal tubercles low or absent; (11) inner metatarsal tubercle oval, two-to-three times as long as round outer metatarsal tubercle; supernumerary plantar tubercles low, at the base of Toes III and IV; (12) toes with narrow lateral fringes; webbing absent; fifth toe much longer than third; (13) in life, males with dorsum olive green with an interorbital golden yellow stripe that extends above the eyes and dorsolaterally to the sacrum, and females with dorsum olive brown to dark brown with an interorbital creamy yellow stripe that extends above the eyes and dorsolaterally to the sacrum; venter bright yellow to greenish cream; posterior surfaces of thighs olive green; (14) adults small, SVL in males 19.7–28.8 mm ($\bar{x} = 23.6 \pm 2.77$, $n = 9$), in females 26.3–30.5 mm ($\bar{x} = 27.8 \pm 1.86$, $n = 7$); males with white testes (mesorchium).

Comparison with similar species.—*Eleutherodactylus aureolineatus* differs from all other species of the *E. lacrimosus* assemblage (i.e., *E. apiculatus*, *E. boulengeri*, *E. brevifrons*, *E. bromeliaceus*, *E. dorsopictus*, *E. eremitus*, *E. lacrimosus*, *E. mendax*, *E. petersorum*, *E. prolixodiscus*, *E. schultei*, *E. tayr-*

ona, *E. zimmermanae*) by its olive-green dorsal coloration with a creamy-yellow interorbital stripe that extends above the eyes and dorsolaterally to the sacrum (Figs. 1, 2). Additionally, *Eleutherodactylus aureolineatus* differs from the sympatric *E. lacrimosus* by lacking tubercles on dorsum (few tubercles present in *E. lacrimosus*) and by being larger (see Table 1). Differences among species in the *E. lacrimosus* assemblage are summarized in Table 1.

Description of holotype.—Adult male (QCAZ 20712) with head as wide as long; snout subacuminate in dorsal view and protruding in lateral view, relatively short (snout–eye distance 16.9% SVL), with small papilla at tip (Fig. 3); in lateral view, canthus rostralis distinct; loreal region slightly concave; nostrils protuberant, directed dorsolaterally; interorbital area flat, broader than upper eyelid (upper eyelid width 61.8% interorbital distance); cranial crests absent; upper eyelid lacking tubercles; tympanic membrane not differentiated from surrounding skin; tympanic annulus distinct, round, with supratympanic fold obscuring upper and posterodorsal edges of annulus (Fig. 3); tympanum diameter 34.4% of eye diameter; postrictal tubercles absent. Choanae small, nearly elliptical, not concealed by palatal shelf of maxillary; dentigerous process of the vomer triangular, widely separated, posteromedial to choanae, each bearing two or five small teeth (bilateral variation within individual); shortest distance between dentigerous processes about 36% distance between choanae; tongue longer than wide, granular, with small notch in posterior border.

Texture of skin of dorsum and flanks shagreen, dorsolateral folds absent; venter areolate; discoidal fold low; cloacal sheath absent. Forearm slender; radio–ulna length 20.6% SVL; ulnar tubercles and ulnar fold absent; hand length longer than radio–ulna length (hand length 26.7% SVL); fingers with narrow lateral fringes; relative lengths of fingers I < II < IV < III; palmar tubercle incompletely bifid, thenar tubercle oval (Fig. 4); subarticular tubercles round, prominent; supernumerary palmar tubercles present at the base of all fingers (Fig. 4); disc cover of Finger I slightly expanded, those of Fingers II–IV extensively expanded (Fig. 4); outer discs of fingers as wide as those of toes; all disc covers with elliptical ventral pads defined by circummarginal grooves.

Hind limbs relatively slender; tibia length 53.1% SVL; foot length 82.9% of tibia length; tarsal fold and tarsal tubercles absent; heel (tibiotarsal articulation) lacking tubercles; toes with narrow lateral fringes (Fig. 4); subarticular tubercles round, prominent; inner metatarsal tubercle oval, about 2.4 × the size of subconical outer tubercle; supernumerary plantar tubercles low, at the base of toes (Fig. 4); disc covers slightly expanded; toes with defined pads; disc pads nearly elliptical; relative lengths of toes I < II < III < V < IV (Fig. 4); tip of Toe V reaching proximal border of distal subarticular tubercle of Toe IV; tip of Toe III reaching distal border of medial subarticular tubercle of Toe IV.

Coloration of holotype in life.—Dorsum light olive green with an interorbital creamy yellow stripe that extends above the eyes and dorsolaterally to the sacrum, dorso-lateral portion of stripe faint; surfaces of hind limbs and forearm olive green; dorsal surface of arm greenish yellow; flanks olive green with lighter flecks. Venter bright yellow; throat greenish cream, becoming pale gray towards the jaw; ventral surfaces of hind limbs greenish salmon; tibiofibula externally visible, white; sides of head olive green, becoming greenish cream towards the lips. Iris reddish bronze with reddish brown median horizontal streak (S. R. Ron, field notes, 8 May 2002).

Coloration of holotype in ethanol.—Dorsum brown with an interorbital whitish stripe that extends above the eyes and dorsolaterally to the sacrum, posterior portion of stripe faint; surfaces of limbs brown; flanks light brown; groin cream. Throat, venter, and underside of limbs cream; palms and soles cream with some brown pigmentation on external fingers and toes.

Measurements of holotype (mm).—SVL = 24.3; tibia length = 12.9; foot length = 10.7; head length = 9.4; head width = 9.3; upper eyelid width = 2.1; interorbital distance = 3.4; eye diameter = 3.2; eye-to-nostril distance = 2.9; snout-to-eye distance = 4.1; tympanum diameter = 1.1; eye-to-tympanum distance = 1.1; internarial distance = 1.8; radioulna legth = 5.0; hand length = 6.5; finger I length = 4.3; finger II length = 4.4. For morphometric variation, see Table 2.

TABLE 1.—Diagnostic morphological characters in species of the *Eleutherodactylus lacrimosus* assemblage. For *E. lacrimosus*, SVL is given for lowland (<800 m) and highland (900–1100 m) populations (adults only).

	SVL males	SVL females	Tubercles on upper eyelid	Ulnar tubercles	Tarsal tubercles	Dorsal coloration in life	Source
E. apiculatus	17.8–21.8	21.6–26.3	One small nonconical tubercle	Absent	Present, but indistinct	Tan or yellowish tan with or without irregular shaped blotches; some with middorsal yellow stripe or fine yellow stripes	Lynch and Duellman, 1997; this work
E. aureolineatus	19.7–28.8	26.3–30.5	Absent or one low tubercle present	Low or absent	Low or absent	Olive green with creamy yellow interorbital bar and dorsolateral stripes that extend posterolateraly to the level of sacrum	This work
E. boulengeri	18.6–25.6	27.3–33.8	Present, numerous and nonconical	Present	Low or absent	Orange-tan to brown with darker spots or marks; some with dark dorsolateral stripes; interorbital bar usually present	Lynch, 1981; this work
E. brevifrons	15.1–19.7	21.2–25.0	Low or absent	Absent or present, but indistinct	Low or absent	Pale yellow to brown with indistinct to bold brown markings washed with green; some with dorsalateral stripes	Lynch, 1981; this work
E. bromeliaceus	16.7–23.2	22.9–28.1	Two or three small tubercles	Absent	Present, low	White with or without spots and/or reticulation	Lynch, 1979
E. dorsopictus	19.0–22.0	21.6–31.6	?	Present, small	Low or absent	?	Rivero and Serna, 1988 "1987"
E. eremitus	17.2–21.8	27.1–27.6	One conical tubercle or several small tubercles	Absent or present, but indistinct	Present, small	Green, usually with darker markings; some with black spots or redish brown dorsaleteral stripes	Lynch and Duellman, 1997; this work
E. lacrimosus	Low: 16.1–20.0 High: 19.6–23.7	Low: 20.6–24.4 High: 24.4–32.5	Absent	Absent	Absent	Pale golden brown with or without brown spotting	Lynch and Duellman, 1980
E. mendax	19.4–21.7	22.6–28.0	Low or absent	Present	Present	Green with various markings; some with orange-tan or yellow-tan dorsolateral stripes	Duellman, 1978*a*; this work
E. olivaceus	17.8–20.7	—	Two or three small tubercles	Present, small	Present, small	Olive green with black spots and markings; cream interorbital bar present	Köhler et al., 1998

TABLE 1.—Continued

	SVL males	SVL females	Tubercles on upper eyelid	Ulnar tubercles	Tarsal tubercles	Dorsal coloration in life	Source
E. petersorum	14.5–19.9	20.3–23.1	One conical tubercle	Absent	Absent	Usually uniform pale green to dull green; some tan or brown with or without brown markings	Lynch and Duellman, 1980
E. prolixodiscus	19.3–25.4	23.0–26.7	Low or absent	Present, low	Absent	Dorsum with distinct green patch; canthal and postocular stripe (ending about sacrum) present	Lynch, 1978; this work
E. schultei	23.5–26.6	28.4–34.0	Numerous, low	Present, low	Numerous, low	Tan, reddish brown, or green, bordered or not by narrow dark brown line from snout to point above vent	Duellman, 1990
E. tayrona	15.3–25.1	22.6–30.2	Low or absent	Low or absent	Absent	Reddish-brown; some with cream to dull orange vertebral stripe	Lynch and Ruíz-Carranza, 1985; this work
E. zimmermanae	19.1–21.2	22.4–25.8	Several tubercles	Present	Present	Light to medium brown with darker markings; yellow interorbital bar present or absent	Heyer and Hardy, 1991

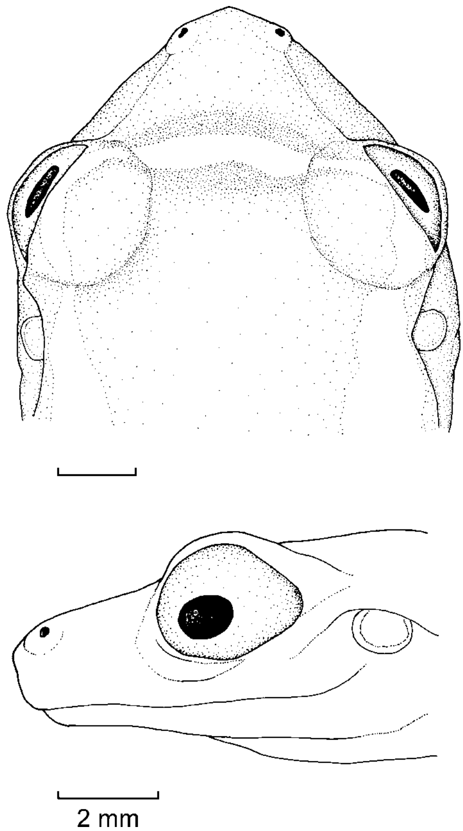

FIG. 3.—Dorsal (A) and lateral (B) views of head of holotype of *Eleutherodactylus aureolineatus*, QCAZ 20712, SVL = 24.3 mm.

Variation.—In some specimens, the snout is round in dorsal view and lacks the papilla at tip (QCAZ 20713, KU 123402, DFCH-USFQ 0559). In one female (DFCH-USFQ 0736), the papilla is poorly defined. On the inner margin of the tarsus of most individuals (KU 104623, 106967, 123402, 148902, 148906, DFCH-USFQ 0734, 0443, TCWC 90335–42), three low tubercles are evident under magnification. The absence of tarsal and ulnar tubercles in some of the specimens of *Eleutherodactylus aureolineatus*, including the holotype, may be a preservation artifact. We have observed that low tubercles are distinguishable in living individuals, but seem to be absent when examining preserved material.

The number of teeth on the dentigerous processes of the vomers is variable; some specimens (KU 148906, QCAZ 19534, 20713,

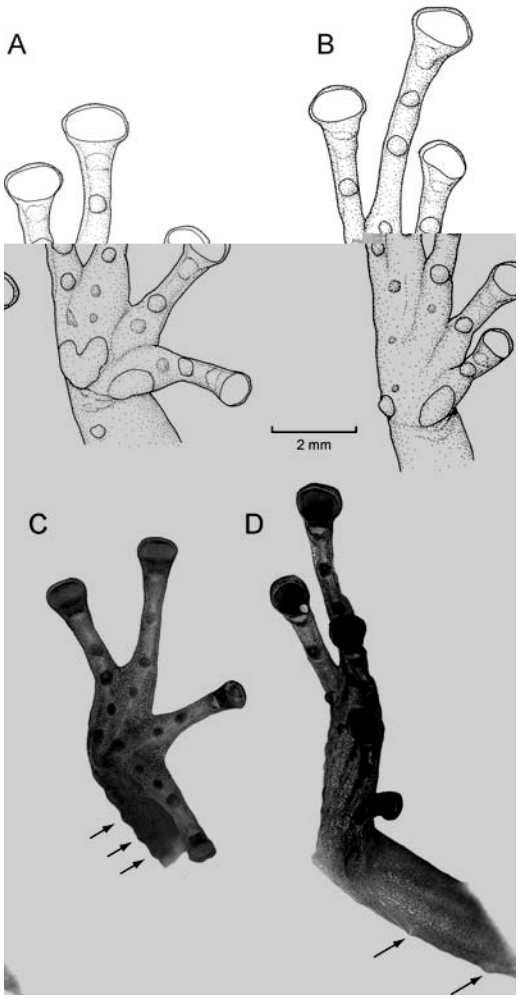

FIG. 4.—Ventral view of hand and foot of *Eleutherodactylus aureolineatus*. (A) Hand, QCAZ 19534, female; (B) foot, QCAZ 19534, female; (C) hand and forearm, arrows indicate low ulnar tubercles, TCWC 90338, male; (D) foot and tarsus, arrows indicate low tarsal tubercles, TCWC 90338, male.

TABLE 2.—Measurements (in mm) and morphological proportions (in percentages) of adult males and females of *Eleutherodactylus aureolineatus* (range over mean ± standard deviation).

	Males $n = 9$	Females $n = 7$
SVL	19.7–28.8	26.3–30.5
	23.6 ± 2.77	27.5 ± 1.58
Tibia length	11.5–15.3	13.5–15.4
	12.8 ± 1.33	14.5 ± 0.68
Foot length	9.2–12.6	11.3–12.5
	10.4 ± 1.24	11.9 ± 0.40
Head length	8.6–11.1	10.1–10.8
	9.1 ± 0.87	10.4 ± 0.22
Head width	8.7–12.0	10.2–12.2
	9.5± 1.19	11.1 ± 0.70
Upper-eyelid width	2.1–2.9	2.3–2.9
	2.3 ± 0.29	2.5 ± 0.21
Interorbital distance	2.7–4.3	3.3–4.3
	3.2 ± 0.56	3.7 ± 0.33
Eye diameter	2.7–4.1	3.3–4.0
	3.25 ± 0.42	3.6 ± 0.27
Eye-to-nostril distance	2.6–3.6	3.0–3.4
	2.9 ± 0.34	3.3 ± 0.15
Snout-to-eye distance	3.9–5.2	4.2–5.0
	4.2 ± 0.45	4.7 ± 0.29
Tympanum diameter	1.0–1.5	1.2–1.5
	1.2 ± 0.18	1.3 ± 0.15
Eye-to-tympanum distance	0.7–1.6	0.9–1.6
	1.1 ± 0.34	1.2 ± 0.27
Internarial distance	1.7–2.5	2.0–2.7
	1.9 ± 0.29	2.2 ± 0.25
Radioulna length	4.9–6.7	5.7–6.4
	5.35 ± 0.62	6.0 ± 0.27
Hand length	5.8–7.9	7.4–8.0
	6.5 ± 0.74	7.6 ± 0.25
Finger I length	2.8–4.85	3.9–5.3
	4.0 ± 0.66	4.9 ± 0.46
Finger II length	4.0–5.5	5.1–5.7
	4.8 ± 0.76	5.3 ± 0.30
Tibia length/SVL	50.4–58.4	48.8–58.2
Foot length/SVL	40.9–46.7	41.0–46.2
Head width/SVL	38.3–44.2	38.6–42.5
Head length/SVL	36.8–44.7	33.8–39.5
Radioulna length/SVL	20.6–25.9	18.7–24.2
Upper eyelid width/ Interorbital distance	60.0–86.2	60.5–81.8
Tympanum diameter/ Eye diameter	34.4–43.3	34.3–42.1
Finger I length/Finger II length	88.7–97.7	90.1–96.6

DFCH-USFQ 0734, TCWC 90335, 90337, 90338, 90340, 90342) have 5 or 6 teeth, one specimen (TCWC 90339) has 4 teeth, whereas others (KU 104623, 106967, 123402, DFCH-USFQ 0443, 0736, TCWC 90336, 90341) have only 1 to 3 or lack them altogether (KU 148902, TCWC 90334). Two to three small ulnar tubercles are present in CRG 931, TCWC 90335, 90337–40, 90342. In life, males have a pale (DFCH-USFQ 0443, TCWC 90339) or dark (QCAZ 20713, DFCH-USFQ 0734, TCWC 90335, 90338, 90341) olive-green dorsum; the interorbital stripe is bright golden to yellow during night and pale golden during day, and it extends above the eyes and dorsolaterally down to the sacrum or to mid-flanks; coloration of ventral surfaces of arms and legs is similar to that on venter. Females have a darker coloration, with olive brown to dark brown dorsal coloration and the

interorbital stripe is creamy yellow (DFCH-USFQ 0736, TCWC 90337, 90340, 90342), coloration of ventral surfaces of arms and legs are dark brown, unlike venter coloration. Venter coloration varies from bright yellow (QCAZ 20712, DFCH-USFQ 0736, 443, TCWC 90335) and pale cream (DFCH-USFQ 0734, TCWC 90336, 90339, 90341), to greenish creamy (QCAZ 20713, TCWC 90337, 90338, 90340, 90342). Posterior surfaces of thighs vary from olive green to dark brown. Juvenile (DFCH-USFQ 0559) with dark brown dorsum, ventral surfaces white bluish, posterior surfaces brown with indistinct darker transversal bands and flecks, cream interorbital stripe, iris dark brown. In preservative, the soles and palms have a pale brown coloration (CRG 931; DFCH-USFQ 0736); the dorsum is creamish brown (KU 148906), reddish brown (DFCH-USFQ 0443) or dark brown (DFCH-USFQ 0736) with cream dorsolateral stripes.

Distribution and natural history.—*Eleutherodactylus aureolineatus* has been found at localities below 350 m in elevation, in the upper Amazon Basin of eastern Ecuador and Peru (Fig. 5). The vegetation type at the Ecuadorian localities is Amazonian Evergreen Lowland Forest (Palacios et al., 1999). The YSRS and the TBS are located on the bank of the Río Tiputini at elevations between 190–250 m. Limoncocha is a oxbow lake on the north bank of the Río Napo at an elevation of 220 m. At these localities, the vegetation is composed of terra firme forest (nonflooded forest), varzea (flooded forest), and seasonally flooded forest. The vegetation type and climate at Santa Cecilia (Provincia de Sucumbíos, 340 m) have been described in detail by Duellman (1978*b*). On 7 May 2002, the holotype and one subadult male (QCAZ 20713) were collected by day in a tank bromeliad, at a height of 25 m, on a tree in terra firme forest. In the same bromeliad, an adult male and at least 10 tadpoles of *Osteocephalus planiceps* (e.g., QCAZ 20873) were found. On 7 May 2002, in a tree hole 7 m below the same bromeliad, an adult male and female and several tadpoles (QCAZ 20875) of *Phrynohyas resinifictrix* were found; the next day, an additional adult female of *P. resinifictrix* was collected in the same hole (S. R. Ron, fieldnotes). An adult female *E. aureolineatus* (QCAZ 19534) was

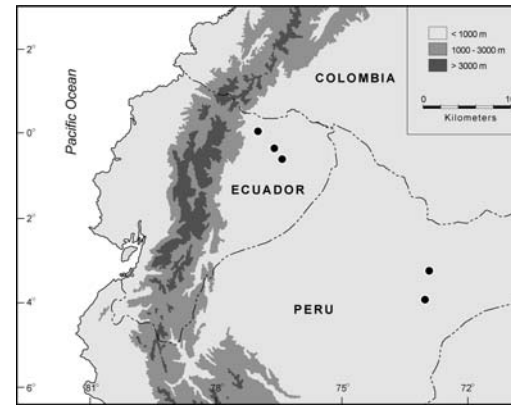

FIG. 5.—Distribution of *Eleutherodactylus aureolineatus* (circles). Map modified from Torres-Carvajal (2005).

collected by night over a window on a building of the YSRS on 3 December 2001. An adult male *E. aureolineatus* (DFCH-USFQ 0443) was collected while calling by night over a leaf ca. 45 m height on a Ceiba tree in terra firme forest. A subadult male (DFCH-USFQ 0734) and an adult female (DFCH-USFQ 0736) were collected by day inside a bromeliad ca. 40 m height on a tree in terra firme forest (D. F. Cisneros-Heredia, fieldnotes). A female *E. aureolineatus* (not collected) was observed during day inside a bromeliad ca. 40 m height, together with an adult *Dendrobates ventrimaculatus* (D. F. Cisneros-Heredia, fieldnotes). A juvenile *E. aureolineatus* (TCWC 90334) was collected by night ca. 30 m height on a handrail of a wooden canopy tower surrounding a Ceiba tree in terra firme forest at TBS on 18 May 04; two adult males (TCWC 90335, 90338), one adult female (TCWC 90337) and one juvenile female (TCWC 90336) were collected by day inside a bromeliad ca. 38 m height on a tree in terra firme forest during bromeliad patch sampling on 31 July 2004; on the same tree, an adult male (TCWC 90339), an adult female (TCWC 90340) and a juvenile male (TCWC 90341) were collected by day inside a bromeliad ca. 35.5 m height on 31 July 2004 (S. F. McCracken, fieldnotes). An adult female (TCWC 90342) was collected by day inside a bromeliad ca. 23.5 m height on a tree in terra firme forest during bromeliad patch sampling on 8 Aug. 2004; on the same tree, an *E. aureolineatus* (not collected) was observed by day inside a bromeliad ca. 23.5 m height on

8 Aug. 2004 (S. F. McCracken fieldnotes). Two males *E. aureolineatus* (KU 148902, 148906) were found at night on low vegetation (W. E. Duellman, fieldnotes); one juvenile (KU 123402) was found on forest floor by day (M. L. Crump, fieldnotes), while another juvenile (DFCH-USFQ 0559) was found in low vegetation (50 cm) by night (D. F. Cisneros-Heredia, fieldnotes). Twelve out of fifteen adults with ecological data have been found at heights >20 m suggesting that *E. aureolineatus* is predominantly a canopy dweller.

Etymology.—The specific name *aureolineatus* comes from the Latin words *aureus* meaning golden, and *linea* meaning line. The name is used in reference to the dorsolateral golden stripe characteristic of the new species.

Remarks.—Most of the diversity of the *Eleutherodactylus lacrimosus* assemblage is found in the cloud forest of the Andes. Only five species (*E. aureolineatus*, *E. bromeliaceus*, *E. lacrimosus*, *E. mendax*, and *E. zimmermanae*) are known from the Amazonian lowlands (<1000 m; see IUCN et al., 2004).

Discussion

Neglect of Canopy in Amphibian Inventories?

Most amphibian inventories in tropical rainforests are carried out at ground level, typically along shallow strata (only ~2 m), characterized by higher humidity and lower ambient temperature than other microhabitats. Therefore, accounts of the diversity, community composition, and abundance of amphibians in these structurally complex forests are biased toward a relatively localized environmental space. *Eleutherodactylus aureolineatus* and other members of the *lacrimosus* assemblage are good examples of species that can be overlooked as a consequence of microhabitat sampling bias.

This bias could be influential in inventories on which visual encounter surveys (VES), transect surveys, or quadrats are the predominant sampling methods. An example is given by inventories carried out in the YSRS and at the TBS. At the YSRS, between 1995 and 2003, a total of 1540 specimens, belonging to 72 amphibian species, have been collected (QCAZ database). Despite the large sampling effort, only one *E. aureolineatus* (QCAZ 19534) has ever been collected below the canopy. The only additional *E. aureolineatus* known from this locality (QCAZ 20712–13) were collected during sporadic canopy searches (especially in tank bromeliads) carried out during one week in May 2002.

At the TBS, between 1998 and 2001, almost 600 specimens, belonging to 87 species of amphibians were collected (Cisneros-Heredia 2003, D. F. Cisneros-Heredia, unpublished data). All paratypes (except for one juvenile found near the floor, DFCH-USFQ 0559) were collected in the canopy. Aside from the type series, nine additional specimens were also collected during the yearly canopy surveys (these specimens were not preserved). Also, *E. aureolineatus* seems to be an abundant species in the canopy; bromeliad patch sampling of 40 bromeliads among eight trees resulted in the collection of eight specimens.

The specimens of *Eleutherodactylus aureolineatus* from the YSRS represent 13% of the total number found in the canopy searches, and the specimens from the TBS represent 27%. These results suggest that *E. aureolineatus* is a proportionally more abundant anuran within higher strata of the forest. In addition, at YSRS, the canopy searches yielded 13 specimens belonging to 6 species: *Dendrobates* aff. *ventrimaculatus*, *Nyctimantis rugiceps*, *Osteocephalus deridens*, *O. fuscifacies*, *O. planiceps*, and *Phrynohyas resinifictrix*. At the TBS, the canopy searches yielded 32 records belonging to 13 species: *Hyalinobatrachium munozorum*, *Cochranella* sp., *Dendrobates ventrimaculatus*, *D. duellmani*, *Eleutherodactylus lacrimosus*, *Gastrotheca longipes*, *Nyctimantis rugiceps*, *Osteocephalus deridens*, *O. planiceps*, *O. taurinus*, *Phrynohyas coriacea*, *P. resinifictrix*, and *Sphaenorhynchus carneus*. Bromeliad patch sampling yielded 11 specimens belonging to two additional species: *Dendrobates ventrimaculatus* and *Eleutherodactylus* sp. Similarly to *E. aureolineatus*, all these species found in canopy situation have been extremely rare during VES, and three (*Osteocephalus deridens*, *O. fuscifacies*, *Dendrobates duellmani*) were undescribed until recently (Jungfer et al., 2000; Schulte, 1999); the scarcity of these

species in herpetological collections is likely an artifact of survey methodology.

Although our sampling effort was limited, the results are consistent with the suggestion that canopy surveys can improve species richness assessments and inventory efficiency in tropical rainforests (e.g., Longino and Colwel, 1997; Kalko and Handley, 2001). Sampling methodologies that distribute capture effort more evenly among vertical strata of rainforests have the potential to enhance significantly our understanding of tropical amphibian communities.

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Appendix I

Specimens Examined

Eleutherodactylus apiculatus (KU 212534–38, paratypes). *Eleutherodactylus boulengeri* (KU 169056–61, paratypes). *Eleutherodactylus brevifrons* (KU 169006–13, paratypes). *Eleutherodactylus bromeliaceus* (KU 174524–25, paratypes). *Eleutherodactylus eremitus* (KU 140878, 179085–86; paratypes). *Eleutherodactylus lacrimosus* (KU 110782, neotype; 148889–908, 123391–98, DFCH-USFQ D50). *Eleutherodactylus mendax* (KU 173234, holotype; 171897, paratype). *Eleutherodactylus petersorum* (KU 143508, holotype). *Eleutherodactylus prolixodiscus* (KU 132727–33, paratypes). *Eleutherodactylus schultei* (KU 209498–504, paratypes).

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THREE NEW SPECIES OF *COPHIXALUS* (ANURA: MICROHYLIDAE) FROM SOUTHEASTERN NEW GUINEA

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Abstract: We describe three new species of a cryptic species complex of *Cophixalus* from southeastern New Guinea and adjacent islands. They are readily distinguished from all other Papuan species by their small size, presence of vocal slits in males, absence of toe webbing, relatively long legs, short snouts, and vertical lores. Their calls consist of a series of high-pitched peeps. Intraspecific color pattern is highly variable and variant patterns are shared among species. Members of this complex can be distinguished from each other on the basis of adult body size, extent of development of the first finger and disc, snout width, tympanum size, and advertisement calls. The new species are among the most common frogs where found. Two of the species are currently known only from their type localities, but the third ranges more broadly in the Southeast Peninsula of New Guinea and D'Entrecasteaux Islands.

Key words: Anura; *Cophixalus*; Microhylidae; New Guinea; New species

In the course of conducting herpetological surveys in Milne Bay Province, Papua New Guinea, during 2002, we found an undescribed species of *Cophixalus* to be among the most common components of the anuran community at a number of locations. It has been known for approximately 30 years and was featured in Menzies (1975:pl. 12C) but has not received a name or formal description. Menzies (1975:60) further noted that a second, similar species might replace this species at higher elevations. In expanding our initial surveys to additional localities, apparent differences in call parameters lent support to Menzies' supposition that more than one species was involved, although morphologically they are virtually impossible to tell apart in the field. Additional collections and recordings of similar animals from Central Province made it clear that the situation was more complicated than suggested by Menzies. It is now apparent that the frog referred to as "*Cophixalus* species" by Menzies (1975:59–60) is actually a complex of cryptic species. Here we describe three of these species but note that additional members may remain to be discovered. This brings the

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total number of Papuan members of the genus to 20 and the total for the genus (ranging from Halmahera to Australia) to 34 (Günther, 2003; Kraus and Allison, 2000).

Materials and Methods

Specimens were fixed in 10% buffered formalin and transferred to 70% ethanol for storage. All measurements were made with digital calipers or an optical micrometer to the nearest 0.1 mm, with the exception that disc widths were measured to the nearest 0.01 mm. Measurements, terminology, and abbreviations follow Zweifel (1972, 1985) and Kraus and Allison (2001): body length from snout–vent (SVL); tibia length from heel to skin fold of knee (TL_{fold}); tibia length from heel to outer surface of flexed knee (TL_{knee}); diameter of eye (EY); distance from anterior corner of eye to center of naris (EN); internarial distance, between centers of external nares (IN); distance from anterior corner of eye to tip of snout (SN); head width at widest point, typically at the level of the tympani (HW); head length, from tip of snout to posterior margin of tympanum (HL); horizontal tympanum diameter (TY); hand length from proximal edge of palm to tip of 3rd finger (HandL); foot length from proximal edge of sole to tip of 4th toe (FootL); width of the third finger disc (3rd F); width of the fourth toe disc (4th T). We also introduce a new measure, length of the first finger, from the most proximal margin of webbing between the first and second fingers to the tip of the disc (1st F). We provide two measures of TL to facilitate comparison with all earlier studies of the genus, which have generally evolved from using TL_{fold} (e.g., Zweifel, 1956) to TL_{knee} (e.g., Zweifel, 1985).

We recorded calls in the field using a Sennheiser K6 microphone and either a Sony Professional Walkman WM-D6C cassette recorder or a Sony MDSJE480 minidisc recorder. Call structure was analyzed using the computer program Avisoft-SASLab Pro(v4.34).

We confirmed by dissection generic assignment of the frogs using the presence of an eleutherognathine jaw, absence of clavicles and procoracoids, presence of expanded finger discs larger than toe discs, fifth toe shorter than the third, *M. depressor mandibulae* arising mostly from the dorsal musculature, and alary process of premaxilla projecting dorsally (Burton and Zweifel, 1995; Menzies and Tyler, 1977; Parker, 1934; Zweifel and Parker, 1989). Type specimens are deposited in the Bernice P. Bishop Museum, Honolulu (BPBM) and Papua New Guinea National Museum and Art Gallery, Port Moresby (PNGNM).

Pairwise statistical comparisons of SVL means utilized Student's *t*-test in SigmaStat, version 2.0. All other statistical comparisons involved general linear model ANOVA to determine if two-parameter regressions (most commonly one morphometric parameter against SVL) varied among samples. Significant pairwise differences were detected using Tukey's test. These tests were performed using Minitab 14. To save space, we summarize morphometric differences among samples or species with simple bivariate ratios. In the accompanying tables we highlight those ratios whose constituent variables have significantly different relationships among strata (sexes, geographic samples, species) in the ANOVA tests. A posteriori canonical variates and discriminant function tests were performed using PAST, version 1.32, to evaluate how well the presumptive species could be discriminated from each other in multivariate space.

Unless otherwise noted, all latitude and longitude coordinates use the Australian Geodetic Datum, 1966 (AGD 66).

Cophixalus **variabilis** *sp. nov.*

Holotype.—BPBM 20165 (field no. FK 10633), adult male (Figs. 1, 2), collected by F. Kraus on SE slope Mt Pekopekowana, 10.2851° S, 150.1822° E (WGS 84), 330 m, Milne Bay Province, Papua New Guinea, 24 May 2004.

Paratypes.—Papua New Guinea: Milne Bay Province: near Upaelisafupi Stream, Cloudy Mts, 10.4971° S, 150.2330° E (WGS 84), 715 m, 10–16 April 2002 (BPBM 15772–803); same locality, 11–20 April 2002 (PNGNM 23747–51, 23838–47); Cloudy Mts, 10.5079° S, 150.2227° E (WGS 84), 1010 m, 19 April 2002 (BPBM 15804); Cloudy Mts, 10.5095° S, 150.2224° E, 980–1000 m, 23 April 2002 (BPBM 15805–08); same data as holotype but 7 May 2002 (BPBM 15809–10); along Wailahabahaba Creek, SE slope Mt Pekopekowana, 10.2826° S, 150.1548° E (WGS 84),

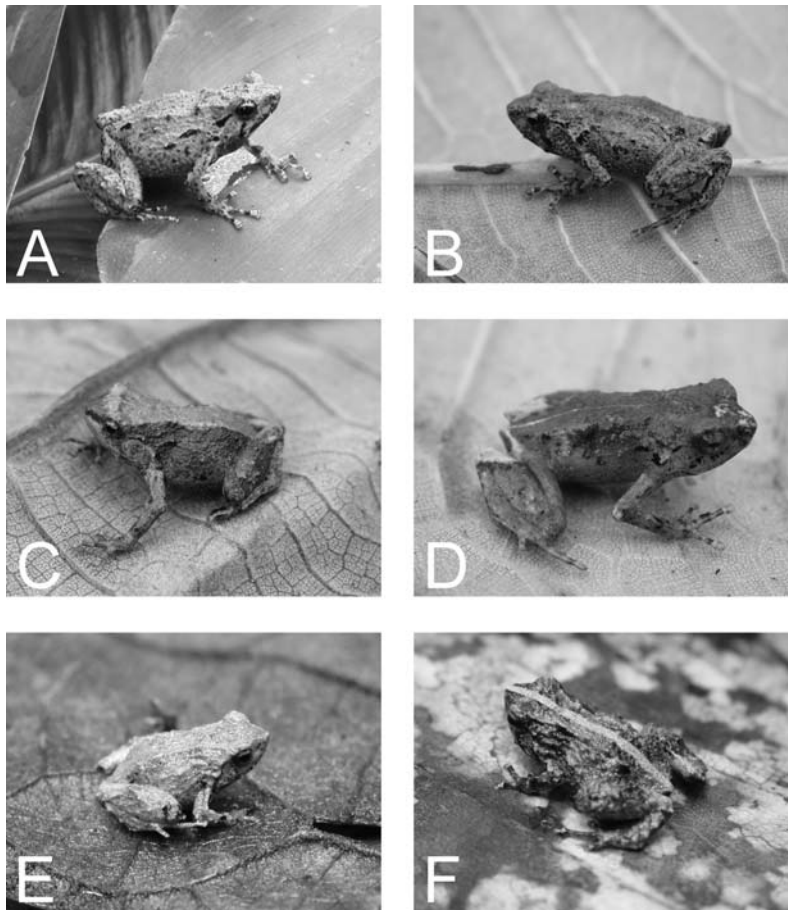


FIG. 1.—(A) *Cophixalus variabilis*, paratype (BPBM 15772), male, Cloudy Mountains, Milne Bay Province; (B) *C. timidus*, paratype (BPBM 18092), female, Mt Simpson, Milne Bay Province; (C) *C. timidus*, paratype (BPBM 18096), female, Mt Simpson, Milne Bay Province; (D) *C. timidus*, paratype (BPBM 18104), female, Mt Simpson, Milne Bay Province; (E) *C. sisyphus*, paratype (BPBM 19302), male, Mt Obree, Central Province; and (F) *C. sisyphus*, paratype (BPBM 19303), male, Mt Obree, Central Province.

590–615 m, 9–10 May 2002 (BPBM 15811–14); same locality, 14–17 May 2002 (PNGNM 23850–51); along Sagabada River, SE slope Mt Pekopekowana, 10.2820° S, 150.1493° E, 1600 m, 12 May 2002 (BPBM 15815); SE slope Mt Pekopekowana between 10.2815° S, 150.1616° E, 620–680 m, 13 May 2002 (BPBM 15816–21, PNGNM 23848–49); Central Province: Moroka, 9.4290° S, 147.5932° E, 302 m, 21 March 2005 (BPBM 21886–89).

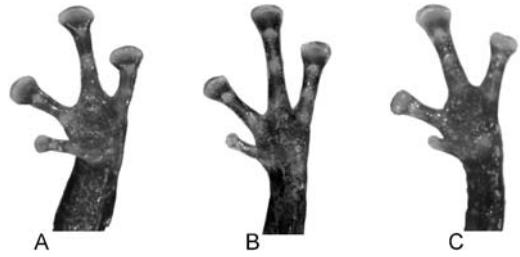
Referred specimens.—Papua New Guinea: Milne Bay Province: E slope Oya Tabu (= Mt Kilkerran), Fergusson Island, 9.4576° S, 150.7888° E (WGS 84), 960 m, 23 August 2002 (BPBM 16273–74, PNGNM 23852); NE slope Oya Tabu, Fergusson Island, 9.4588° S, 150.7787° E, 1500 m, 28 August 2002 (BPBM 16275); NE slope Oya Tabu, Fergusson Island, 9.4548° S, 150.8043° E (WGS 84), 320–360 m, 31 August 2002 (BPBM 16276–78, PNGNM 23853–54); S slope Oya Waka, Fergusson Island, 9.4562° S, 150.5596° E (WGS 84), 980 m, 9–13 September 2002 (BPBM 16279–85, PNGNM 23855–56); near Saidowai, Normanby Island, 9.9560° S, 150.9508° E (WGS 84), sea level, 1 October 2002 (BPBM 16286).

Diagnosis.—A small (adult males 13.6–18.6 mm, adult females 14.5–19.7 mm) species of *Cophixalus* having a tuberculate dorsum; well-developed first finger (1^{st} F/HandL = 0.15–0.28); well-developed, expanded, flattened discs on all fingers and toes; toes free of

webbing; vocal slits in males; sexual monomorphism in tympanum size (TY/SV = 0.035–0.075 in males, 0.045–0.071 in females); moderately long legs (TL_{knee}/SVL = 0.46–0.58, TL_{fold}/SVL = 0.41–0.53); a relatively short, broad snout (EN/IN = 0.72–1.00); vertical lores; ventral pectoral spots usually obscure or absent; shanks typically banded or mottled with dark brown or black; heavily melanized ventral surfaces in most individuals, and a call consisting of a series of 1–31 peeps.

Cophixalus variabilis is distinguished from *C. ateles*, *C. bewaniensis*, *C. pipilans*, *C. pulchellus*, *C. shellyi*, and *C. sphagnicola* by its tuberculate dorsum, variegated or striped color pattern, and in having the first finger of normal length, not reduced in size, with a disc; from *C. verrecundus* in having discs on the fingers and toes; from *C. tagulensis* in having the toes free of webbing; from *C. daymani* in having vocal slits in males, vertical lores, and longer legs (TL_{fold}/SVL = 0.31–0.38 in *C. daymani*); from *C. parkeri* and *C. kaindiensis* in having the third toe distinctly longer that the fifth (subequal in *C. parkeri* and *C. kaindiensis*); and from *C. nubicola* in its longer legs (TL_{fold}/SVL = 0.35–0.38 in *C. nubicola*). It is distinguished from all remaining Papuan *Cophixalus* by its much smaller size and heavily melanized ventral surfaces but also differs from *C. cheesmanae* and *C. verrucosus* in its short, broad (vs. pointed) snout; from *C. cryptotympanum* in having vocal slits in males and a tuberculate dorsum; and from *C. biroi* in its vertical lores and more variable color pattern.

Description of holotype.—An adult male. Head moderately wide (HW/SVL = 0.39), with vertical loreal region; canthus rostralis rounded, slightly concave when viewed from above; nostrils directed laterally, much closer to tip of snout than to eyes; internarial distance considerably larger than distance from naris to eye (EN/IN = 0.80, IN/SVL = 0.096, EN/SVL = 0.077); snout rounded and projecting when viewed from the side, angulate when viewed from above; eyes moderately large (EY/SVL = 0.12); eyelid approximately 3/4 the width of the interorbital distance; tympanum indistinct and small (TY/SVL = 0.064), without a clear annulus. Dorsal and lateral surfaces smooth (probably an artifact of preservation). Supratympanic fold absent. Ventral surfaces



FIG

generally smooth but weakly granular on abdomen. Fingers unwebbed, bearing discs with terminal grooves; relative lengths 3 > 4 > 2 > 1; first finger and disc well-developed. Finger discs approximately 2.5 times widths of penultimate phalanges, except for the first finger disc, which is only approximately 1.5 times width of penultimate phalanx (Fig. 2A). Articular tubercles low and indistinct; metacarpal tubercles poorly developed. Toes unwebbed, bearing discs with terminal grooves; relative lengths 4 > 3 > 5 > 2 > 1. Toe discs smaller than those of fingers; disc of fourth toe approximately twice width of penultimate phalanx; disc of first toe approximately same width as penultimate phalanx. Subarticular tubercles lacking but having thicker, lighter skin in same areas; inner metatarsal tubercle narrow and elongate, outer lacking. Hind legs moderately long (TL_{knee}/SVL = 0.49, TL_{fold}/SVL = 0.44).

Dorsum with variegated color pattern. Dorsum posterior to scapular region light brown with orange cast and with few small brown blotches; anterior to scapular region chocolate brown, including top of head and sides of face. Sides with same antero-posterior division of colors but with band of dense dark brown spotting posterior to forearm; anteriorly, from behind eye to behind forearm, ground color light gray. Tops of limbs tan, mottled and blotched with black or dark brown; backs of thighs tan heavily mottled with dark brown; ill-defined triangular dark brown patch surrounds the anus. Short, dark brown postocular line ending approximately halfway to forearm insertion; followed by a dark brown dash above forearm and then the band of dark brown lateral spots. Entire dorsum covered

TABLE 1.—Sexual variation in mensural characters for the Cloudy Mountains sample of *Cophixalus variabilis*. Numbers in parentheses indicate sample sizes.

	Males (20)		Females (21)	
Character	Mean	Range	Mean	Range
SVL (mm)	15.5	13.6–16.9	16.8	14.0–19.4
TLfold/SVL	0.47	0.42–0.51	0.48	0.41–0.51
TLknee/SVL	0.52	0.47–0.56	0.52	0.47–0.56
EN/SVL	0.085	0.073–0.094	0.082	0.071–0.090
IN/SVL	0.099	0.089–0.110	0.096	0.085–0.107
SN/SVL	0.13	0.12–0.15	0.13	0.11–0.15
TY/SVL	0.054	0.040–0.072	0.060	0.045–0.071
EY/SVL	0.13	0.12–0.13	0.12	0.11–0.13
HW/SVL	0.39	0.36–0.43	0.37	0.35–0.40
HL/SVL	0.33	0.31–0.34	0.32	0.26–0.34
HandL/SVL	0.28	0.25–0.32	0.28	0.25–0.32
FootL/SVL	0.47	0.43–0.53	0.48	0.43–0.53
3rd F/SVL	0.059	0.049–0.067	0.062	0.047–0.078
4th T/SVL	0.048	0.040–0.054	0.049	0.039–0.058
EN/IN	0.86	0.79–1.00	0.86	0.75–1.00
EN/SN	0.65	0.57–0.74	0.63	0.54–0.70
EY/SN	0.98	0.87–1.11	0.94	0.81–1.05
3rd F/4th T	1.2	1.0–1.5	1.3	1.1–1.4
HL/HW	0.84	0.76–0.93	0.87	0.79–0.95
1st F/HandL	0.21	0.18–0.26	0.22	0.19–0.25

with minute black punctations, invisible except under magnification. Iris dark brown. Venter light pearl gray, densely dusted with black punctations and flecks, densest from chin to chest and decreasing in density posteriorly; undersides of limbs same.

Measurements (in mm).—SVL = 15.6, TL_{fold} = 6.9, TL_{knee} = 7.6, HW = 6.1, HL = 5.5, IN = 1.5, EN = 1.2, SN = 2.1, EY = 1.9, TY = 1.0, HandL = 3.9, FootL = 7.6, 3rd F = 1.08, 4th T = 0.96.

Variation.—The range of mensural variation in the samples is considerable (Tables 1–3). However, consistent morphological differences between the sexes are virtually nonexistent, judging from comparisons made within the large sample from the Cloudy Mts. For this sample, females are larger than males (t = 3.76, P = 0.001), but a significant interaction does not occur between sex and any of the parameter pairs used in the morphometric ratios. Given this absence of sexual morphometric differences, we pooled males and females for our comparisons of geographic variation among our three largest samples (Table 2).

Body size is significantly larger in specimens from Fergusson Island than in specimens from the adjacent mainland (F = 27.629, df = 2, P < 0.001; Fergusson vs. Cloudy Mts p = 3, q = 9.569, P < 0.001; Fergusson vs. Owen Stanley Mts q = 9.168, P < 0.001); specimens from the two mainland localities cannot be distinguished (q = 0.461, P = 0.943). Morphometric relationships that differ geographically are IN vs. SVL, TY vs. SVL, HW vs. SVL, 3rd F vs. SVL, 4th T vs. SVL, EN vs. IN, EY vs. SN, HL vs. HW, and 1st F vs. HandL (Table 2). The frogs from the Cloudy Mts have significantly wider IN at any given SV than do those from Fergusson Island (T = 2.719, P = 0.0216) and are almost significantly different from the sample from Owen Stanley Mts (T = 2.254, P = 0.0683) but the slopes remain identical. The sample from the Cloudy Mts has wider TY than does that from Fergusson Island for any given SV (T = 4.037, P = 0.0004) but the slope is the same and the remaining pairwise comparisons show no differences. The sample from the Owen Stanley Mts has larger HW for any given SV than does that from Fergusson Island (T = 3.328, P = 0.038) but there is no difference in slopes and all other sample comparisons are identical. The sample from Fergusson Island has smaller 3rd F at any given SVL than do those from the Cloudy Mts (T = 2.996, P = 0.0101) or Owen Stanley Mts (T = 3.683, P = 0.0012), but there is no difference in slopes. The sample from the Owen Stanley Mts has significantly larger 4th T at any given SVL than do those from the Cloudy Mts (T = 3.9824, P = 0.0004) or Fergusson Island (T = 3.927, P = 0.0005), but there is no difference in slope. The sample from Fergusson Island increases more rapidly in EN with increasing IN than do the samples from the Cloudy Mts or Owen Stanley Mts (F = 3.39, df = 2, P = 0.039). The samples differ in the rate at which EY increases with respect to SN (F = 3.56, df = 2, P = 0.033), with that from Fergusson Island increasing at the most rapid rate, that from the Owen Stanley Mts at the slowest rate, and that from the Cloudy Mts intermediate between these extremes. The sample from Fergusson Island has a relatively longer HL for any given HW compared to that from the Owen Stanley Mts (T = 2.7459, P = 0.0195) but neither differs from the sample from the Cloudy Mts and the slopes do not differ, and it has a relatively longer 1st F for any given HandL than do the samples from the Cloudy Mts (T = 2.594, P = 0.0318) or Owen Stanley

TABLE 2.—Geographic variation in mensural characters for three samples of *Cophixalus variabilis* comparing only adults. Numbers in parentheses indicate sample sizes; asterisks indicate character pairs having significantly different covariant relationships among locations using Tukey's test (see text).

	Cloudy Mts (41)		Owen Stanley Mts (18)		Fergusson Island (16)	
Character	Mean	Range	Mean	Range	Mean	Range
SVL (mm)	15.5	13.6–19.4	15.7	14.1–17.9	17.3	15.3–19.7
TLfold/SVL	0.47	0.41–0.51	0.49	0.43–0.53	0.48	0.46–0.52
TLknee/SVL	0.52	0.46–0.56	0.53	0.46–0.58	0.53	0.50–0.57
EN/SVL	0.083	0.071–0.094	0.082	0.073–0.092	0.084	0.075–0.092
IN/SVL*	0.097	0.085–0.110	0.095	0.078–0.104	0.091	0.082–0.098
SN/SVL	0.13	0.11–0.15	0.13	0.12–0.15	0.13	0.12–0.14
TY/SVL*	0.057	0.040–0.072	0.051	0.039–0.075	0.048	0.035–0.066
EY/SVL	0.13	0.11–0.14	0.13	0.12–0.14	0.12	0.12–0.13
HW/SVL*	0.38	0.33–0.43	0.35	0.36–0.43	0.37	0.32–0.39
HL/SVL	0.32	0.26–0.35	0.32	0.28–0.35	0.32	0.30–0.33
HandL/SVL	0.28	0.25–0.32	0.27	0.19–0.34	0.27	0.25–0.30
FootL/SVL	0.48	0.43–0.53	0.48	0.42–0.52	0.47	0.44–0.51
3^{rd} F/SVL*	0.061	0.047–0.078	0.063	0.052–0.070	0.057	0.048–0.065
4^{th} T/SVL*	0.048	0.039–0.058	0.053	0.041–0.062	0.048	0.042–0.055
EN/IN*	0.86	0.79–1.00	0.87	0.74–1.00	0.92	0.82–1.00
EN/SN	0.64	0.54–0.74	0.62	0.55–0.70	0.64	0.58–0.74
EY/SN*	0.96	0.78–1.19	0.97	0.83–1.11	0.95	0.88–1.05
3^{rd} F/4^{th} T	1.3	1.0–1.5	1.2	1.1–1.4	1.2	1.1–1.3
HL/HW*	0.86	0.76–0.95	0.83	0.77–0.90	0.87	0.82–0.98
1^{st} F/HandL*	0.22	0.18–0.26	0.21	0.15–0.25	0.24	0.21–0.28

Mts ($T = 3.140$, $P = 0.0074$) but there is no difference among the slopes.

A number of mensural characters show apparent ontogenetic variation, with adults and juveniles having different covariation slopes for a number of character pairs (Table 3). Juveniles have relatively longer legs (for TL_{fold} vs. SVL, $F = 4.94$, $P = 0.031$; for TL_{knee} vs. SVL, $F = 6.13$, $P = 0.017$), longer snouts (for EN vs. IN, $F = 7.83$, $P = 0.007$; for EN vs. SN, $F = 8.07$, $P = 0.007$), wider heads (HW vs. SVL, $F = 9.78$, $P = 0.003$), and longer feet (for FootL vs. SVL, $F = 4.65$, $P = 0.0036$).

Color variation is considerable. In preservative, most specimens are variegated with black and/or dark brown flecks and spots on a light tan to dark gray ground color. Many specimens have longitudinal striping of two types: of 88 specimens, 24 have a light tan mid-dorsal stripe and 16 have a lighter, tan to russet, mid-dorsal band; a few specimens have both, that is, a narrow mid-dorsal stripe contained within a wider mid-dorsal band. Of the specimens having the narrow tan stripe, 11 also have narrow tan stripes on the backs of the thighs and shanks ($n = 8$) or only the shanks ($n = 3$). Thirty-nine specimens have the heels and proximal upper surfaces of the thighs conspicuously lighter than the surrounding regions, producing a light, triangular posterior patch when the animals sit at rest. Clear lumbar ocelli are present in 26 specimens, obscure ocelli are present in 16, and ocelli are absent in 22. The shanks of most individuals are mottled or banded with darker brown or black. Venters have a straw ground color flecked with dark gray, with the amount of gray flecking varying considerably. In specimens with the least flecking, overall ventral coloration is a dirty light gray; most specimens have a two-toned ventral coloration, with a dark chin and throat followed by a lighter chest and abdomen. One or two (usually one) cream or dirty white pectoral spots are present on each side of the pectoral region in many specimens. In 15 specimens examined, these spots are distinct, in 29 specimens obscure, and in 20 specimens absent.

Color in life.—In life, BPBM 15773 was noted to have a tan dorsal ground color with darker brown wash and some scattered small russet blotches, a light tan mid-dorsal stripe and inguinal ocelli, black blotches in the scapular region, and a gray venter. Others (e.g., BPBM 15798) were noted to have a tan face and heel marks on an otherwise dark brown ground. These are the two most commonly observed color patterns, although the tan

TABLE 3.—Ontogenetic variation in mensural characters for the Cloudy Mts sample of *Cophixalus variabilis*. Adults were determined by sexual maturity (presence of enlarged ova in females and vocal slits in males) and juveniles are those animals smaller than the smallest adult. Numbers in parentheses indicate sample sizes; asterisks indicate character pairs having significantly different covariant relationships between the samples using Tukey's test (see text). Differences in SVL were not compared.

	Adults (41)		Juveniles (7)	
Character	Mean	Range	Mean	Range
SVL (mm)	16.1	13.6–19.4	11.8	10.1–15.4
TL_{fold}/SVL*	0.47	0.41–0.51	0.48	0.41–0.52
TL_{knee}/SVL*	0.52	0.46–0.56	0.53	0.46–0.58
EN/SVL	0.083	0.071–0.094	0.093	0.081–0.109
IN/SVL	0.097	0.085–0.110	0.109	0.099–0.119
SN/SVL	0.13	0.11–0.15	0.15	0.13–0.17
TY/SVL	0.057	0.040–0.072	0.051	0.044–0.065
EY/SVL	0.13	0.11–0.14	0.14	0.13–0.16
HW/SVL*	0.38	0.33–0.43	0.39	0.36–0.45
HL/SVL	0.32	0.26–0.35	0.35	0.31–0.38
HandL/SVL	0.28	0.25–0.32	0.27	0.26–0.30
FootL/SVL*	0.48	0.43–0.53	0.46	0.41–0.52
3^{rd} F/SVL	0.061	0.047–0.078	0.056	0.050–0.062
4^{th} T/SVL	0.048	0.039–0.058	0.048	0.036–0.059
EN/IN*	0.86	0.75–1.00	0.86	0.75–0.93
EN/SN*	0.64	0.54–0.74	0.64	0.60–0.67
EY/SN	0.96	0.78–1.19	0.96	0.85–1.13
3^{rd} F/4^{th} T	1.3	1.0–1.5	1.2	0.9–1.4
HL/HW	0.86	0.76–0.95	0.89	0.83–0.95
1^{st} F/HandL	0.22	0.18–0.26	0.18	0.17–0.20

ground color can also be predominantly russet and some animals are entirely tan with a few black flecks (e.g., BPBM 15772; Fig. 1A). Occasional specimens have a dark ground color with a narrow, light tan mid-dorsal stripe and others are dark brown with a broad, russet mid-dorsal band. Venters are almost always so heavily flecked with melanin as to appear dark gray, but occasional specimens are light gray.

Call.—We recorded 24 complete calls from nine individuals (Table 4; Fig. 3). The average call consists of 12–13 peeping notes (range 1–31) with a mean repetition rate of 2.36 notes/s (range 0.84–3.32 notes/s). The notes averaged 114 ms in duration (range 78–196 ms) and the intervals between notes averaged 414 ms (range 196–1070 ms). The mean dominant frequency was 4175 Hz.

The holotype (BPBM 20165) produced two different types of calls and was observed to alternate between them (Table 4; Figs. 3A–F). The first two complete calls that we recorded had a mean repetition rate of 1.85 notes/s while the next three calls had a repetition rate of 3.27 notes/s. There were also differences in the number of notes per call. The mean number of notes in the first two calls was 17.5 (range 10–25). This decreased to 9.7 (range 5–14) for the next three calls. BPBM 20165 was the only individual that we directly observed alternating between the two different calling rates, but this behavior could account for the rather large spread that we observed in call repetition rate (1.54–3.32 notes/s for mainland populations of *Cophixalus variabilis*). BPBM 20165 also had a shorter mean call note (84 ms) than did the other individuals recorded from the New Guinean mainland (mean = 119 ms; n = 15 calls from six individuals).

The two individuals from Fergusson Island (BPBM 16273–74) had a much slower note repetition rate (Table 4; Fig. 3G–I) than did those from the New Guinean mainland. The mean repetition rate for the two specimens from Fergusson Island was 0.85 notes/s (n = 4; range 0.84–0.86 notes/s) compared to 2.67 notes/s for the seven specimens from the mainland (n = 20; range 1.53–3.33 notes/s). These differences mainly reflect differences in the duration of the internotes of these two populations. The notes in the population from Fergusson Island, which averaged 136 ms in durationrange 102–196 ms), were only slightly longer than those for mainland populations, which averaged 110 ms (range 78–133 ms). However, the mean internote duration for the population from Fergusson Island was 1042 ms (range 990–1070 ms) compared to a mean of 281 ms (range 196–53
the New Guinean mainland.

During drought conditions in August and September, 2002, males on Fergusson Island were only heard to call on the four nights (out of five weeks of field activity) having rain. The two individuals from Fergusson Island were recorded on one of these four nights and the generally dry conditions may have affected their calling rate. We heard only four individuals calling irregularly during the first few hours of darkness. In our experience, other species of New Guinean frogs tend to call in small numbers at irregular intervals and at slower rates under drought conditions than they do during wet weather. Unfortunately, we do not have data for the populations from Fergusson Island during wet weather, but our overall impression of the call was that

it seemed relatively tepid compared to other populations of *Cophixalus variabilis* and its close relatives observed under wet conditions.

Individuals were observed to call both day and night but predominantly from dusk through the first several hours of darkness. Calling during daytime was more frequent under cloudy conditions or immediately following a rain but never was observed to involve as many animals as nocturnal calling. Males most often called from exposed sites on vegetation 1–2 m above ground, but daytime calling was conducted from hidden locations within hollow trees, under bark, or even in underground burrows.

Two individuals from the New Guinean mainland were recorded during the afternoon. Their calls ($n = 10$) averaged 5.1 notes (range 1–29) with a repetition rate of 2.96 notes/s. The other five individuals from the mainland produced calls ($n = 10$) that averaged 16.9 (range 5–29) notes and had a mean repetition rate of 2.41 notes/s. The duration of the notes was similar in the two groups (116 ms during the day and 105 ms at night). The internote duration in the diurnal calls was slightly shorter than for that for calls recorded at night (215 ms vs. 341 ms). Dominant frequencies were similar (4190 Hz for the diurnal calls; 4307 Hz for nocturnal calls).

In 13 of the 23 calls with two or more notes, the first note is the longest note in the call (in some cases by only a few ms). In the holotype (BPBM 20165), the first note is the longest in only one of five complete calls.

Ecological notes.—The species ranges from sea level (Normanby Island) to 1500 m (Fergusson Island), but most of our records occurred from 300–1000 m. The species was always found in closed-canopy lowland and mid-elevation rainforest, except for the elevational outliers. The sea-level specimen was found in a sago swamp; the 1500 m specimen in a more open montane forest dominated by *Metrosideros* (Myrtaceae). Where found, the species appears to be widely distributed throughout the forest, showing no obvious tendency to cluster near streams, unlike some other members of the genus (Menzies, 1975: 59).

Animals of both sexes make no apparent attempt to hide themselves at night and are easily encountered fully exposed while perching on vegetation. In this choice of perch sites this species closely resembles species of *Albericus*. During the above-mentioned drought, several specimens were captured hiding in moist soil beneath rocks alongside a small forested stream at 320–360 m. Except for two males calling during the daytime, these were the only animals to be seen on the ground.

Judging from observations made incidental to dissections, ants appear to form a significant portion of the diet for this species.

Syntopic congeners include *Cophixalus verrucosus* and an undescribed *Cophixalus* related to *C. ateles*. The former is a larger species with similar perching habits to *C. variabilis* but shows some tendency to cluster around stream courses; the latter is a slightly smaller species that typically inhabits the ground or vegetation within ca. 20 cm of the ground.

Etymology.—The masculine Latin adjective "variabilis" means "changeable" and refers to the great color-pattern and call-rate variation seen in this species.

Distribution.—We have collected *Cophixalus variabilis* at several localities in southeastern Milne Bay Province (Fig. 4), including the Cloudy Mts (700–1000 m), Owen Stanley Mts (300–600 m), Fergusson Island (300–1500 m), and Normanby Island (sea level). Additionally, we have collected the species near Aieme Creek (300 m), east of Port Moresby, in Central Province (Fig. 4). We presume the species to be restricted to the Southeast Peninsula and adjacent islands.

Remarks.—The values in calling rate of animals from Fergusson Island fall outside the already wide range of variation observed in mainland specimens of *Cophixalus variabilis* (Table 4) and differ as greatly as that seen in the closely related species described next. Nonetheless, we tentatively include our material from the D'Entrecasteaux Islands in *C. variabilis* for two reasons. First, except for a tendency toward larger body size, we can find no morphological features that serve to distinguish D'Entrecasteaux material from mainland material. Second, the only calls we could record of animals from Fergusson Island were obtained during a prolonged drought. It was our impression that these frogs, and other syntopic species, were calling in a sluggish

TABLE 4.—Call characteristics for *Cophixalus variabilis*, *C. timidus*, and *C. sisyphus*.

Species/Specimen	Call no.	Locality	Time (h)	Elevation (m)	Temperature (C)	Total notes in call	Mean note duration (s)	Mean internote duration (s)	Repetition rate (notes/s)	Dominant frequency (Hz)
Cophixalus variabilis										
Uncaptured No. 1	A	Cloudy Mts	ca. 1800–2000	715	NR	29	0.112	0.477	1.696	4050
Uncaptured No. 2	A	”	1230	”	27.5	2	0.111	0.222	2.843	4080
”	B	”	”	”	”	5	0.117	0.236	2.801	4270
”	C	”	”	”	”	1	0.123	—	—	4030
”	D	”	”	”	”	2	0.121	0.236	2.659	4240
”	E	”	”	”	”	2	0.121	0.232	2.658	4350
”	F	”	”	”	”	2	0.131	0.217	2.687	4410
BPBM 15772	A	”	1840	”	23.0	27	0.122	0.532	1.530	4350
Uncaptured No. 3	A	”	1920	”	23.4	20	0.132	0.282	2.406	4290
”	C	”	”	”	”	19	0.133	0.269	2.481	4350
Uncaptured No. 4	A	”	”	”	”	10	0.125	0.279	2.469	4210
BPBM 15782	A	”	1340	”	24.5	10	0.110	0.197	3.240	4230
”	B	”	”	”	”	11	0.108	0.197	3.264	4150
”	C	”	”	”	”	4	0.107	0.199	3.211	4030
”	D	”	”	”	”	12	0.108	0.196	3.276	4110
BPBM 20165	A[1]	Owen Stanley Mts	1830	330	23.6	1	0.080	—	—	4380
”	B	”	”	”	”	10	0.078	0.463	1.851	4260
”	C	”	”	”	”	25	0.082	0.458	1.851	4220
”	D	”	”	”	”	5	0.078	0.226	3.257	4630
”	E	”	”	”	”	10	0.087	0.217	3.325	4450
”	F	”	”	”	”	14	0.096	0.208	3.263	4260
BPBM 21886	A	Moroka	1830	302	25.5	14	0.098	0.547	1.551	4260
”	B	”	”	”	”	12	0.102	0.550	1.532	4160
”	C	”	”	”	”	16	0.102	0.535	1.569	4180
BPBM 16273	A	Fergusson Island	2040	960	18.8	11	0.102	1.062	0.858	3920
”	B	”	”	”	”	16	0.121	1.070	0.840	3930
BPBM 16274	A	”	2050	”	”	28	0.196	0.990	0.842	3730
”	B	”	”	”	”	31	0.125	1.047	0.853	3640
Cophixalus timidus										
BPBM 18098	A	Mt Simpson	1100	2170	22.3	9	0.229	0.882	0.898	4000
”	B	”	”	”	”	13	0.228	0.859	0.918	4080
”	C	”	”	”	”	12	0.220	0.877	0.910	4000
”	D	”	”	”	”	12	0.239	0.873	0.898	3940
”	E	”	”	”	”	11	0.243	0.835	0.926	3950
BPBM 18107	A	”	1920	1490	18.0	14	0.203	0.967	0.854	4500
”	B	”	”	”	”	10	0.213	0.956	0.855	4660
”	C	”	”	”	”	9	0.194	0.948	0.874	4710
BPBM 18108	A	”	1930	”	”	12	0.264	1.127	0.718	4840
”	B	”	”	”	”	13	0.256	1.147	0.713	4710
”	C	”	”	”	”	13	0.185	0.896	0.922	4600
”	D	”	”	”	”	13	0.192	0.887	0.924	4550
”	E	”	”	”	”	14	0.265	1.043	0.764	4600
Uncaptured No. 5	A[2]	”	”	”	”	13	0.193	0.888	0.989	4490
Cophixalus sisyphus										
BPBM 18316	A[3]	Mt Obree	2115	600	22.0	9	0.145	0.309	2.196	4580
”	B	”	”	”	”	10	0.159	0.304	2.148	4460
”	C	”	”	”	”	10	0.160	0.305	2.142	4600
BPBM 19299	A	”	1910	1610	20.2	7	0.183	0.452	1.569	5000
”	B	”	”	”	”	7	0.221	0.513	1.353	4860
”	C	”	”	”	”	6	0.223	0.504	1.365	4620
”	D	”	”	”	”	6	0.219	0.489	1.404	4890
BPBM 19300	A	”	1925	”	”	7	0.183	0.452	1.569	4940
”	B	”	”	”	”	7	0.191	0.459	1.535	4890
”	C	”	”	”	”	7	0.194	0.476	1.484	4710
BPBM 19301	A	”	2030	”	”	7	0.179	0.447	1.597	5100
”	B	”	”	”	”	5	0.196	0.445	1.548	5190

TABLE 4.—Continued.

Species/Specimen	Call no.	Locality	Time (h)	Elevation (m)	Temperature (C)	Total notes in call	Mean note duration (s)	Mean internote duration (s)	Repetition rate (notes/s)	Dominant frequency
BPBM 19306	A	"	2105	"	17.8	8	0.195	0.534	1.367	4990
"	B	"	"	"	"	8	0.202	0.530	1.361	4840
"	C	"	"	"	"	8	0.202	0.523	1.374	4830
BPBM 19308	A	"	1950	"	19.2	8	0.158	0.451	1.636	5230
BPBM 19316	A	"	2030	1795	16.5	8	0.166	0.487	1.524	5570
"	B	"	"	"	"	8	0.159	0.488	1.540	5600
"	C	"	"	"	"	8	0.167	0.466	1.571	5630

[1] Partial call – presumed last note of series.
[2] Two notes cannot be accurately measured because of interference from another frog; call statistics based on 11 notes and 8 internotes; repetition rate based on entire call.
[3] Partial call – call statistics based on 8 full notes included in recording.

fashion during this drought (when calling at all, which was extremely infrequently) and we are not convinced that the slow call rates obtained by us are not an artifact of the adverse weather conditions. It remains to obtain calls from specimens from the D'Entrecasteaux Islands during wet weather conditions to determine whether the apparent call differences seen in our material are consistent, and hence of potential taxonomic importance, or merely vary with weather conditions. Until that time, it seems most prudent to include these samples within *C. variabilis*. Because of their questionable status, calls from the animals from Fergusson Island will not be used in comparisons with the new species that follow.

Cophixalus **timidus** *sp. nov.*

Holotype.—BPBM 18098 (field no. FK 7472), adult male (Figs. 1, 2), collected by F. Kraus on NE slope Mt Simpson, 10.0316° S, 149.5767° E, 2170 m, Milne Bay Province, Papua New Guinea, 21 February 2003.

Paratypes.—Papua New Guinea: Milne Bay Province: NE slope Mt Simpson, 10.0380° S, 149.5984° E, 1800 m, 17 February 2003 (BPBM 18092); same data as holotype but 19 February 2003 (BPBM 18093–97); same data as holotype (BPBM 18099–105, PNGNM 24002); N slope Mt Simpson, 10.0364° S, 149.5749° E, 2480 m, 21 February, 2003 (BPBM 18106); 0.5 km S Bunisi, 10.0209° S, 149.5947° E, 1490 m, 23 February 2003 (BPBM 18107–12); same locality but 24 February 2003 (BPBM 18113); NE Bunisi, 10.0140° S, 149.6129° E, 1520 m, 26 February 2003 (BPBM 18114); ca. 1 km S Bunisi, 10.0245° S, 149.5947° E, 1490–1540 m, 27 February 2003 (BPBM 18115–17); Bunisi, 10.0171° S, 149.6002° E, 1420 m, 25 February 2003 (PNGNM 24003–24006).

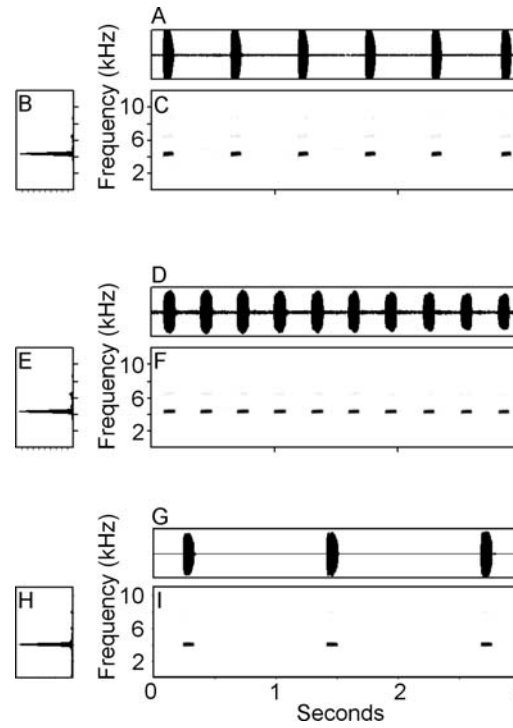


FIG. 3.—(A) Waveform, (B) power spectrum, and (C) spectrogram of a slow-call sequence of *Cophixalus variabilis*, BPBM 20165, holotype, from southern Owen Stanley Mts; recorded 1830 h, air temperature 23.6 C. (D)–(F) same data for a fast-call sequence from the same animal. (G)–(I) same data for a call from BPBM 16273, Oya Tabu, Fergusson Island; recorded 2040 h, air temperature 18.8 C.

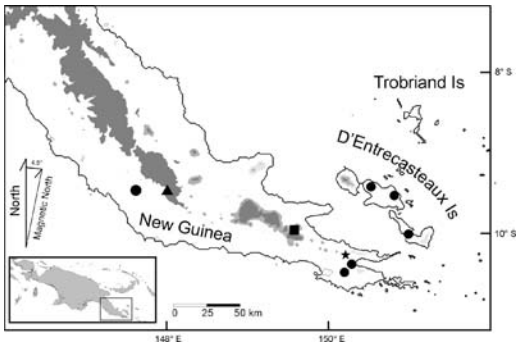


FIG. 4.—Map of southeastern New Guinea and adjacent islands, showing the ranges of *Cophixalus variabilis* (filled circles; star is type locality), *C. timidus* (square), and *C. sisyphus* (triangle).

Diagnosis.—A small (adult males 13.5–17.5 mm, adult females 14.4–21.1 mm) species of *Cophixalus* having a tuberculate dorsum; well-developed first finger (1^{st} F/HandL = 0.09–0.26); discs with well-defined terminal grooves on all fingers and toes except the first finger, which has a narrower, less flattened disc that either lacks a terminal groove or has it weakly developed (present typically but not exclusively in large females); toes free of webbing; vocal slits in males; sexual dimorphism in tympanum size (TY/SVL = 0.031–0.052 in males, 0.048–0.084 in females); relatively short legs (TL_{knee}/SVL = 0.42–0.52, TL_{fold}/SVL = 0.37–0.46); a relatively short, broad snout (EN/IN = 0.75–1.00); vertical lores; light yellow blotch in the groin; 1–4 (usually 1) small yellow spots on each side of the pectoral region; shanks typically uniform dark gray; and a call consisting of a series of 9–14 peeps.

Cophixalus timidus differs from all previously described Papuan *Cophixalus* in the same suite of characters as exhibited by *C. variabilis*, with which it is very similar, and *Cophixalus timidus* differs from *C. variabilis* in having (1) sexual dimorphism in tympanum size; (2) somewhat shorter legs (TL_{knee}/SVL = 0.42–0.52 vs. 0.46–0.58 in *C. variabilis*); (3) disc on first finger less well developed, usually barely wider than penultimate phalanx, and not as flattened as in *C. variabilis*; (4) usually two (sometimes more) small yellow pectoral spots surrounded by black, which are more obvious than in *C. variabilis*; (5) typically a light yellow blotch in the groin; (6) generally no dark banding on the shanks; (7) longer call notes (mean 0.185–0.265 ms vs. 0.078–0.133 ms in *C. variabilis*); and (8) slower call rate (mean 0.713–0.989 notes/s vs. 1.530–3.325 notes/s in mainland *C. variabilis*).

Description of holotype.—An adult male. Head moderately wide (HW/SVL = 0.42), with vertical loreal region; canthus rostralis rounded, straight when viewed from above; nostrils directed laterally, much closer to tip of snout than to eyes; internarial distance considerably larger than distance from external naris to eye (EN/IN = 0.88, IN/SVL = 0.103, EN/SVL = 0.090); snout slightly projecting when viewed from the side, shallowly angulate when viewed from above; eyes moderately large (EY/SVL = 0.12); eyelid approximately 2/3 the width of the interorbital distance; tympanum indistinct and small (TY/SVL = 0.038). Dorsal and lateral surfaces weakly tuberculate. Supratympanic fold weakly developed. Ventral surfaces generally smooth but weakly granular on abdomen. Fingers unwebbed, bearing discs with terminal grooves; relative lengths 3 > 4 > 2 > 1; first finger and disc moderately well-developed. Finger discs approximately twice widths of penultimate phalanges, except for first finger disc, which is just barely wider than penultimate phalanx (Fig. 2B). Articular tubercles low and indistinct; metacarpal tubercles poorly developed. Toes unwebbed, bearing discs with terminal grooves; relative lengths 4 > 3 > 5 > 2 > 1. Toe discs smaller than those of fingers, that of fourth toe approximately 1.5 times width of penultimate phalanx, that of first approximately same width as penultimate phalanx. Subarticular tubercles lacking but with thicker, lighter skin in some areas; inner metatarsal tubercle narrow and elongate, outer lacking. Hind legs relatively short (TL_{knee}/SVL = 0.46, TL_{fold}/SVL = 0.42).

Dorsum with brown ground color heavily and uniformly stippled with tiny black and silver punctations, imparting an overall uniform dark gray appearance. Vestigial black postocular bar present on each side; a few small black spots present above forearm insertions. Narrow cream cresent on each side of lumbar region; remnants of lumbar ocelli but lacking central dark blotches. Dark interrupted band on forearm; legs unbanded. Iris dark brown with numerous tiny silver specks arrayed in a largely radial pattern. Venter light straw

heavily stippled with tiny black punctations, densest on chin and throat, slightly sparser on posterior of abdomen and thighs. Pair of small cream spots on the pectoral region.

Measurements (in mm).—SVL = 15.6, TL_{fold} = 6.5, TL_{knee} = 7.2, HW = 6.5, HL = 5.2, IN = 1.6, EN = 1.4, SN = 2.0, EY = 1.9, TY = 0.6, HandL = 4.2, FootL = 6.8, 3^{rd} F = 0.94, 4^{th} T = 0.83.

Variation.—Mensural variation in the samples is not great, although sexual differences exist (Table 5). Females are generally larger than males ($t = 5.536$, $P < 0.001$). The tympana of females are noticeably larger than those of males and their relative size increases with increasing SVL, whereas that of males decreases slightly ($F = 4.30$, $P < 0.001$). Females have larger toe discs that increase with increasing SV relative to those of males (for 4^{th} T vs. SVL, $F = 2.22$, $P = 0.035$).

Only two juveniles were available for comparison and these have relatively wider and longer snouts (IN/SVL = 0.115–0.118, SN/SVL = 0.16) and larger heads (HW/SVL = 0.42, HL/SVL = 0.37–0.40) than do adults (Table 5).

TABLE 5.—Sexual variation in mensural characters for the type series of *Cophixalus timidus* from Mt Simpson. Numbers in parentheses indicate sample sizes; asterisks indicate character pairs having significantly different covariant relationships between the sexes using Tukey's test (see text).

	Males (14)		Females (15)	
Character	Mean	Range	Mean	Range
SVL (mm)	14.7	13.5–17.5	17.5	14.4–21.1
TLfold/SVL	0.43	0.37–0.46	0.41	0.38–0.45
TLknee/SVL	0.48	0.42–0.52	0.46	0.42–0.49
EN/SVL	0.088	0.080–0.096	0.087	0.081–0.093
IN/SVL	0.097	0.087–0.103	0.096	0.085–0.110
SN/SVL	0.14	0.12–0.14	0.14	0.12–0.15
TY/SVL*	0.043	0.031–0.052	0.070	0.058–0.084
EY/SVL	0.13	0.12–0.14	0.13	0.12–0.14
HW/SVL	0.39	0.35–0.42	0.38	0.34–0.42
HL/SVL	0.33	0.30–0.36	0.34	0.33–0.37
HandL/SVL	0.26	0.22–0.28	0.26	0.24–0.27
FootL/SVL	0.44	0.37–0.49	0.43	0.40–0.46
3^{rd} F/SVL	0.059	0.045–0.075	0.056	0.046–0.068
4^{th} T/SVL*	0.050	0.043–0.055	0.048	0.045–0.055
EN/IN	0.91	0.86–1.00	0.91	0.82–1.00
EN/SN	0.64	0.56–0.70	0.64	0.60–0.69
EY/SN	0.96	0.84–1.05	0.95	0.84–1.05
3^{rd} F/4^{th} T	1.2	1.0–1.6	1.2	1.0–1.4
HL/HW	0.86	0.80–0.92	0.91	0.82–0.96
1^{st} F/HandL	0.16	0.13–0.26	0.17	0.12–0.21

Color pattern of *Cophixalus timidus* is not as variable as in *C. variabilis*. The majority of specimens are dorsally dark gray in alcohol, many uniformly so but most with a few scattered black flecks or small blotches. A few specimens are light gray mottled with black and dark brown, one is light brown with similar mottling. A narrow, light mid-dorsal stripe is seen in only six of the 31 specimens, but is distinct in only one; a single specimen has a wide, light-gray mid-dorsal band. One of the individuals having a light mid-dorsal stripe also has light stripes on the proximal portion of the back of each thigh but these extend only approximately one-third the length of the thigh. Tan heels are seen in eight specimens and, as in *C. variabilis*, are correlated with presence of mid-dorsal stripe (4 specimens) or band (1 specimen). Shanks typically lack any trace of dark banding, but irregular bands are present on the shanks of three, two of which also have tan heels. Clear lumbar ocelli are present in 22 of 31 specimens; of those without, six (of nine) have the dark central blotch of the expected ocellus but lack its light anterior and lateral margins. Venters have a straw ground color heavily flecked with dark gray in all specimens, imparting a dark gray appearance to the venter overall. In a few specimens the gray flecking is somewhat less dense, imparting a slightly lighter color to the abdomen and proximal undersides of the thighs. In those specimens, overall ventral coloration appears two-toned to the naked eye, with a dark chin and throat followed by a lighter chest and abdomen. One to four (usually one) distinct, cream spots are present on each side of the pectoral regions in all except one specimen.

Color in life.—In life, BPBM 18092 was noted to have "Dorsum brown with yellow lumbar ocelli and a few yellow flecks on snout. Legs somewhat lighter; heels tan, margined in black. Occasional black flecks on sides and limbs. Tops of thighs and forearms burnt orange. Venter light yellow heavily dusted with gray; under legs same. Three cream spots on chest. Posterior belly and groin lemon yellow dusted with gray. Iris bronze with black horizontal streaks." BPBM 18095–96 had similarly dark brown dorsa but BPBM 18097 had an ochre dorsum and yellow on the backs of the thighs as well as the groin. BPBM 18110 was noted to have the dorsum dark brown

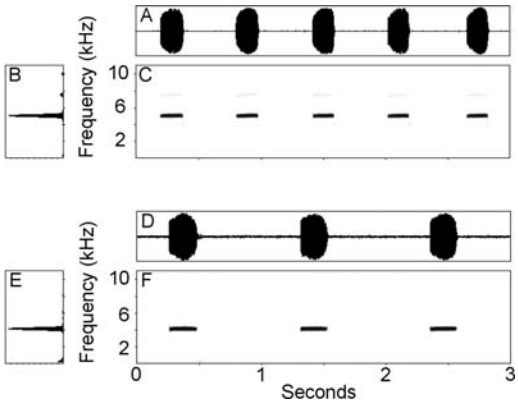


FIG. 5.—(A) Waveform, (B) spectrogram, and (C) power spectrum of a call sequence of *Cophixalus timidus*, BPBM 18098, holotype, from Mt Simpson; recorded 1100 h, air temperature 22.3 C. (D)–(F) same parameters for call sequence of *Cophixalus sisyphus*, BPBM 19300, holotype, from Mt Obree; recorded 1920 h, air temperature 20.2 C.

mottled with tan, tan heels, and tan mid-dorsal stripe and tan stripes on the backs of the thighs. Its venter was dark gray with minute light gray flecks, its iris was tan, and in contrast to most other specimens it lacked the yellow patches in the groin. The dorsum of PNGNM 24005 was dark burnt orange.

Call.—We recorded 14 complete calls from four individuals (Table 4; Fig. 5A–C). The average call consists of 12 peeping notes (range 9–14) with a mean repetition rate of 0.94 notes/s (range 0.71–0.99 notes/s). The notes averaged 223 ms in duration (range in call means 185–265 ms) and the intervals between notes averaged 937 ms (range in call means 823–1147 ms). The mean dominant frequency was 4402 Hz (range 3940–4880 Hz). In all calls the first note was longer than the succeeding notes, averaging 325 ms (range 235–367 ms) compared to 215 ms (range 142–291 ms) for subsequent notes.

As for *Cophixalus variabilis*, animals were heard to call both day and night but the large majority called during the first several hours of darkness. Daytime calling was only observed when animals were safely sequestered in difficult-to-reach refugia. Males called from 0–2 m above the ground on available vegetation. Unlike *C. variabilis* and the species to follow, males of *C. timidus* could be very wary and difficult to capture, especially at upper elevation sites.

Ecological notes.—This species was found to occur in closed-canopy mid-elevation rainforest, montane cloud forest, and open montane mixed shrub-grassland (with *Styphelia* and *Deschampsia* as common elements). Streams were virtually absent from these areas, so any tendency to cluster near streams could not be assessed.

Specimens collected in mid-elevation (~1500 m) rainforest behaved similarly to *Cophixalus variabilis* in calling behavior, calling while perched on stems or leaves of shrubs or from within *Pandanus* leaf axils, and not being unduly difficult to obtain. Individuals observed in the upper-elevation (~2500 m) open grassland/shrubland called most frequently from low grass tussocks and were virtually impossible to collect while calling. Most specimens obtained from this general area were obtained in daytime by removing standing cover of a *Dicranopteris linearis* thicket and raking through the wet leaf litter underneath. This site was a forest-fernland ecotone on a former landslip at 2170 m elevation.

Syntopic congeners include *Cophixalus verrucosus* and two undescribed *Cophixalus* of unclear relationships. *Cophixalus verrucosus* is a larger species also scandent on low vegetation but which shows some tendency to cluster around stream courses; one of the undescribed forms is a dwarf species also found in the *Dicranopteris* leaf litter from which several *C. timidus* were obtained; the second undescribed species was only found on the ground near a mid-elevation (1500 m) stream.

Etymology.—The masculine Latin adjective "timidus" means "fearful" and refers to the wary calling behavior of this species, which contrasts with that of its close relatives described herein.

Distribution.—We have collected or observed *C. timidus* at several localities on the northern slope of Mt Simpson, ranging in elevation from 1400–2500 m. It is currently known only from this area.

Cophixalus **sisyphus** sp. nov.

Holotype.—BPBM 19300 (field no. FK 8910), adult male (Figs. 1, 2), collected by F. Kraus on W slope Mt Obree, 9.4456° S,

148.0064° E, 1580–1640 m, Central Province, Papua New Guinea, 30 January 2004.

Paratypes.—Papua New Guinea: Central Province: 1.5–2 km E Dorobisoro, 9.4592° S, 147.9372° E, 600 m, 7 October 2003 (BPBM 18316); same data as holotype (BPBM 19299, 19301–05); same data as holotype but 31 January 2004 (BPBM 19306); W slope Mt Obree, 9.4447° S, 148.0092° E, 1640–1680 m, 31 January 2004 (BPBM 19307); same data as holotype but 2 February 2004 (BPBM 19308–11); W slope Mt Obree, 9.4583° S, 148.0272° E, 1870 m, 4 February 2004 (BPBM 19312–14); W slope Mt Obree, 9.4574° S, 148.0277° E, 1760–1870 m, 5 February 2004 (BPBM 19315–19, PNGNM 24007–11).

Diagnosis.—A small (adult males 12.0–14.1 mm, adult females 12.7–13.6 mm) species of *Cophixalus* having a tuberculate dorsum; poorly developed first finger (1st F/HandL = 0.09–0.14); discs with well-defined terminal grooves on all fingers and toes except the first finger, which has a poorly developed, unflattened disc usually lacking a terminal groove (but is weakly developed in one large female); toes free of webbing; vocal slits in males; sexual dimorphism in tympanum size (TY/SVL = 0.039–0.068 in males, 0.071–0.081 in females); relatively short legs (TL_{knee}/SVL = 0.43–0.52, TL_{fold}/SVL = 0.37–0.46); a relatively short, broad snout (EN/IN = 0.73–0.87); vertical lores; 1–4 (usually 1) small yellow spots on each side of the pectoral region; and a call consisting of a series of 5–10 peeps.

Cophixalus sisyphus differs from all previously described Papuan *Cophixalus* except *C. ateles*, *C. bewaniensis*, *C. pipilans*, *C. pulchellus*, *C. shellyi*, and *C. sphagnicola* in the same suite of characters as exhibited by *C. variabilis* and *C. timidus*, except that it shares with *C. ateles*, *C. bewaniensis*, *C. pipilans*, *C. pulchellus*, *C. shellyi*, and *C. sphagnicola* a shortened first finger lacking a well-developed disc. It differs from all six of these in its tuberculate dorsum and variegated or striped color pattern.

Cophixalus sisyphus differs from *C. variabilis* in having (1) smaller body size (SVL = 12.0–14.1 mm vs. 13.6–19.7 in *C. variabilis*); (2) sexual dimorphism in tympanum size; (3) a shorter first finger (1st F/HandL = 0.09–0.14 vs. 0.15–0.28 in *C. variabilis*) with a poorly developed, unflattened disc almost always lacking a terminal groove (vs. a wide, flattened disc with a well-developed terminal groove in *C. variabilis*); (4) somewhat shorter legs (TL_{knee}/SVL = 0.43–0.52 vs. 0.46–0.58 in *C. variabilis*); (5) usually two (sometimes more) small yellow pectoral spots surrounded by black, which are more obvious than in *C. variabilis*; and (6) longer call notes (0.158–0.223 ms vs. 0.107–0.159 ms in *C. variabilis*).

Cophixalus sisyphus differs from *C. timidus* in having (1) smaller body size (SVL = 12.0–14.1 mm vs. 13.6–19.7 in *C. timidus*); (2) broader snout (IN/SVL = 0.102–0.117, EN/IN = 0.73–0.87 vs. IN/SVL = 0.085–0.110, EN/IN = 0.75–1.00 in C. *timidus*); (3) a shorter first finger (1st F/HandL = 0.09–0.14 vs. 0.12–0.26 in *C. timidus*); (4) absence of a light yellow blotch in groin; and (5) faster call rate (1.353–2.196 notes/s vs. 0.713–0.989 notes/s in C. *timidus*).

Description of holotype.—An adult male. Head moderately wide (HW/SVL = 0.39), with slightly oblique loreal region; canthus rostralis rounded, straight when viewed from above; nostrils directed laterally, much closer to tip of snout than to eyes; internarial distance considerably larger than distance from external naris to eye (EN/IN = 0.80, IN/SVL = 0.109, EN/SVL = 0.088); snout slightly projecting when viewed from the side, shallowly angulate when viewed from above; eyes moderately large (EY/SVL = 0.13); eyelid approximately 2/3 the width of the interorbital distance; tympanum indistinct and small (TY/SVL = 0.058). Dorsal and lateral surfaces rugosely tuberculate. Supratympanic fold weakly developed. Ventral surfaces granular. Fingers unwebbed, bearing discs with terminal grooves except on first finger; relative lengths $3 > 4 > 2 > 1$; first finger very short (1st F/HandL = 0.10), poorly developed, disc absent. Finger discs approximately 1.5 times widths of penultimate phalanges (Fig. 2C). Articular tubercles low and indistinct; metacarpal tubercles absent. Toes unwebbed, bearing discs with terminal grooves; relative lengths $4 > 3 > 5 > 2 > 1$. Toe discs approximately same size as those of fingers, that of fourth toe approximately 1.5 times width of penultimate phalanx, that of first little wider than penultimate phalanx. Subarticular tubercles lacking; inner metatarsal tubercle narrow, elongate, and poorly developed; outer

TABLE 6.—Sexual variation in mensural characters for the type series of *Cophixalus sisyphus* from Mt Obree. Numbers in parentheses indicate sample sizes; asterisk indicates character pair having significantly different covariant relationship between the sexes using Tukey's test (see text).

	Males (24)		Females (3)	
Character	Mean	Range	Mean	Range
SVL (mm)	13.3	12.0–14.1	13.3	12.7–13.6
TLfold/SVL	0.43	0.39–0.46	0.44	0.43–0.44
TLknee/SVL	0.48	0.43–0.52	0.49	0.49–0.50
EN/SVL	0.087	0.079–0.096	0.091	0.088–0.094
IN/SVL	0.110	0.100–0.117	0.108	0.104–0.110
SN/SVL	0.14	0.12–0.15	0.15	0.15–0.16
TY/SVL*	0.052	0.039–0.063	0.078	0.071–0.081
EY/SVL	0.13	0.12–0.15	0.14	0.13–0.14
HW/SVL	0.39	0.36–0.43	0.37	0.36–0.40
HL/SVL	0.33	0.30–0.35	0.34	0.33–0.35
HandL/SVL	0.25	0.23–0.27	0.26	0.24–0.27
FootL/SVL	0.41	0.38–0.44	0.41	0.40–0.43
3^{rd} F/SVL	0.054	0.045–0.063	0.053	0.050–0.057
4^{th} T/SVL	0.055	0.049–0.060	0.052	0.047–0.056
EN/IN	0.79	0.73–0.87	0.84	0.80–0.86
EN/SN	0.62	0.58–0.72	0.60	0.57–0.63
EY/SN	0.93	0.81–1.11	0.90	0.86–0.95
3^{rd} F/4^{th} T	1.0	0.9–1.1	1.0	0.9–1.1
HL/HW	0.84	0.77–0.90	0.90	0.85–0.96
1^{st} F/HandL	0.10	0.09–0.14	0.11	0.09–0.14

lacking. Hind legs relatively short (TL_{knee}/SVL = 0.45, TL_{fold}/SVL = 0.41).

Dorsum with dark gray central hourglass pattern extending from between eyes to above vent, border slightly darker than center, anterior end brown, with narrow light gray vertebral stripe on posterior half; vestige of light gray crescent on each side of lumbar region of hourglass. Sides lateral to hourglass uniform light gray. Light gray patch on top of snout anterior to eyes, this mottled with dark gray blotches. Black bar extends from behind eye to corner of jaw. Dark band on center of each shank; dark patch on each knee; posterior of tarsus black. Iris dark brown heavily stippled with silver. Venter gray densely stippled with minute black and silver punctations and with an irregular patchwork of small brown spots, best developed under thighs and on margin of chin.

Measurements (in mm).—SVL = 13.7, TL_{fold} = 5.6, TL_{knee} = 6.2, HW = 6.5, HL = 5.2, IN = 1.6, EN = 1.4, SN = 2.0, EY = 1.9, TY = 0.6, HandL = 4.2, FootL = 6.8, 3^{rd} F = 0.94, 4^{th} T = 0.83.

Variation.—Mensural variation in the samples is slight (Table 6). Few females were collected, making comparison of the sexes difficult, but in contrast with *Cophixalus variabilis* and *C. timidus*, there is no observed sexual size dimorphism in our sample of *C. sisyphus* (Table 6). However, as for *C. timidus*, sexual dimorphism in tympanum size is obvious, with the tympana of females noticeably larger than those of males. Female tympana increase in relative size with increasing SVL, whereas those of males decrease slightly ($F = 2.22$, $P < 0.036$). Juveniles are also not available in our sample, making ontogenetic comparisons impossible.

Color pattern variation in *Cophixalus sisyphus* is considerable, resembling *C. variabilis* in this respect and differing from *C. timidus*. In preservative, the dorsa may be more or less uniformly gray or with a broad, mid-dorsal hourglass band. Of the (largely) uniformly colored specimens, six are uniform light gray, six are light gray with small black flecks or blotches, four are uniform dark gray with a light gray triangular patch on the top of the snout, and two are dark gray with scattered small black flecks. Of the specimens with the hourglass pattern, three have a dark gray hourglass with light gray sides, three have the hourglass light gray with dark gray sides, and three have the hourglass light gray with light gray sides. In all cases, the lateral margins of the hourglass are rimmed with black. Five specimens have a narrow light gray mid-dorsal stripe, which may occur in combination with either the uniform or hourglass-patterned dorsa, and one of these has similar narrow stripes on the backs of each thigh and shank. Half of the specimens have a single, central dark band on each shank and half have no banding. Seven specimens have tan heels. Fifteen specimens have lumbar ocelli, but in all but two or three of these the ocelli are obscure; eleven specimens lack lumbar ocelli entirely. Venters have a light gray ground color heavily and uniformly stippled/suffused with dark gray, giving a uniformly dark gray appearance to the entire venter, with no contrast apparent to the naked eye between the intensity of coloration on the chin/throat vs. chest/abdomen. One to four (usually one) distinct, cream pectoral spots are present on each side of the pectoral regions in all except one specimen.

Color in life.—In life, BPBM 18316 was noted to have "Dorsum variegated dark and

light mud brown, with two brown-yellow lumbar hemi-ocelli. Venter dark gray, flecked with light gray, being more heavily flecked posteriorly. Rear of thighs gray-brown with pale brown flecks. Iris light mud brown." BPBM 19299, from 1000 m higher elevation, had "Dorsum reddish brown with scattered small black blotches (mostly laterally), an ochre vertebral stripe, and a ridge running behind eye to suprascapular region. Iris reddish brown. Black chevron above anus. Face gray to black. Hidden surfaces of thighs brown stippled with gray. Chin black, remainder of venter light gray heavily stippled with dark gray, so overall appearance is almost black." In contrast, BPBM 19300 (the holotype) was noted to have a tan ground color with a dorsal brown hourglass blotch and a tan iris; BPBM 19301 to have a tan mid-dorsum, brown sides, and a narrow black stripe intervening between the two; BPBM 19304 to have a uniformly russet-brown dorsum; PNGNM 24008 a brown dorsum with a tan vertebral stripe and dark brown dorsolateral stripes bordered below by tan and then yellow brown; and PNGNM 24009 to be uniformly russet.

Call.—We recorded 18 complete calls from seven individuals (Table 4; Fig. 5D–F). The average call consists of 8 peeping notes (range 5–10) with a mean repetition rate of 1.60 notes/s (range 1.35–2.26 notes/s). The notes averaged 187 ms in duration (range in call means 158–223 ms) and the intervals between notes averaged 454 ms (range in call means 304–534 ms). The mean dominant frequency was 4975 Hz (range 4460–5630 Hz). In all the calls the first note was longer than the succeeding notes, averaging 265 ms (range 213–318 ms; $n = 18$) compared to 172 ms (range 131–221; $n = 117$) for subsequent notes.

Animals called perched on leaves 0.15–1.5 m above ground and calling began after dark in all instances observed by us. A train of calls would be delivered every few minutes. Calling animals were not energetic but were not especially shy either.

Ecological notes.—This species was found to occur in somewhat disturbed, closed-canopy, low-elevation rainforest and in primary, closed-canopy, mid-elevation rainforest. Animals largely occupied rather steep slopes but a few were obtained on an adjacent ridgetop as well; none was obtained in the immediate vicinity of streams.

The only syntopic congener found with *Cophixalus sisyphus* was a small terrestrial species that is either referable to *C. ateles* or is a new close relative of that species. An undescribed species of *Cophixalus* also inhabited small stream margins in the nearby vicinity but appeared not to occur syntopically with *C. sisyphus*.

Etymology.—The name is a proper noun in apposition and refers to the founder of Corinth, who was condemned by the gods to rolling a boulder to the top of a mountain only to have it immediately roll down upon attaining the summit, providing him an eternity of futile labor. The name alludes to the seeming task involved in sorting out the taxonomy of the species described herein.

Distribution.—We have collected *C. sisyphus* only on the western slope of Mt Obree, Central Province, at elevations ranging from 600–1800 m.

Discussion

The three members of this species complex are superficially very similar and difficult to distinguish without detailed morphological examination. Nonetheless, each can be differentiated from the others by a combination of subtle differences. Canonical variates analysis separates all three species into cohesive groups and confirms our placement of the specimens from the D'Entrecasteaux Islands within *Cophixalus variabilis* (Fig. 6). If pairwise discriminant functions are run there is clear separation of taxa in all cases, with no misassigned cases for any comparison, and with Hotelling's T^2 values ranging from 1.26×10^{-14} to 2.23×10^{-35}. These results hold true whether the *C. variabilis* sample is restricted to only mainland specimens or includes the material from the D'Entrecasteaux as well. These results are confirmed by general linear model ANOVA analyses of paired variables using Tukey's tests. Although morphological differences in simple summary ratios can be subtle (Table 7), covariate differences are frequently taxonomically discriminating (Table 8).

The most striking feature of the members of this species complex is the great variation in color pattern features, which includes mottling

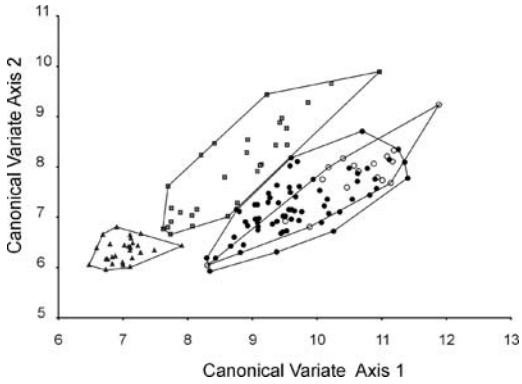


FIG. 6.—Scatter plot of canonical variate axes 1 and 2 with convex hulls delimiting the multivariate ranges for mainland *Cophixalus variabilis* (filled circles), Fergusson Island *C. variabilis* (open circles), *C. timidus* (squares), and *C. sisyphus* (triangles).

and both narrow and broad dorsal striping, tan anal and heel patches, and leg striping, in addition to simply unicolored dorsa. The genetic basis for this variation remains unknown but the phenomenon is not unprecedented. The inclusion of both unicolored/mottled and striped/banded phenotypes within single populations is similar to that seen in *Cophixalus ornatus* from Australia (Zweifel, 1985) and in some Caribbean species of the unrelated *Eleutherodactylus* (Schwartz and Henderson, 1991). Within our complex, *Cophixalus timidus* is slightly anomalous in showing a more limited range of color pattern features and a lower frequency of the more striking features such as dorsal striping, banding, and tan heels.

The call rate variation in *Cophixalus variabilis* is another unusual feature requiring comment inasmuch as that parameter is often useful in distinguishing closely related species of Papuan microhylids (e.g., Kraus and Allison, 2002; Zweifel, 2000). Indeed, we use that character to distinguish *C. timidus* from the other two members of the complex. Specimens of *C. variabilis* typically call at two different rates within any given chorus, the rates differing by a factor of approximately two. Given this variation, it might be wondered if we have inadvertently confounded two syntopic species in our description of *C. variabilis*. But this interpretation is obviated by our directly observing the holotype to alternate between the slow and fast call rates within the course of a few minutes. No other calling specimens were in the area at this time. Furthermore: (1) *C. variabilis* is morphologically cohesive (Fig. 6) and we could discern no distinguishing morphological features in either univariate or multivariate space either within or among geographic samples; (2) other relevant call

TABLE 7.—Variation in mensural characters among the three species of *Cophixalus* comparing only adult males. Numbers in parentheses indicate sample sizes.

	Cophixalus variabilis (49)		*Cophixalus timidus* (14)		*Cophixalus sisyphus* (24)	
Character	Mean	Range	Mean	Range	Mean	Range
SVL (mm)	15.9	13.6–18.6	14.7	13.5–17.5	13.3	12.0–14.1
TLfold/SVL	0.48	0.42–0.53	0.43	0.37–0.46	0.43	0.39–0.47
TLknee/SVL	0.53	0.46–0.58	0.48	0.42–0.52	0.48	0.43–0.52
EN/SVL	0.084	0.073–0.094	0.088	0.080–0.096	0.087	0.079–0.096
IN/SVL	0.096	0.078–0.110	0.097	0.087–0.103	0.110	0.100–0.117
SN/SVL	0.13	0.12–0.15	0.14	0.12–0.14	0.14	0.12–0.15
TY/SVL	0.050	0.035–0.075	0.043	0.031–0.052	0.052	0.039–0.068
EY/SVL	0.13	0.12–0.14	0.13	0.12–0.14	0.13	0.12–0.15
HW/SVL	0.37	0.35–0.43	0.39	0.35–0.42	0.39	0.36–0.43
HL/SVL	0.32	0.28–0.35	0.33	0.30–0.36	0.33	0.30–0.35
HandL/SVL	0.27	0.19–0.32	0.26	0.22–0.28	0.25	0.23–0.27
FootL/SVL	0.48	0.42–0.53	0.44	0.37–0.49	0.41	0.38–0.44
3^{rd} F/SVL	0.060	0.049–0.073	0.059	0.045–0.075	0.054	0.039–0.063
4^{th} T/SVL	0.050	0.040–0.062	0.050	0.043–0.055	0.055	0.044–0.060
EN/IN	0.87	0.79–1.00	0.91	0.86–1.00	0.79	0.73–0.87
EN/SN	0.64	0.55–0.74	0.64	0.56–0.70	0.62	0.58–0.72
EY/SN	0.97	0.86–1.11	0.96	0.84–1.05	0.93	0.81–1.11
3^{rd} F/4^{th} T	1.2	1.0–1.5	1.2	1.0–1.6	1.0	0.9–1.2
HL/HW	0.84	0.76–0.93	0.86	0.80–0.92	0.84	0.77–0.90
1^{st} F/HandL	0.21	0.15–0.26	0.16	0.13–0.26	0.10	0.09–0.14

TABLE 8.—Pairwise covariate differences among the three species of *Cophixalus* for the character pairs in the left-hand column, comparing only adult males. Sample sizes as for Table 7. *C. variabilis* = var, *C. timidus* = tim, *C. sisyphus* = sis.

	Different in slope			Different in Y intercept		
Characters	var vs. tim	var vs. sis	tim vs. sis	var vs. tim	var vs. sis	tim vs. sis
TLfold vs. SVL	$T = 7.987$ $P < 0.0001$	$T = 5.151$ $P < 0.0001$				
TLknee vs. SVL	$T = 7.005$ $P < 0.0001$	$T = 5.110$ $P < 0.0001$				
EN vs. SVL						
IN vs. SVL						
SN vs. SVL					$T = 2.867$ $P = 0.0182$	
TY vs. SVL	$T = 4.506$ $P = 0.0001$					
EY vs. SVL						
HW vs. SVL						
HL vs. SVL		$T = 2.774$ $P = 0.0187$	$T = 2.656$ $P = 0.0255$			
HandL vs. SVL	$T = 2.738$ $P = 0.0205$	$T = 3.663$ $P = 0.0013$				
FootL vs. SVL	$T = 7.117$ $P < 0.0001$	$T = 5.639$ $P < 0.0001$				
3rd F vs. SVL		$T = 3.920$ $P = 0.0005$	$T = 3.041$ $P = 0.0088$			
4th T vs. SVL						
EN vs. IN		$T = 6.763$ $P < 0.0001$	$T = 4.803$ $P < 0.0001$			
EN vs. SN		$T = 3.711$ $P = 0.0011$	$T = 3.086$ $P = 0.0078$			
EY vs. SN		$T = 5.938$ $P < 0.0001$	$T = 3.871$ $P = 0.0006$			
3rd F vs. 4th T		$T = 8.590$ $P < 0.0001$	$T = 4.869$ $P < 0.0001$			
HL vs. HW		$T = 2.569$ $P = 0.0320$	$T = 2.373$ $P = 0.0520$			
1st F vs. HandL	$T = 5.406$ $P < 0.0001$	$T = 4.434$ $P = 0.0001$	$T = 2.488$ $P = 0.0400$			

parameters, such as dominant frequency, and note length are the same within populations for specimens exhibiting the two call rates; (3) though not frequently investigated, variation in notes/s for other Papuan microhylids can be of a similar magnitude as seen in our samples (e.g., Günther, 2000). Given these considerations, we are confident that our mainland samples of syntopic frogs with the fast and slow call rates represent the same species.

The taxonomic status of the frogs from the D'Entrecasteaux Islands is not certain. Morphologically they are indistinguishable from mainland samples of *C. variabilis* (Fig. 6), but our recorded individuals were calling at a rate slower than seen in mainland *C. variabilis*. We suspect the calls of the frogs from Fergusson Island to be atypical and think it inadvisable to draw taxonomic conclusions without having this issue clarified by further recordings. If future research shows the slow calling rate observed in our limited sample is consistent among frogs of this complex from the D'Entrecasteaux Islands, recognition of an additional species may be warranted.

The nearest relatives of the *Cophixalus variabilis* complex are difficult to discern. In quantitative morphometrics, the new species seem to differ least from the considerably larger *C. biroi*, although the species could not easily be confused with each other for size and color-pattern differences alone. The new species are also similar to *C. daymani* in having a short snout and to *C. cryptotympanum* in having vertical lores—both characters of limited occurrence in *Cophixalus*—but both of these species lack vocal slits in males (Zweifel, 1956) and differ in other morphological and color-pattern features. The remaining Papuan *Cophixalus* species appear more

divergent and seem even less likely candidates for any near relationship to the new form. It is conceivable that the nearest relatives of the *C. variabilis* complex may be found in Queensland. In superficial appearance, size, color-pattern variation, and some morphological details, the new species resemble *C. ornatus*; nonetheless, various combinations of snout shape, tibia length, and call differences clearly distinguish the Papuan species from all Australian forms (cf. Zweifel, 1985). Should the Australian species prove to be closer relatives of the *C. variabilis* complex than the currently known Papuan species, it remains uncertain what process would allow sister lineages to occupy the Southeast Peninsula of New Guinea and the Queensland mountains 600–800 km distant, apparently without occupying intervening areas.

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