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A Review of the Frog Genus *Lechriodus* (Leptodactylidae) of New Guinea and Australia

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ABSTRACT

Lechriodus is one of three genera of the Leptodactylidae present in New Guinea. With three species endemic in New Guinea and one in Australia, *Lechriodus* is the only leptodactylid genus predominately Papuan in distribution and diversity. The present revision recognizes four species: *Lechriodus aganoposis*, new species; *L. fletcheri* (Boulenger); *L. melanopyga* (Doria); and *L. platyceps* Parker. The new species has not been mentioned in the literature. The name *L. melanopyga* is applied to the lowland species of the Aru Islands and New Guinea, previously known by this name as well as *L. papuana* and *L. fletcheri* (or combinations thereof). *Phanerotis fletcheri papuana* Roux is a junior synonym of *L. melanopyga*. *Lechriodus fletcheri* is limited in distribution to Australia. *Lechriodus platyceps* and *L. aganoposis* allopatrically share montane habitats in, respectively, the western and eastern parts of New Guinea. The species are distinguished primarily by differences in body size, presence or absence of certain digital tubercles, structure of male nuptial pads, number of skin folds on the dorsum, and pigmentation of the testes. Limited information suggests that mating calls also differ.

INTRODUCTION

The genus *Lechriodus* has been revised only once: by Parker in his 1940 monograph. Parker recognized four species: three on mainland New Guinea, one of which lived also in Australia, and the one on the Aru Islands in the Arafura Sea west of New Guinea. He worked with an

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extreme dearth of material, for he examined only eight specimens (none at all of one nominal species), including the holotypes of only two of the four species. Hence, it is not astonishing that some of his conclusions as to distribution and relationships now require modification.

My interest in *Lechriodus* was stimulated while I was participating in the Seventh Archbold Expedition to New Guinea in 1964 when native collectors brought in specimens of what proved to be an undescribed species of the genus. It proved impractical to describe this new form without reviewing the numerous specimens that have accumulated in collections since Parker's research. Accordingly, I present here the results of this survey of systematics and distribution. I regard the nomenclature now to be on fairly stable ground, although acquisition of additional information, especially that pertaining to mating calls, may show that more species should be recognized. Knowledge of ecology of the four species I recognize ranges from scanty to virtually nonexistent, and information on distribution is spotty. Contributions in either of these areas could bear importantly on my systematic conclusions.

I have directed my attention primarily to the species in New Guinea. I found it necessary to study Australian material in order to place all species in the proper perspective, but I have not sought out recently collected specimens that might add to the distributional information given by Moore (1961).

ACKNOWLEDGMENTS

In gathering material for this study, I not only had to appeal to colleagues in many countries for specimens and other assistance, but also had to retain for unusually long periods specimens sent on loan. I thank these persons for their generosity and patience: Lilia Capocaccia, Museo Civico di Storia Naturale di Genova; Harold Cogger, the Australian Museum, Sydney; Alice G. C. Grandison, British Museum (Natural History), London; D. Hillenius, Zoologisch Museum, Amsterdam; Marinus Hoogmoed, Rijksmuseum van Natuurlijke Historie, Leiden; E. Kramer, Naturhistorisches Museum, Basel; Alan E. Leviton, California Academy of Sciences, San Francisco; James Menzies, University of Papua and New Guinea, Port Moresby; Fred Parker, Daru, Territory of Papua; T. G. Schultz-Westrum, Assenhausen, Germany; K. Somadikarta, Museum Zoologicum Bogoriense, Bogor, Indonesia; O. Stemmler, Naturhistorisches Museum, Basel; Ian Straughan, University of Southern California, Los Angeles; Enrique Tortonese, Museo Civico di Storia Naturale di Genova; Ernest E. Williams, Museum of Comparative Zoology, Harvard University, Cambridge; Alan C. Ziegler, Bernice P. Bishop Museum, Honolulu.

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Abbreviations

AM, the Australian Museum, Sydney
AMNH, the American Museum of Natural History, New York
BBM, Bernice P. Bishop Museum, Honolulu
BMNH, British Museum (Natural History), London
CAS, California Academy of Sciences, San Francisco
MCZ, Museum of Comparative Zoology, Harvard University
MSNG, Museo Civico di Storia Naturale di Genova
MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia
NMB, Naturhistorisches Museum, Basel
RMNH, Rijksmuseum van Natuurlijke Historie, Leiden
SW, Field numbers of T. Schultz-Westrum, specimens in Zoologische Staatssammlung, Munich
ZMA, Zoologisch Museum, Amsterdam

MATERIALS AND METHODS

I have examined 274 specimens of *Lechriodus* in addition to one series of embryos and larvae. Among these are the holotypes of all taxa assigned to the genus.

Measurements

SV, length from snout to vent
HW, head width, taken at the angles of the jaws
IN, internarial distance, taken from center to center of nares
E-N, distance from eye to naris from anterior edge of eye opening to center of naris
TL, tibia length from heel to fold of skin on knee
Eye, length of orbit from anterior to posterior edge of eye opening

The relative sizes of spines comprising male nuptial pads were determined by counting the number in an area of one-quarter or one square mm., as seen through an ocular grid. Other measurements were made with an ocular micrometer or with vernier calipers, as was appropriate.

I have followed conventional procedures in describing bodily proportions as ratios. Unless specified otherwise, these ratios refer to adult individuals and presumably are not greatly influenced by ontogenetic variation.

Where elevation of a collecting site is given, it is noted first in feet or meters as it appeared in the original field data or publication, then in parentheses converted and rounded to the nearest 10 feet or 10 meters. This presentation preserves the degree of precision given in the original data and does not impose spurious precision in converting from feet to meters or vice versa.

The synonymies include all new names, new combinations of names, and misapplied names that have come to my attention. I have not cited in the synonymies (but have attempted to include elsewhere) references of no taxonomic consequence but of other scientific pertinence.

LECHRIODUS BOULENGER

Asterophrys (*non* Tschudi, 1838): DORIA, 1874, p. 355.

Batrachopsis (*non* Fitzinger, 1843) BOULENGER, 1882a, p. 439 (type-species apparently by monotypy, *Asterophrys melanopyga* Doria; see discussion that follows).

Lechriodus BOULENGER, 1882b, p. 116 (substitute name for *Batrachopsis* Boulenger 1882a, a junior homonym of *Batrachopsis* Fitzinger, 1843; type-species as in *Batrachopsis* Boulenger).

Phanerotis BOULENGER, 1890, p. 594 (type-species by monotypy *Phanerotis fletcheri* Boulenger 1890).

Ranaster: NIEDEN, 1923, p. 536 (in part).

DIAGNOSIS: A genus of the leptodactylid subfamily Cycloraninae (as defined by Parker, 1940, and Lynch, 1971), with the following diagnostic combination of characters: maxillary teeth present; vomerine teeth behind level of choanae; no dentary pseudo-teeth; pupil horizontal; fronto-parietal foramen absent or bones narrowly separated; digital webbing sparse, not penetrating between outer metatarsals; first finger not opposable to remainder; toes with small terminal discs.

Among the frogs of New Guinea, *Lechriodus* is likely to be confused only with species of the ranid genus *Platymantis* Günther. Despite superficial similarity, they are readily distinguished in that the vomerine teeth of *Lechriodus* are in two nearly contiguous transverse rows behind the internal nares, whereas in *Platymantis* these teeth are in small, widely separated groups between and behind the nares. If any doubt remains following examination of the teeth, dissection of the pectoral girdle will show the arciferal condition in *Lechriodus* and the firmisternal condition in *Platymantis*.

For keys distinguishing *Lechriodus* from other Australian leptodactylids, see Parker (1940), Moore (1961), and Lynch (1971). However, some characters thought by Parker (1940) and Lynch (1971) to be diagnostic of *Lechriodus* evidently are not. These are taken up in the descriptive material that follows.

CONTENT: I recognize four species: *Lechriodus melanopyga* (Doria), *L.*

fletcheri (Boulenger), *L. platyceps* Parker, and *L. aganoposis*, new species.

DESCRIPTION: Members of the genus *Lechriodus* are moderately broad-headed frogs (head width about 40% of snout-vent length), with prominent eyes (orbit length about 12% of snout-vent length) and long legs (tibia length averages about 52% of snout-vent length). The toes (but not the fingers) bear small terminal discs, and have only slight basal webbing. Generally there is a prominent supratympanic skin fold, and often one or more pairs of folds are present on the dorsum. The maximum size (snout-vent length) varies interspecifically from 52 mm. to 95 mm. More detailed descriptions of external morphology are given in the species accounts.

Noble (1924, p. 11, figs. 5, 7) described and figured the thigh and ventral body musculature of *Lechriodus platyceps* (as *L. melanopyga*).

Both Parker (1940) and Lynch (1971) described the skeleton. My remarks here are confined largely to exceptions to statements by these authors. Parker did not indicate what skeletal material he examined. However, Dr. Grandison at my request kindly examined the specimens in the British Museum used by Parker in the preparation of his monograph, and she has no doubt (*in litt.*) that his account of the osteology was based on one of the paratypes of *Lechriodus platyceps* Parker, BMNH 78.2.11.5 (now registered as BMNH 1947.2.18.64). Lynch (1971, p. 227) examined one dry skeleton (AMNH 59488) and one cleared and stained specimen of *L. fletcheri* (CAS 82221). I have examined the following specimens: *L. fletcheri* (AMNH 59488, complete dry skeleton); *L. melanopyga* (AMNH 86680, skull and anterior vertebrae); *L. platyceps* (AMNH 74180, skull and anterior vertebrae); and *L. aganoposis* (AMNH 74646, complete dry skeleton).

Parker and Lynch considered *Lechriodus* lacking a frontoparietal fontanelle. The specimen of *L. aganoposis* has distinct gaps between the frontoparietal bones at their anterior and posterior ends, although the bones are virtually in contact in the middle. The total exposed area is less than is illustrated for *Limnodynastes* by Lynch (1971, fig. 61, p. 87).

Lechriodus was said by Parker and Lynch to have the cervical and second vertebrae free in contrast to their fusion in some other cycloranine genera. In the four specimens that I examined these vertebrae are fused (fig. 1). The specimen of *L. platyceps* that I examined has also the third and fourth vertebrae fused into the same mass in an apparently abnormal condition. Indications from my specimens are that fusion is the more usual condition, although additional data are needed to substantiate this supposition. In any event, it is clear that the free condition of these vertebrae is not diagnostic of the genus. Dasgupta and Grewal (1970) found as high as 12 percent fusion of vertebrae in natural populations of frogs, with the

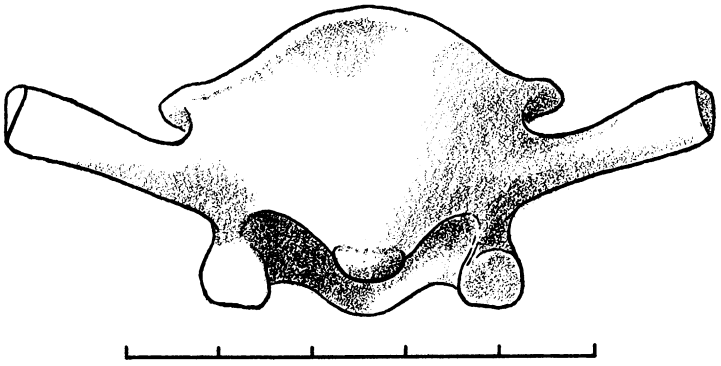

FIG. 1. *Lechriodus melanopyga*, AMNH 86680, first vertebra (fused first and second) in ventral view; scale in mm.

commonest fusion being between the first and second vertebrae. They attribute the condition in *Rana cyanophlyctis* to a simple dominant gene. Thus, it may be that in *Lechriodus* the fusion of vertebrae or its absence are genetically controlled polymorphic states.

Two other minor departures from the skeletal conditions listed in Lynch's "Diagnostic definition" (1971, p. 85) may be noted: the nasal bones are separate, not "apparently in median contact"; the dentigerous rami of the vomers are narrowly separated, not "in tenuous median contact."

Using Parker's (1940, pp. 12–13) key to the genera of the Cycloraninae, confusion could occur at couplet B (1–2), which presents the alternatives of no frontoparietal foramen or a large frontoparietal foramen. If the foramen seen in my specimen of *Lechriodus aganoposis* were considered large, the specimen would key to *Limnodynastes*. If the foramen were ignored, the specimen (and others with no foramen) would key best to *Lechriodus* (the alternative being *Adelotus*), although the fusion of the first two vertebrae would still render the keying less than certain.

A point of possible confusion in Lynch's generic key (1971, pp. 71–72) is in couplet 15, "Tympanum clearly visible externally" (*Lechriodus*) contrasted to "Tympanum partially or completely concealed." I find the tympanum in many specimens of *Lechriodus* to be indistinct, often partly covered with minute warts like those on adjacent areas. Such specimens could be keyed out as *Limnodynastes*.

The larva of only one species has been described: see the species account for *Lechriodus fletcheri*.

NOTES ON NOMENCLATURE: Boulenger (1882a) included only *B. melanopyga* (Doria) in his new genus *Batrachopsis*, so *Asterophrys melanopyga*

seems to be the type-species by monotypy. However, the two specimens that formed the basis of Boulenger's description belong to *Lechriodus platyceps* rather than *L. melanopyga*. This is a case of misidentification of a type-species, as discussed in Article 70 of the International Code of Zoological Nomenclature. In compliance with Article 70(a), I have brought this case to the attention of the International Commission of Zoological Nomenclature (Zweifel, In press), requesting that *melanopyga* be designated type-species.

The principal systematic problem involving *Lechriodus* was the family to which the genus belonged. Boulenger (1882a, p. 439) placed his new genus *Batrachopsis* (and, hence, its replacement name *Lechriodus*) in the Pelobatidae, and in 1890 described *Phanerotis* in the Cystignathidae (= Leptodactylidae). The distinction of these genera was questioned by Fry (1915, p. 74), who wrote: "So complete is the resemblance of *Phanerotis* to *Lechriodus* that it is difficult to find even specific characters with which to distinguish them." Neither Nieden (1923, pp. 49, 537) nor van Kampen (1923, pp. 16, 18) followed Fry's lead, however. Both authors placed *Lechriodus* (still called *Batrachopsis* by van Kampen, who considered *Batrachopsis* Fitzinger a *nomen nudum*) in the Pelobatidae and *Phanerotis* (considered a synonym of *Ranaster* by Nieden) in the Cystignathidae. It remained for Noble (1924, p. 11) to confirm *Lechriodus* as a "toothed bufonid" (leptodactylid of present authors), and thus dispose of the only supposed pelobatid of the Australo-Papuan region. He based his decision on the structure of the pectoral and thigh musculature and presence of the double condylar articulation of the urostyle. Later, Noble (1931, p. 497) casually referred *Phanerotis* to the synonymy of *Lechriodus* with a parenthetical statement: "*Lechriodus* (including *Phanerotis*, which apparently has the same shaped pupil) has the toes only slightly webbed."

INTERGENERIC RELATIONSHIPS: Lynch (1971) placed *Lechriodus* in the tribe Limnodynastini of the subfamily Cycloraninae, along with the genera *Adelotus*, *Limnodynastes*, *Kyarranus*, and *Philoria*. He considered *Lechriodus* in many respects to be the most primitive genus of Limnodynastini, but cited the supposed nonfusion of first and second vertebrae as a possibly advanced character. Present knowledge that these vertebrae are normally fused eliminates this presumably advanced state (but I can find no statement explaining why the fused state is the more primitive).

Newly acquired information (see Description, above) indicates that *Lechriodus* is less distinct from *Limnodynastes* than was apparent to Parker and Lynch. I do not imply that *Lechriodus* should be merged with *Limnodynastes*, for I regard the species of *Lechriodus* as constituting a natural group worthy of generic rank, but the evidence points to *Limnodynastes* as

the genus most closely related to *Lechriodus*.

DISTRIBUTION: Frogs of the genus *Lechriodus* have been found throughout much of New Guinea, excluding the higher montane areas and the northern slopes of the eastern "tail" of the island (fig. 2). They are present on the Aru Islands, but have been reported from no other island satellites of New Guinea except Mansiman (see account of *L. platyceps*). In Australia,

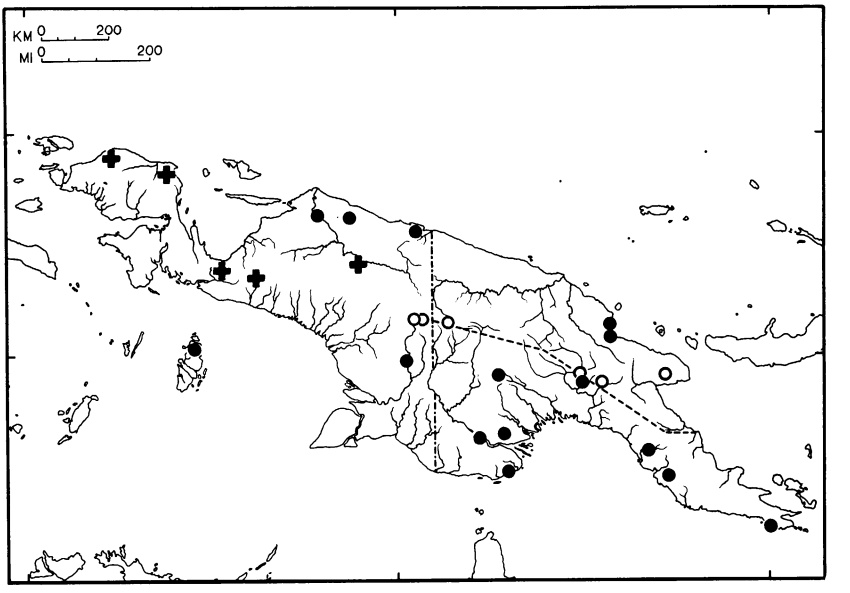

FIG. 2. Distribution of the species of *Lechriodus* in New Guinea: crosses, *L. platyceps*; solid circles, *L. melanopyga*; open circles, *L. aganoposis*.

Lechriodus apparently ranges along the east coast from the base of the Cape York Peninsula in Queensland south to Ourimbah (north of Sydney) in New South Wales, but records are lacking for most of the stretch of Queensland within this range (Moore, 1961, p. 173, fig. 6).

KEY TO THE SPECIES OF *Lechriodus*

1. A tubercle near the base of each finger (fig. 8) . . . . . *melanopyga*
   No such tubercles, although unpigmented spots may be present (fig. 11). . 2
2. Size smaller—adult males less than 50 mm. SV, adult females 53 mm. or less; back with no more than one (paravertebral) pair of elongate skin folds, often none. . . . . *fletcheri*
   Size larger—adult males *ca.* 64–78 mm. SV, adult females *ca.* 66–82 mm., rarely to 95 mm.; usually with two or three distinct pairs of elongate skin

folds on back and sides 3

3. Male nuptial pads composed of coarse, conical elements, *ca.* 4 to 20 per square mm.; chin immaculate or variously patterned with fine melanic stippling, but without large, black spots on chin or chest; testes pale . . *platyceps*

Male nuptial pads composed of extremely fine asperities, hundreds per square mm.; chin and chest often with some large black spots but in some immaculate; testes pigmented, in some virtually black . . . . . *aganoposis*

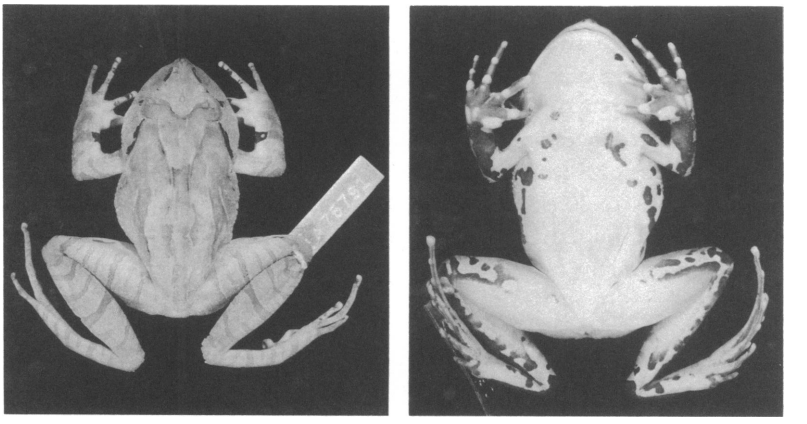

FIG. 3. *Lechriodus aganoposis*, AMNH 75791, *left*, holotype male, dorsal view; AMNH 75790, *right*, paratype, female, ventral view. Both approximately ×0.5.

Lechriodus aganoposis, NEW SPECIES

Figure 3

HOLOTYPE: AMNH 75791, adult male, Numbut, Mt. Rawlinson, *ca.* 4200 ft. (*ca.* 1280 m.), Morobe District, Territory of Papua-New Guinea, collected by natives for H. M. Van Deusen, Seventh Archbold Expedition, June 20, 1964.

PARATYPES: AMNH 75790, same data as holotype; AMNH 74646 [skeleton], Gang Creek, Mt. Rawlinson, 4500 ft. (1370 m.), Morobe District; MCZ Y00400 and 68342, Karimui, Chimbu District; MCZ 53098, Purosa, Eastern Highlands District; MCZ 81632, Tifalmin, West Sepik District; RMNH 17005, west side of Mt. Antares, 1500 m. (4920 ft.), about 20 km. W Sibil (Mabilibol), Star Mountains, West Irian (camp 39A of Kalkman, 1963); RMNH 17006 (4 specimens), Sibil, Star Mountains, 1260 m. (4130 ft.), West Irian; BBM 3156, Sibil Valley, 1250 m. (4100 ft.), Star Mountains, West Irian; RMNH 17007, "probably Katem," about 20 km. S and 20 km. E Sibil, Star Mountains, West Irian.

DIAGNOSIS: *Lechriodus aganoposis* differs from the other species of its genus

in possessing the following combination of characters: adult males 64 to 73 mm. snout-vent length, adult females 66 to 77 mm.; nuptial pads of males (on first and second fingers) composed of minute asperities, hundreds per square mm.; usually four to six prominent longitudinal folds on the back and sides.

Lechriodus melanopyga and *L. fletcheri* resemble *L. aganoposis* in the nature of the nuptial pads, but both are smaller species than *aganoposis*: males reach 48 mm. and females 60 mm. (but rarely more than 53 mm.) snout-vent length. These two species typically lack the prominent skin folds of *aganoposis*, or have only a paravertebral pair, and *melanopyga* differs additionally in having a tubercle at the base of each finger.

Lechriodus platyceps is as large as or larger than *L. aganoposis* and has the same skin folds. Males, however, have relatively much coarser nuptial spines—about 4 to 20 per square mm. Another difference is that the testes of *platyceps* I examined are unpigmented or virtually so, whereas those of *aganoposis* are partly brown to virtually black (as they are in *melanopyga* and *fletcheri*).

DESCRIPTION OF HOLOTYPE: Head broad, about as wide as body, width about 45 percent of snout-vent length. Snout sloping, somewhat pointed as viewed from above; loreal region concave, oblique; canthal angle sharp; nostrils slightly closer to eyes than to tip of snout; distance from eye to naris greater than internarial distance. Top of head concave anterior to mid-ocular line. Eyes moderately large, orbit length about 11 percent of snout-vent length, interorbital span about 80 percent of width of upper eyelid. Tympanum slightly smoother than surrounding skin, horizontal diameter 78 percent length of orbit.

Relative lengths of fingers, $3 > 2 > 1 > 4$; a large, rounded inner metacarpal tubercle and lesser middle and outer tubercles; subarticular tubercles rounded and prominent; no small tubercles at bases of fingers; finger tips rounded, neither dilated nor grooved; fingers not webbed; nuptial pad of fine horny asperities (about 400 per square mm.) occupies most of dorsal and inner lateral surfaces of first finger, with more of same material on second finger and inner metacarpal tubercle. Hind limbs long, tibia length 54 percent of snout-vent length; relative lengths of toes, $4 > 3 > 5 > 2 > 1$; inner metatarsal tubercle three times as long as wide; no other metatarsal tubercles present, but numerous tiny warts present on sole; subarticular tubercles single, rounded; tips of toes very slightly expanded but not grooved; toes with basal webbing (extending to proximal subarticular tubercle) and lateral fringes.

Dorsal surface of body and limbs with rather generally distributed soft (not horny), tiny warts. A U-shaped skin fold between eyes with a poste-

riorly directed projection from right side; a pair of folds beginning at eyelids, converging slightly in scapular region, and passing almost to end of body with slight interruptions posteriorly; second pair of folds from scapular region (fold on right contacting paravertebral fold anteriorly) almost into groin; another short, diagonal fold on each side; a strong fold from posterior corner of eye passing over upper edge of tympanum terminating behind axilla. Ventral surfaces wholly smooth.

Ground color of dorsal surfaces light tan (in preservative). A dark brown streak from nostril to eye, continued behind eye following postocular skin fold to postaxillary region; a small dark blotch beneath eye. Body without darker marking except for narrow dark lines following some skin folds. Hind limbs with narrow tan crossbars. Palm and forearm largely dark brown beneath with extensions dorsally on wrist. Sole, under side of tarsus, and anterior side of tibia dark brown. Posterior surface of thigh uniform brown, only slightly darker than dorsal surface; a triangular brown patch with apex on cloacal opening. Two dark spots on chest, a dark streak on under side of upper arm, and dark spots laterally on abdomen.

MEASUREMENTS OF HOLOTYPE (in MM.): Length from snout to vent 66.4; tibia length 35.0; head width 29.0, head length (tip of snout to angle of jaws) 24.7; diameter of orbit 7.4; horizontal diameter of tympanum 5.8; internarial distance 5.8; distance from eye to naris 7.5.

VARIATION: Ranges and means of proportions within the type series of 13 preserved specimens (excluding one skeleton) are given in table 1. One specimen is a juvenile, and provided the lowest E-N/IN ratio (because of its relatively larger eyes). Otherwise, ontogenetic variation is not evident in this small sample. Each specimen has a skin fold between the eyes, although in some it is straight rather than U-shaped. Every specimen has the paravertebral and adjacent (dorsolateral) skin folds well developed, but not all have the additional short lateral fold seen in the holotype. The postocular fold is strong, straight, and diagonal in all specimens.

I recorded in my field notes (paraphrased here) the following description of a living individual (AMNH 74646, female): gray dorsally with slight greenish tinge most evident on head; loreal stripe and supraocular markings black; upper third of iris golden, lower two-thirds dark gray with faint golden suffusion; pupil horizontal; dark bars of hind limbs composed of paired black lines with slightly paler areas in between; under surfaces of hind limbs and groin faint peach; sole and posterior surface of tarsus black; palms black except for white subarticular and inner metacarpal tubercles; chin, chest, and abdomen white with a few black markings.

Dorsal color and pattern show little variation. Two specimens have a dark brown ground color (rather than light tan), and one of these has

TABLE 1

BODY PROPORTIONS IN SPECIES OF *Lechriodus*

Species	N	TL / S–V		HW / S–V		IN / S–V		E–N / IN	
		Mean ± σ_m	Range	Mean ± σ_m	Range	Mean ± σ_m	Range	Mean ± σ_m	Range
L. melanopyga									
Aru Islands	2[a]	0.505	— (0.50, 0.51)	0.410	— (0.41)	0.066	— (0.062–0.070)	1.66	— (1.61–1.71)
Didessa	7	0.529	— (0.48–0.57)	0.429	— (0.39–0.44)	0.067	— (0.065–0.068)	1.71	— (1.61–1.77)
Boze	10	0.527 ± 0.005	(0.51–0.56)	0.422 ± 0.003	(0.41–0.44)	0.073 ± 0.001	(0.069–0.078)	1.50 ± 0.02	(1.40–1.64)
Brown River	38	0.537 ± 0.004	(0.47–0.60)	0.396 ± 0.002	(0.37–0.42)	0.074 ± 0.001	(0.067–0.081)	1.31 ± 0.01	(1.20–1.45)
L. fletcheri	32	0.518 ± 0.003	(0.48–0.56)	0.388 ± 0.002	(0.36–0.43)	0.073 ± 0.001	(0.064–0.077)	1.30 ± 0.01	(1.18–1.43)
L. aganoposis	13	0.526 ± 0.005	(0.49–0.55)	0.426 ± 0.004	(0.41–0.45)	0.089 ± 0.001	(0.080–0.099)	1.17 ± 0.02	(1.09–1.33)
L. platyceps									
Vogelkop	9	0.576 ± 0.005	(0.56–0.60)	0.447 ± 0.007	(0.42–0.49)	0.086 ± 0.002	(0.077–0.095)	1.27 ± 0.03	(1.18–1.42)
Wissel Lakes ♂♂	41	0.536 ± 0.003	(0.48–0.57)	0.412 ± 0.002	(0.38–0.45)	0.082 ± 0.001	(0.073–0.089)	1.18 ± 0.01	(1.08–1.26)
Wissel Lakes ♀♀	31	0.527 ± 0.004	(0.47–0.57)	0.407 ± 0.002	(0.38–0.44)	0.078 ± 0.001	(0.073–0.087)	1.23 ± 0.01	(1.15–1.32)

[a] Holotype and topotype.

the top of the head anterior to a line across the eyelids colored pale brown. Some specimens have dark markings on the back more evident than in the holotype, but these still tend to be concentrated along the skin folds. Four specimens have the chin immaculate, two show a light marginal infuscation, and seven have sharply defined black spots, variable in size and number but almost wholly marginally situated. Only two specimens lack black spots laterally on the abdomen.

COMPARISON WITH OTHER SPECIES: *Lechriodus aganoposis* is not known to be sympatric with any other species of the genus, so inferences as to the level of relationship between *aganoposis* and the other nominal species must be based on degree of morphological divergence and on indications of the presence or absence of intergradation. I attribute importance to the considerable difference in size between *aganoposis* on the one hand and *melanopyga* and *fletcheri* on the other, and assume that this would inhibit free interbreeding between *aganoposis* and either of the other two forms were they to come in contact. Nine miles separate the closest localities for *aganoposis* at Karimui, *ca.* 3600 ft., and *melanopyga* at Soliabeda, *ca.* 2000 ft. The single specimen from Soliabeda is a male of 42 mm. snout-vent length evidently just attaining sexual maturity (vocal sac openings present but no nuptial pads). It is of the single-striped morph, with moderately distinct paravertebral folds but without the other folds seen in *aganoposis*. In head width (HW/S-V = 0.40) and internarial distance (IN/S-V = 0.073) it is within the range of *melanopyga* and outside the range of *aganoposis* (table 1). Most important for its determination as *melanopyga*, it possesses the hand tubercles typical of that species.

Lechriodus aganoposis and *L. platyceps* are the same size, so this potential isolating mechanism is absent. The difference between the two forms in the nature of the male nuptial pads is, I think, of significance because of the intimate relationship of these structures to the actual mating process. Principally for this reason I regard *aganoposis* and *platyceps* as different species rather than as geographic races of a single species.

As to ways of distinguishing among specimens of *aganoposis* and the other species, there is little to be added to what has been given in the foregoing diagnosis. The chin and chest of *aganoposis* are immaculate, or marked with a variable number of large dark spots. Most specimens of *platyceps*, including all from the Tigi Lakes region, have a distinctly different pattern: melanophores are concentrated in tiny brown spots, densely scattered over the whole region or arranged partly this way and partly in scrollwork-like figures or vermiform lines. This aspect of pigmentation might be of use should specimens come to hand from the area west of the westernmost locality for *aganoposis* in the Star Mountains (Sibil Valley). The minimum

distance between localities for the two species is about 140 miles (Sibil Valley and Idenburg River).

ECOLOGICAL NOTES: Native collectors obtained the specimens of *L. aganoposis* taken on the Huon Peninsula; the exact conditions of capture are unknown. The Gang Creek camp was in "evergreen oak and mixed forest" (Van Deusen, 1966, p. 453), but we could not be certain that the frogs were obtained in this virgin forest and not in areas disturbed by native agriculture.

Kalkman (1963, p. 255) described "Camp 39A" at 1500 m. on Mt. Antares, where a specimen was taken on the Netherlands New Guinea Expedition of 1959. Here there was a circular hollow about 100 m. in diameter, mainly covered with grasses, surrounded by primary montane forest with trees 15 to 25 m. high and very rich in mosses and epiphytes. During the collector's stay of 14 rainy days, water came to cover about a quarter of the hollow to a depth of up to 2 m. Several specimens were taken in the Sibil Valley (*ca.* 1250 m.), which Kalkman (1963, p. 250) characterized as follows: "swampy grasslands alternating with scattered trees and tree-groups, thickets and a marsh type of riverbank-forest."

Exact altitudinal data do not accompany all the specimens, but from available information it appears that *Lechriodus aganoposis* lives at moderate elevations, not reaching down into nonmontane areas or up into high mountains. Apparently the lowest station for the species is Karimui, which is at 3650 ft. (1110 m.; Diamond, 1967, p. 2). Four other localities lie between about 4100 and 4900 ft. (1250–1500 m.). Possibly the highest locality is Purosa. Brass (1964, p. 198) described a camp near Purosa at 6400 ft. (1950 m.), but the specimen was not collected on this expedition and may have come from a lower elevation.

NOMENCLATURAL HISTORY: I find no references in the literature that clearly pertain to this species. The only possible reference is that of Boettger (1894, p. 112) to *Batrachopsis melanopyga* from an unspecified locality in southeast New Guinea. (The collector, Richard Semon, visited several coastal localities between Yule Island and Milne Bay [Semon, 1899].) Boettger described the specimen as "Ein junges ♂" with a "Kopfrumpflänge 50 mm." The species to be expected in the collection area is *L. melanopyga*, but adult males of this species are not known to attain even 50 mm. Possibly the sex or size was given incorrectly, for it does not seem from Semon's itinerary that he collected at a high enough elevation to obtain *aganoposis*. Unfortunately, the specimen is not in the Senckenberg Museum, where I presume it would have been deposited (Konrad Klemmer, personal commun.).

ETYMOLOGY: The name *aganoposis* combines the Greek words *aganos*

(gentle, kind) and *posis* (husband), alluding to the structure of the male nuptial pads (in contrast to those of *L. platyceps*).

DISTRIBUTION: *Lechriodus aganoposis* is confined to New Guinea, and is found on the Huon Peninsula and along the central mountainous spine of the island from Purosa in the Eastern Highlands District, Territory of Papua-New Guinea, west to the Sibil Valley in West Irian (fig. 2). It is likely that the range of the species extends both to the east and west of the limits presently known in the central mountains. See under "Holotype" and "Paratypes" for locality data and specimens examined.

Lechriodus fletcheri (Boulenger)

Phanerotis fletcheri BOULENGER, 1890, p. 594 (type locality, Dunoon, Richmond River, New South Wales, Australia; holotype, BMNH 1947.2.18.67 [formerly 1890.7.28.1], collected by Richard Helms in 1890). FRY, 1913, p. 48; 1915, p. 69. ANDERSSON, 1916, p. 10. VAN KAMPEN, 1923, p. 18 (in part).

Lechriodus fletcheri: LOVERIDGE, 1935, p. 22 (new combination; Loveridge, Parker [1940, p. 26, in part], and Gorham [1966, p. 124] all credited Noble [1931, p. 497] with this combination, but it does not appear in the reference cited). LYNCH, 1971, p. 86.

[*Lechriodus*] *f*[*letcheri*]. *fletcheri*: LOVERIDGE, 1956, p. 2 (in part; new combination).

DIAGNOSIS: *Lechriodus fletcheri* males reach a known maximum snout-vent length of 48 mm. and in females 52 mm. This relatively small size distinguishes these Australian frogs from adults of the Papuan species *L. aganoposis* and *L. platyceps*, whose adult males are at least 64 mm. in length, and whose females measure at least 66 mm. *Lechriodus platyceps* differs additionally in having coarse rather than exceedingly fine spines in the male nuptial pads, and both of these Papuan species have two or three pairs of longitudinal skin folds on the back, compared with one pair at most in *fletcheri*.

The other Papuan species, *L. melanopyga*, is morphologically distinguishable from *L. fletcheri*, in that *melanopyga* possesses a small tubercle near the base of each finger, whereas *fletcheri* has no tubercles proximal to the large, rounded subarticular tubercles except the metacarpal tubercles.

DESCRIPTION: The following description is a composite, based on specimens from Ulong, New South Wales.

Head broad, as wide as or slightly narrower than body; width about 39 percent of snout-vent length. Snout sloping, bluntly pointed to slightly more rounded as seen from above; loreal region oblique, shallowly concave; canthal angle moderately sharp; nostrils closer to tip of snout than to eyes; internarial distance less than distance from eye to naris. Top of head slightly concave to virtually flat. Eyes moderately large, orbit length about 12 percent of snout-vent length. Tympanum moderately distinct.

Relative lengths of fingers, 3 > 2=1=4, or 3 > 2 > 1=4 (1, 2, and 4 very similar in length); a large, rounded inner metacarpal tubercle and lesser middle and outer metacarpal tubercles (last sometimes obsolete); prominent, rounded subarticular tubercles, but no additional small tubercle between inner metacarpal tubercle and subarticular tubercle of first finger, rarely even a trace of such tubercles at bases of other fingers; finger tips rounded, neither expanded nor grooved; fleshy, basal webbing present, with a tubercle in web between first and second fingers. Males with nuptial pads composed of extremely fine, black spicules on first, second, and (usually) third fingers; females with first and especially second fingers broadened laterally. Hind legs long, tibia length about 52 percent of snout-vent length; relative lengths of toes, 4 > 3=5 > 2 > 1; inner metatarsal tubercle three times as long as wide; no other metatarsal tubercles; subarticular tubercles single, rounded; tips of toes rounded, slightly expanded, not grooved; toes with scant webbing, barely reaching to level of first subarticular tubercle; males with broad fringes on toes, each fringe broader than half width of body of digit; females lacking such fringes.

All specimens with straight, diagonal skin fold from posterior corner of eye, across top margin of tympanum a variable distance onto flank; no specimens with distinct, continuous folds on back (but see "Variation"), a few specimens with short or discontinuous folds; interocular fold rarely present. Males with minute, black, horny spicules over entire dorsal surfaces of head, body, and limbs; spicules present also on under surfaces of feet, toe fringes, and in line along under side of margin of lower jaw; females with spicules present but much less well developed.

Dorsal ground color (in preservative) gray to dark brown, usually virtually immaculate, rarely (especially in dark phase) with obscure, darker markings; dark postocular-supratympanic stripe in all specimens; canthal dark stripe rarely present; hind limbs barred dorsally; posterior surfaces of thighs through cloacal area dark gray-brown; same color present on anterior surfaces and on groin, or these areas much paler; under side of tibia and foot dark gray-brown; chin all pale or with dusky marginal band; never any dark spotting on chin or chest; remainder of venter pale and immaculate except for marginal impingement of dorsal pigmentation.

See Slevin (1955, p. 372) and Moore (1961, p. 169) for descriptions of color in life. For photographs of *L. fletcheri*, see Moore (1961, pl. 34, fig. 3), Cogger (1960, p. 9), and Slevin (1955, fig. 12).

MEASUREMENTS OF HOLOTYPE (IMMATURE FEMALE, IN MM.): Length from snout to vent 32.4; tibia length 17.8; head width 12.7; head length

11.9; diameter of orbit 4.3; horizontal diameter of tympanum 2.2; internarial distance 2.6; distance from eye to naris, 3.4.

VARIATION: Ranges and means of proportions are presented in table 1, and some aspects of variation are treated in the foregoing description. An adult male (AMNH 58953) lacks the black epidermal spines so conspicuous in the specimens from Ulong. The latter specimens were breeding when collected (Slevin, 1955, p. 372), and it may be that such rich development of these structures is limited to individuals in breeding condition.

The distinctness of epidermal folds may vary somewhat, according to the state of preservation of the specimen or other undetermined factors. For example, the folds appear much less distinct in the preserved specimen than they show in the same living individual illustrated by Moore (1961, pl. 34, fig. 3).

The largest of 21 male specimens I measured has a snout-vent length of 48.4 mm., the largest of 10 females, 51.5 mm. Moore (1961, p. 170) mentioned males as small as 42.2 mm. snout-vent length with well-developed nuptial pads, and I have examined a female of 45 mm., gravid and with spatulate fingers. These sizes may approximate the sizes at which sexual maturity is attained.

EARLY STAGES: The reader is referred to Moore (1961, pp. 171–173) for an account of the embryonic and larval development of this foam-nesting species. As a supplement to Moore's description, I present illustrations of one of Moore's larval specimens and of its mouth parts (fig. 4). Martin (1967, fig. 7:4B) illustrated a hatchling larva, and Salthe (1963, p. 164) figured the egg capsule. Lynch (1971, p. 86) characterized the larva of *Lechriodus* as having "2/3 tooth rows." I think that 5/3 would be a more correct designation. I presume that Lynch was misled by Moore's (1961, p. 171) reference to "three (rarely, four) short rows on each side of the jaws." In my interpretation, these are anterior (upper) rows.

COMPARISON WITH OTHER SPECIES: In almost all respects, *Lechriodus fletcheri* greatly resembles *Lechriodus melanopyga*. The two are virtually the same size and there appear to be no significant differences between them in proportions (table 1). Color-pattern differences may be present but are not adequately defined in preserved specimens. (The apparent absence of the striped morph in *fletcheri* needs to be verified with larger numbers of specimens.) In spite of these similarities, I regard the two as separate species, basing my opinion primarily on the differences in the mating calls (described below). I think it a reasonable assumption that the female frogs would not react positively to the call of the other species, because the nature and magnitude of the differences in the calls are of the sort com-

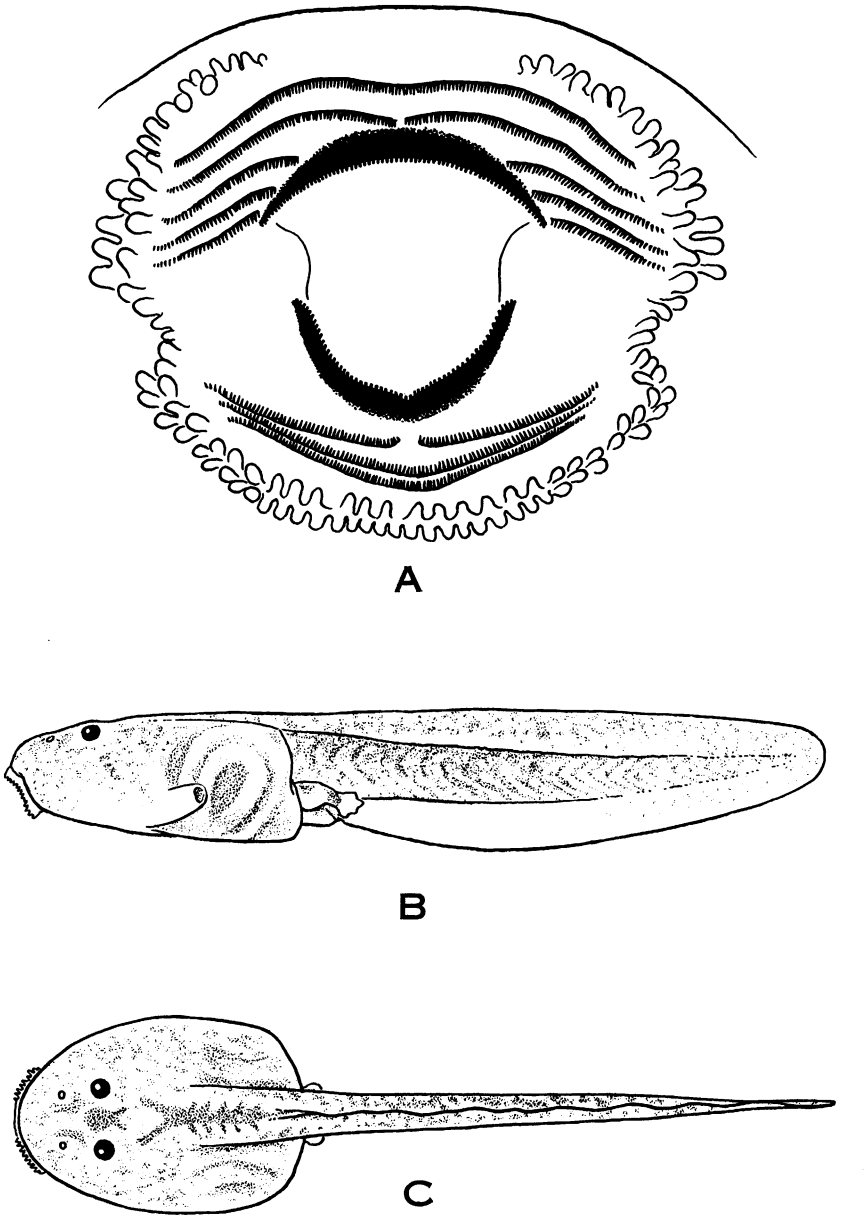

FIG. 4. *Lechriodus fletcheri*, AMNH 86679, larva, stage 35 (Gosner, 1960), total length 27 mm. A. Mouth parts (semi-diagrammatic). B. Lateral view. C. Dorsal view.

monly found between sympatric species. Thus, the calls would serve as premating isolating mechanisms were the two species ever to come in contact.

There is a seemingly trivial but constant morphological character that distinguishes the species. *Lechriodus melanopyga* has near the base of each finger a small but distinct tubercle, much smaller than the subarticular tubercles and unpigmented in contrast to the remainder of the palm. The corresponding regions of *L. fletcheri* are smooth; there are no tubercles, although the spots may be indicated by absence of pigment. Another difference is in the relative lengths of the fingers: in *fletcheri* the first, second, and fourth are very similar in length, whereas the fourth finger of *melanopyga* is distinctly shorter than the others.

No comparison between *L. fletcheri* and the other two species is needed to supplement the information in the diagnosis.

MATING CALL: Through the courtesy of Dr. Ian Straughan, I have received a reduced photographic copy of an audiospectrogram of the call of *Lechriodus fletcheri*, recorded at Lamington National Park, Queensland, at an air temperature of 19.3° C. (Unfortunately, the original tape-recording or audiospectrogram could not be obtained for me.) The individual notes in the call were approximately 0.1 sec. in length and were uttered at a rate of almost four per second. The pulse rate within each cannot be resolved on the copy at hand, but the notes clearly were not broken into discrete pulses ("trills") which would appear as separate vertical streaks on the audiospectrogram.

In contrast, the mating call of *L. melanopyga* (see account of that species and fig. 9) consists of individual notes that are longer (more than 0.2 sec. at 26° C.), are composed of a small number of quite distinct pulses, and are uttered at a slower rate (nine notes in 20 sec.). The differences in length and rate of call presumably would be increased were the frogs calling at the same temperature.

Moore (1961, p. 171) characterized the call of *L. fletcheri* as "a single note that may be described as 'g-a-r-r-up.' Each note . . . has a duration of about one second. It is repeated at short intervals." This description implies a call different from either that recorded in New Guinea (*melanopyga*) or in Queensland. Obviously, additional information is needed to test my hypothesis, which assumes that the calls recorded were typical mating calls of the two nominal species.

ECOLOGICAL NOTES: Moore (1961, p. 171) summarized what little is known of the ecology of this species. Various authors (Moore, 1961; Slevin, 1955; Cogger, 1960) have referred to it as a species of the rain forest. Eggs are deposited in foam nests in standing or slow-moving water and develop

unusually rapidly (Moore, 1961, p. 172). The larvae are voracious predators, even cannibalistic (Moore, 1961), although Martin (1967, p. 187) doubts whether these larvae are predacious in uncrowded conditions. Littlejohn (1967) briefly mentioned *L. fletcheri* in a discussion of anuran zoogeography.

DISTRIBUTION AND SPECIMENS EXAMINED: *Lechriodus fletcheri* is confined to eastern Australia; published records for New Guinea are based on misidentifications of *L. melanopyga*. There are several records for the species in the region between Ourimbah, New South Wales, and extreme southeastern Queensland, but a gap of some 800 miles separates the localities in southeastern Queensland from the northernmost record at Ravenshoe, at the base of the Cape York Peninusla (Moore, 1961, fig. 6). The specimen from Ravenshoe is identifiable as *fletcheri* on the basis of the absence of tubercles at the bases of the finger and is not, as might have been suspected, the Papuan species. To what extent the range actually is disjunct remains to be determined.

I have examined 33 transformed specimens and one embryonic-larval series (see Moore, 1961, p. 173, for additional locality records): Queensland: Near Ravenshoe (AMNH 19947); Binna Burra, 3000 ft. (910 m.) (AMNH 58953; 59488 [skeleton]); Bower Bird Creek near Binna Burra (AMNH 86679; embryos and larvae). New South Wales: Vicinity north of Ulong, *ca.* 1800 ft. (550 m.) (CAS 82201–82212, 82214–82216, 82218–82223, 82225–82231); Salisbury, 1000 ft. (300 m.) (MCZ 18170); Cascade, Darringo, 3000 ft. (910 m.) (MCZ 18171); Dunoon, Richmond River (BMNH 1947.2.18.67, formerly 1890.7.28.1, holotype of *Phanerotis fletcheri* Boulenger).

Lechriodus melanopyga (Doria)
Figures 5–7

Asterophrys melanopyga DORIA, 1874, p. 355 (type locality, Wokam Island, Aru Islands, Indonesia; holotype, MSNG 29736, collected by Odorado Beccari in 1874). PETERS AND DORIA, 1878, p. 97 (in part).

Batrachopsis melanopyga: BOULENGER, 1882a, p. 439 (in part; new combination). BOULENGER, 1898, p. 710. LUCAS, 1898, p. 359. ROUX, 1910, p. 247. VAN KAMPEN, 1923, p. 17 (in part). CAPOCACCIA, 1957, p. 211.

Phanerotis fletcheri: ANDERSSON, 1913, p. 75. LAMPE, 1913, p. 86. ANDERSSON, 1916, p. 10 (in part). VAN KAMPEN, 1923, p. 18 (in part).

Lechriodus melanopyga: VAN KAMPEN, 1909, p. 45 (in part). FRY, 1913, p. 48; 1915, p. 73. NIEDEN, 1923, p. 49 (in part). PARKER, 1940, p. 25. LOVERIDGE, 1948, p. 322. GORHAM, 1966, p. 125.

Lechriodus (Batrachopsis) melanopyga: VAN KAMPEN, 1906, p. 178 (new combination).

Batrachopsis (Lechriodus) melanopyga: VAN KAMPEN, 1919, p. 51 (in part; new combination).

Phanerotis fletcheri papuana ROUX, 1927, p. 122 (type locality, "Region of Lake Sentani, northern Dutch New Guinea" [near Djayapura, formerly Hollandia, West Irian]; holotype, NMB 3887, collected by P. Wirz).
Lechriodus fletcheri: PARKER, 1940, p. 26 (in part). GORHAM, 1966, p. 124 (in part).
Lechriodus papuanus: PARKER, 1940, p. 27 (new combination). FORCART, 1946, p. 123. LOVERIDGE, 1948, p. 322; 1956, p. 2. LYNCH, 1971, p. 86.
Lechriodus platyceps PARKER, 1940, p. 29 (in part, specimen from Upper Tor River).
[*Lechriodus*] *f*[*letcheri*]. *fletcheri:* LOVERIDGE, 1956, p. 2 (in part; new combination).
[*Lechriodus*] *f*[*letcheri*]. *papuanus:* LOVERIDGE, 1956, p. 3 (new combination).
Lechriodus melanopygus: LYNCH, 1971, p. 86 (unjustified emendation of ending).

DIAGNOSIS: *Lechriodus melanopyga* may be differentiated from all other *Lechriodus* species by its possession of a small but distinct, unpigmented tubercle near the base of each finger (fig. 8). Other species lack any such tubercles, although their positions may be marked by unpigmented spots. In addition, *melanopyga* differs from the Papuan species *platyceps* and *aganoposis* by its smaller size: males measure less than 50 mm. snout to vent, compared with a minimum of 64 mm. in adult males of the other two species; comparable measurements for females are 60 mm. (but rarely more than 53 mm.) and 64 mm. Individuals of the two large species commonly have two or three pairs of longitudinally oriented skin folds on the back, whereas *melanopyga* has at the most one distinct pair. An additional character distinguishing *melanopyga* from *platyceps* is the coarse nature of the nuptial pads of the latter, compared with the exceedingly fine-grained structures of *melanopyga*.

Lechriodus melanopyga closely resembles *L. fletcheri* of Australia in morphology, except for the digital tubercles discussed above. Apparently the two differ in their mating calls (see account of *L. fletcheri*).

DESCRIPTION: The following description is composite, based on specimens from several localities. Details of variation are discussed in a following section.

Head broad, as wide as or slightly narrower than body, width averaging about 40 to 43 percent of snout-vent length; snout sloping in profile rounded as seen from above; loreal region oblique, slightly concave; canthal angle distinct but not sharp; nostrils closer to tip of snout than to eye; internarial distance less than distance from eye to naris. Top of head virtually flat. Eyes moderately large, orbit length about 12 percent of snout-vent length; eyelid broader than interorbital space. Tympanum moderately distinct, separated from posterior corner of eye by a distance slightly less than half tympanic diameter.

Relative lengths of fingers, $3 > 1 > 2 > 4$ (or $1 = 2$; 4 always distinctly shortest); a large, elongate but rounded inner metacarpal tubercle and smaller, lower middle and outer metacarpal tubercles (last in some cases

FIG. 5. *Lechriodus melanopyga* (AMNH 81222), female, unstriped color phase, SV 43 mm.

missing); prominent, rounded subarticular tubercles; a small, round, unpigmented tubercle near the base of each finger (fig. 8); finger tips rounded, not broadened or grooved; fleshy, basal webbing present, with a tubercle in web between first and second fingers. Males with nuptial pads of extremely fine, black asperities on first and second fingers; females with first and second fingers slightly broadened laterally. Hind legs long, tibia length averaging about 50 to 54 percent of snout-vent length; relative lengths of toes, $4 > 3 > 5 > 2 > 1$, or less often, $3 = 5$; inner metatarsal tubercle rounded, more than twice as long as wide, no other metatarsal tubercles present; subarticular tubercles large, prominent, rounded; tips of toes rounded, slightly expanded but not distinctly grooved; webbing scant, reaching first subarticular tubercle or (fifth toe) slightly beyond; males with narrow dermal fringe on toes, less than one-half width of body of digit; fringes not developed in females.

A fold of skin, often not well defined, from posterior corner of eye across top edge of tympanum to above axillary region or flank; a pair of converging interscapular folds usually distinguishable; rarely, a pair of paravertebral folds continuous with interscapular folds and distinct for full length of dorsum; occasional individuals with numerous small, irregular

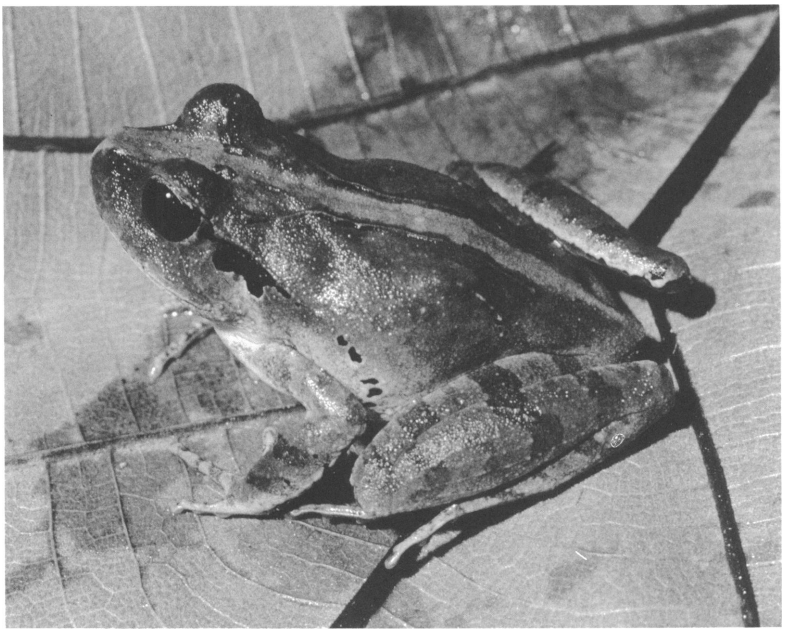

FIG. 6. *Lechriodus melanopyga* (AMNH 81226), female, striped color phase, SV 52 mm.

folds on dorsum, but no specimens with more than one pair of long, continuous folds; interocular fold in some cases present. Dorsal surfaces smooth to minutely warty, but never with horny spicules.

Dorsum gray to gray-brown in preservative, obscure darker markings visible in some, or concentrations of dark pigment present along skin folds; rarely a light, middorsal stripe (see Variation); usually a dark stripe, wavy-edged beneath, following postocular stripe; in some cases a dark canthal stripe, or entire loreal area dark. Hind limbs crossbarred dorsally; tarsal area and sole dark brown, under side of tibia slightly lighter; posterior surface of thigh (including cloacal region) uniform moderately dark to dark brown; anterior side of thigh and groin similar but generally paler. Ventral surface from chin through thighs pale and immaculate except for occasional presence of small clumps of melanophores marginally on chin; never any large, black spots on any ventral surface.

I recorded the colors in life (here paraphrased from my field notes) of two frogs from Brown River. AMNH 81222, subadult female (fig. 5): dorsal ground color greenish gray with a faint trace of darker mottling of same shade; a narrow, dark interocular line; a small brown dot at posterior

end of each weak scapular fold; postorbital marking dark brown; lateral ground color pinkish gray rather than greenish gray; a dull greenish gray patch rather distinctly outlined in groin; posterior surface of thigh dark greenish brown except for an irregular yellowish gray spot; upper surface of thigh pinkish gray with slightly darker crossbands; under side of foot dark brown, almost black; ventral surfaces white, unmarked; pupil diamond-shaped, long axis horizontal; iris largely dark brown to black, but a band of greenish speckling prominent in upper third. AMNH 81226, adult female (fig. 6): similar to individual described previously, but ground color darker (metachrosis?) and a distinctive yellowish brown dorsal stripe between paravertebral skin folds.

Two exceptionally large females from Didessa measure 60 mm. and another measures 58 mm., snout to vent (see Variation); the largest male measures 48 mm. snout to vent. To judge from the sample from Brown River, males evidently mature at a snout-vent length of about 38 to 40 mm. Fifteen mature males (with vocal sac openings and most with nuptial pads) measure 38 to 47 mm.; five males measuring 37 to 39 mm. lack vocal sac openings and nuptial pads, and one with a snout-vent length of 38 mm. lacks pads but has one vocal slit open. Females mature at a slightly larger size than males. Sixteen gravid females measure 46 to 53 mm., whereas seven in the range from 40 to 43 mm. have enlarged but unpigmented ova. Nine specimens in the range from 35 to 39 mm. are immature. (The sample studied includes an additional 31 juvenile specimens.)

MEASUREMENTS OF HOLOTYPE (FIG. 7, ADULT FEMALE, IN MM.): Length from snout to vent 47.3; tibia length 23.5; head width 19.2; diameter of orbit 5.5; horizontal diameter of tympanum 2.8; internarial distance 3.3; distance from eye to naris 5.3.

VARIATION: Ranges and means of selected proportions are presented in table 1. There appears to be geographic variation in at least one proportion, the internarial distance. The ratio IN/S-V averages lower among seven specimens from Didessa (0.067) than in 38 adults from Brown River (0.074). Ratios are low also in the type and topotype of *melanopyga* from the Aru Islands (0.062 and 0.070) and in the single specimen from Tanah Merah in West Irian (0.068). These localities are all at about the same latitude and are the northernmost for the species. The ratio E-N/IN shows even greater difference, but I regard it as less reliable because ontogenetic variation in eye size influences the measurement of eye-naris distance.

The series from Didessa is remarkable also in that among only seven specimens there are three females measuring 58 to 60 mm. snout-vent length, whereas the largest female from elsewhere in the Territory of Papua measures only 53 mm. Specimens from Boze (south of the mouth

FIG. 7. *Lechriodus melanopyga* (MSNG 29736), holotype, copied from Doria (1874, pl. 12).

of the Fly River) and from the Aramia River (north of the mouth of the Fly River) resemble those from Brown River in the IN/S-V ratio and include no exceptionally large individuals (N = 15), so it presently appears that the tendency to larger size and narrower internarial distance is limited to the area from Mt. Bosavi (Didessa is on its northern slope) westward.

The variation seen in dorsal skin folds and in color pattern suggests a polymorphic condition such as is seen among species of several families of frogs, including the Leptodactylidae (e.g., Main, 1965; Lynch, 1966).

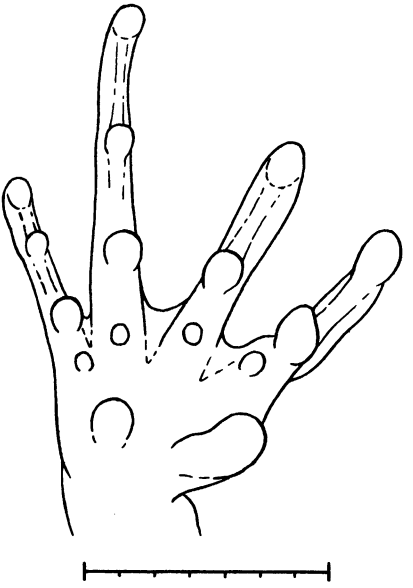

FIG. 8. *Lechriodus melanopyga*. Palmar view of right hand of adult female to show tubercles at bases of fingers (compare fig. 11).

The commonest combination of characters (seen in 64 of 92 specimens from Brown River) is: dorsal skin folds weak (in scapular region) or absent; ground color uniform or faintly mottled; a strong postocular dark stripe present (fig. 5). Another group (22 specimens) differs in that the postocular stripe is absent or is represented by only a tiny spot, and the dorsum is more distinctly mottled. The third form (4 specimens) has the postocular stripe of the first form and a light-colored vertebral band, bordered by essentially continuous paravertebral folds (fig. 6). The fourth form (2 specimens) lacks postocular and vertebral stripes but has numerous short skin folds on the dorsum, each emphasized by an accumulation of melanic pigment.

The four classes distinguished above are readily identified among preserved specimens, although this classification does not exhaust the variability. For example, three of the 64 specimens in the first group have the facial area anterior to the eye dark rather than the same paler color as on top of the head. Possibly living frogs could be classified in more numerous categories, but I noted no others among 23 living frogs I examined.

In contrast to the situation in the sample from Brown River, where the striped morph amounts to less than 4 percent of the sample, three of the seven frogs from Didessa belong to this class. The remaining four from Didessa are of the first class, commonest at Brown River, as are all 10 from

Boze. This is, together with the difference in maximum size and internarial proportion, another indication of genetic differentiation in the Didessa population. The holotype of *melanopyga* also evidently is of the striped morph (fig. 7).

EARLY STAGES: The eggs and larvae have not been described.

COMPARISON WITH OTHER SPECIES: See accounts of the other species for comparisons additional to those in the foregoing diagnosis.

MATING CALL: Through the courtesy of James Menzies, I have studied the mating call of *L. melanopyga*, recorded by Mr. Menzies at Brown River, Territory of Papua, at an air temperature of 26° C. The call consists of a series of pulsed notes, each note about 0.25 sec. in length (fig. 9). The individual most prominent in the recording uttered nine notes in 20 seconds, each one including seven or eight discrete pulses easily resolved by the human ear. Energy is broadly distributed throughout the pulses, although there appears to be a slight peak at about 400–500 Hz. Judged from what could be heard in the background, the call described is typical of those being given in the chorus recorded. See account of *L. fletcheri* for a discussion comparing the calls of the two species.

ECOLOGICAL NOTES: I find nothing in the literature on the ecology of this species. The only individual I collected personally was found at night on the floor of lowland rain forest (elevation 20 m.) near Brown River.

NOMENCLATURAL HISTORY: The *Lechriodus* of the Aru Islands has con-

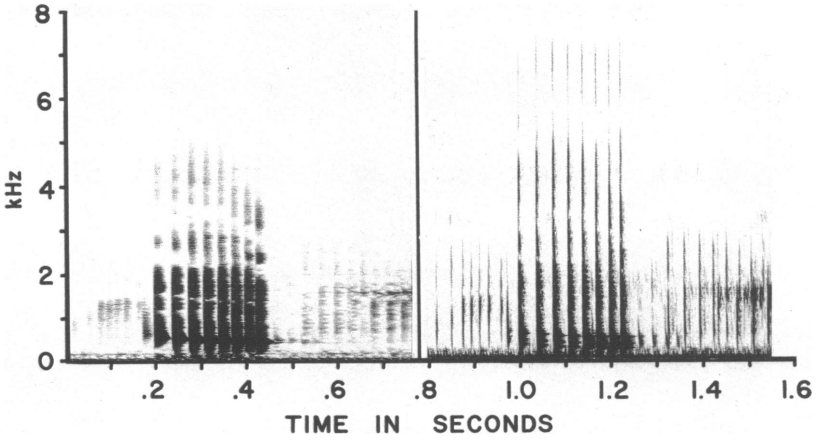

FIG. 9. Audiospectrogram of mating call of *Lechriodus melanopyga*, recorded at an air temperature of 26° C. at Brown River, Territory of Papua by J. Menzies. Same call shown twice; *at left* graphed with narrow band (45 Hz.) filter, *at right* with wide band (300 Hz.).

sistently been referred to the species *melanopyga* by all authors treating it, but the frogs of the mainland of New Guinea have been referred to *melanopyga* as well as being confused with both *platyceps* and *fletcheri*. The confusion began early, when Peters and Doria (1878, p. 87) referred specimens of *platyceps* from the Vogelkop Peninsula to *Asterophrys melanopyga*. Shortly thereafter, Boulenger (1882a, p. 439) proposed the new generic name *Batrachopsis* with *melanopyga* as type species, but his specimens were *platyceps*. Andersson (1913, 1916) recognized the great similarity between *Phanerotis fletcheri* Boulenger of Australia and a specimen from Bogadijm, and referred his Papuan specimen to Boulenger's species. He did not consider *melanopyga* in his discussions. Van Kampen (1923) included both *Batrachopsis melanopyga* and *Phanerotis fletcheri* in the Papuan fauna. However, the specimens he examined evidently included both *melanopyga* and *platyceps*, and he followed Andersson in recording *fletcheri*. Parker (1940) restricted *melanopyga* to the Aru Islands and assigned a Papuan specimen of the species (from Vikaiku) to *fletcheri*. He also cited as *platyceps* literature records from St. Joseph's River and Fife Bay for specimens that I have examined and identify as *melanopyga*.

A paper by Loveridge (1956) on the "rediscovery of . . . *Lechriodus papuanus* in New Guinea" requires somewhat more discussion. Roux (1927) described *Phanerotis fletcheri papuana* (Lake Sentani, West Irian), which Parker (1940) raised to species status. The species evidently was known to Parker only from the published description of the juvenile female holotype, and he recognized that examination of additional specimens might change the picture. Loveridge secured six specimens from the Aramia River in which the variation in a supposedly diagnostic character, dorsal skin folds, bridged the difference between *papuanus* and *fletcheri*. With this difference disposed of, he noted only color differences between *papuanus* and *fletcheri*, and returned *papuanus* to the trinomial designation. *Lechriodus melanopyga* at no time intruded upon the discussion. The basis for subspecific distinctness accorded *papuanus* by Loveridge (1956, p. 2) was color: "Color above pale brown with traces of a blackish brown line from end of snout along the canthus to the eye . . ." (*fletcheri*); "Color above light gray, a white, finely black-edged, shieldlike patch on snout which may merge with two similar, but smaller, anteorbital patches . . ." (*papuanus*). The difference in ground color could be no more than individual variation. The white markings on Loveridge's specimens from the Aramia River (which I have examined) are not distinctive pigmentary patches but are abraded areas from which the epidermis is gone. The pattern of abrasions is such as would be produced if the frog repeatedly forced its snout through the wire mesh of a cage.

The holotype of *Phanerotis fletcheri papuana* possesses tubercles at the bases of the fingers (O. Stemmler kindly verified this for me), so I do not hesitate to refer the taxon to the synonymy of *melanopyga*.

Lechriodus melanopyga has not been recorded from New Guinea under that name since Parker (1940) restricted the name to the frogs of the Aru Islands. Some Papuan *melanopyga* were misidentified as *L. platyceps*, others as *L. fletcheri* or *L. fletcheri papuanus*.

DISTRIBUTION AND SPECIMENS EXAMINED: I have examined 130 specimens that I refer to this species. *Lechriodus melanopyga* is found on the Aru Islands and at elevations from sea level up to about 2000 feet on the southern watershed of New Guinea from the eastern tip of the island (Fife Bay) west at least to the Digoel River (fig. 2). On the north coast of New Guinea, *melanopyga* ranges from Astrolabe Bay near Madang to the Mamberamo River in West Irian, a distance of some 600 miles, but there are only five verified localities and four specimens extant from this vast area (the specimen from Bogadjim, Astrolabe Bay, was destroyed in the Second World War).

Indonesia: Aru Islands, Wokam Island (MSNG 29736, holotype of *Asterophrys melanopyga* Doria); Aru Islands (BMNH 82.7.14.31).

West Irian: Tanah Merah, Digoel River (RMNH 17014); Upper Tor River (ZMA 5799, paratype of *Lechriodus platyceps* Parker); Mamberamo River (MZB 58); Region of Lake Sentani (NMB 3887, holotype of *Phanerotis fletcheri papuana* Roux).

Territory of Papua and New Guinea: Western District: Didessa, N side of Mt. Bosavi (SW 139, 336 [3], 373 [2], unnumbered [1]); Aramia River (MCZ 28382–28386); Fly River, East bank opposite Sturt Island (AMNH 44792); Boze, Binaturi River (AMNH 82281, MCZ 65996, 65997, 80023–80029). Chimbu District: Soliabeda (MCZ Y-40896). Central District: Brown River, Karema and vicinity (AMNH 79953–79955, 81222–81244, 86680 [+ skull]; BBM 1188; MCZ Y-40555 [23], Y-40564–40567, Y-40583 [37]); St. Joseph's (Angabunga) River (AM R4618); Vikaiku, St. Joseph's River (BMNH 97.12.10.164; MSNG 29927); Igibirei, *ca.* 200 m. (660 ft.) (MSNG, unnumbered [1]). Milne Bay District: Fife Bay (AM R6511, 6512). Madang District: Jagaum Hospital, near Madang (SW 88); Bogadjim, Astrolabe Bay (Andersson, 1913; Lampe, 1913).

Lechriodus platyceps Parker
Figure 10

Asterophrys melanopyga: PETERS AND DORIA, 1878, p. 97 (in part).

Batrachopsis melanopyga: BOULENGER, 1882, p. 439 (in part; new combination). VAN KAMPEN, 1923, p. 17 (in part).

Lechriodus melanopyga: VAN KAMPEN, 1906, p. 163 (new combination). NIEDEN, 1923, p. 49 (in part). NOBLE, 1924, p. 11, figs. 5, 7; 1931, p. 113, fig. 38.

Lechriodus (Batrachopsis) melanopyga: VAN KAMPEN, 1906, p. 178 (new combination).
Batrachopsis (Lechriodus) melanopyga: VAN KAMPEN, 1919, p. 51 (in part; new combination).
Lechriodus platyceps PARKER, 1940, p. 28 (type locality, "Arfak, Dutch New Guinea" [Arfak Mountains, Vogelkop Peninsula, West Irian]; holotype, BMNH 1947.2.18.63 [formerly 1876.7.18.6], collected by A. A. Bruijn). LOVERIDGE, 1948, p. 322. GORHAM, 1966, p. 125. LYNCH, 1971, p. 86.

DIAGNOSIS: The principal distinguishing features of this species are its large size (males to 72 mm. snout-vent length, females to 95 mm.), the usual presence of at least four elongate dermal skin folds (paravertebral and dorsolateral), and the relatively large nuptial spines on the fingers of the male.

Lechriodus aganoposis resembles *L. platyceps* in the first two characteristics mentioned above, but the nuptial spines are so small that they are indistinguishable except under magnification.

Lechriodus fletcheri and *L. melanopyga* are smaller (males to 48 mm. snout-vent length, females rarely as large as 60 mm.) than *L. platyceps*, have at the most one pair (paravertebral) of elongate skin folds, and have minute nuptial spines like those of *L. aganoposis*. An additional feature distinguishing *L. melanopyga* is the presence of a tubercle at the base of each finger (fig. 8); such structures are lacking in *L. platyceps* (fig. 11).

DESCRIPTION: This description is composite. Additional aspects of variation are taken up in a following section.

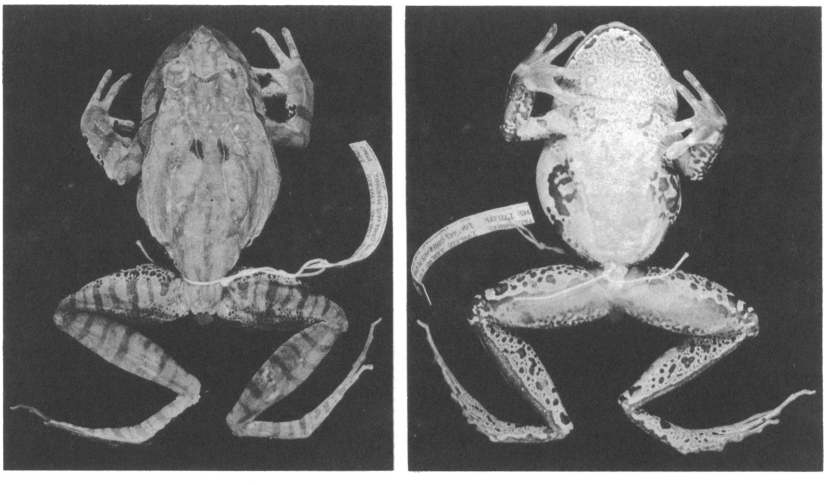

FIG. 10. *Lechriodus platyceps* (RMNH 17001), female, dorsal view left, ventral view right, ×0.5.

Head broad, as wide as or slightly narrower than body, width averaging 41 to 45 percent of snout-vent length; snout sloping in profile, rounded as seen from above; loreal region oblique, slightly concave; canthal angle sharp, emphasized by a slight ridge of skin; internarial distance slightly smaller than distance from eye to naris; nostrils closer to tip of snout than to eye. Top of head slightly concave anterior to interorbital line. Eyes moderately large, orbit length about 12 percent of snout-vent length; eyelid broader than interorbital distance. Tympanum obscure to moderately distinct, generally as pustulose as surrounding skin.

Relative lengths of fingers, $3 > 1 > 2 > 4$ (or $1 = 2$); inner metacarpal tubercle large, rounded; middle metacarpal tubercle smaller, lower and less distinct; outer tubercle absent or scarcely evident; subarticular tubercles rounded, prominent; no tubercles at bases of fingers; finger tips rounded, neither grooved nor expanded; fleshy, basal webbing between fingers. Males with nuptial pads of relative coarse, horny asperities (*ca.* 4–30 per square mm.) on dorsal and inner surface of first finger, dorsal surface of second finger, and on hallux-like projection of inner metacarpal tubercle (fig. 11, left); females with markedly broadened flanges on first and second fingers (fig. 11, right). Hind legs long, tibia length averaging 53 to 58

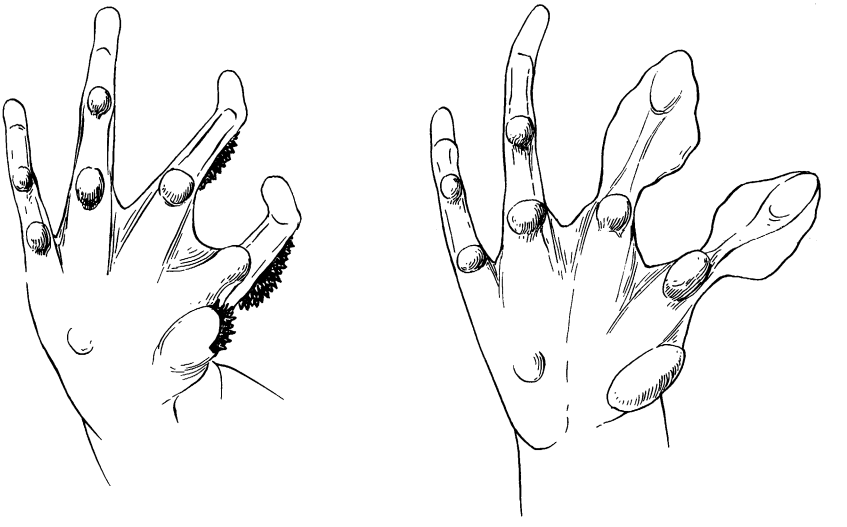

FIG. 11. *Lechriodus platyceps*. Palmar views of right hands of male (left) and female, to show absence of tubercles at bases of fingers (compare fig. 8), nuptial spines of male and flanged fingers of female (figures originally published in Noble, 1931, fig. 38).

percent of snout-vent length; relative lengths of toes, $4 > 5 \cong 3 > 2 > 1$; inner metatarsal tubercle rounded, about twice as long as wide, no other metatarsal tubercles present; subarticular tubercles rounded, relatively low; tips of toes rounded, slightly expanded, not grooved; toes with basal web extending no farther than proximal subarticular tubercle; toes with narrow dermal fringes, best developed in males.

Dorsum typically with four elongate skin folds: paravertebral pair converging from posterior edges of orbits toward scapular region, then running parallel or diverging slightly, terminating at or posterior to sacral region; dorsolateral pair arising from paravertebral pair in scapular region, diverging and then running parallel to paravertebral pair, or arising in scapular region (but not connecting to paravertebral folds) and running posteriorly parallel to paravertebral pair. Interocular fold present, may extend slightly onto eyelids and may have posterior projections. Dorsal surface with numerous tiny warts, tipped with black, horny, pointed caps in some males; venter smooth except for black asperities in a row around edge of chin, expanding to cover region of symphysis.

Noble (1924, p. 11, figs. 5, 7) described and figured the thigh and ventral body musculature of a specimen of "*Lechriodus melanopyga*" provided by van Kampen. I have examined a specimen of *L. platyceps* (MZB 225 from "Northern New Guinea") that has been dissected in just the way illustrated by Noble, and I consider it to be the one Noble used.

Dorsal ground color generally dark to light gray in preservative; area between paravertebral folds often somewhat darker, especially posteriorly; area anterior to interocular fold often lighter; dark markings frequently associated with interocular fold and with folds in scapular region; rarely, irregular black splotches scattered over dorsal surface of body; black-tipped warts of some males may impart black-speckled appearance, especially laterally. Canthal dark line more or less distinct; invariably a black post-ocular mark, wavy-edged beneath, extending across top edge of tympanum, generally terminating above arm. Sides of abdomen with large black blotches or coarsely mottled, less often unmarked. Limbs crossbanded dorsally; anterior side of thigh rarely unmarked, usually with small to large rounded brown spots and heavy, dark markings just proximal to knee; posterior surface of thigh uniformly dark or finely spotted or mottled; sole and under side of tarsal area uniform dark brown; tibia with black streak on anterior side, spotted beneath. Throat pale, pigmented with light speckling of melanophores least dense in posterior-central region, or with elaborate mixture of spots, vermiform lines and amoeba-shaped figures. Chest sometimes unpigmented, but more often bearing extension of throat pattern. Abdominal area ventrally immaculate.

I have not examined living individuals of this species, but notes by H. Boschma accompanying specimens he collected in the Wissel Lakes region indicate that the ground color in life is generally some shade of gray, often with a greenish tinge. Some specimens also had pink in their pattern, so the general effect evidently is much the same as in *Lechriodus aganoposis* and *L. melanopyga*. The iris is brown with gold in its upper part.

The series of specimens from the Wissel Lakes region includes 55 males ranging in size from 64 to 78 mm. (snout-vent length), mean 72.4 mm., and 32 females, 72 to 82 mm., mean 77.4 mm. The largest specimen examined is a female from "South of Geelvink Bay" that measures 95 mm. from snout to vent. The only juvenile specimen I examined is a male 43 mm. in length, whose immaturity is attested by the absence of vocal sac openings and nuptial pads (*L. melanopyga* matures at a size slightly smaller than this).

MEASUREMENTS OF HOLOTYPE (ADULT FEMALE, IN MM.): length from snout to vent 78.2; tibia length 44.6; head width 34.6; head length 27.6; diameter of orbit 8.4; horizontal diameter of tympanum 4.7; internarial distance 6.6; distance from eye to naris 7.8.

VARIATION: Ranges and means of selected proportions are presented in table 1. Frogs from the Vogelkop Peninsula appear to have relatively longer hind legs and relatively wider heads than do those from the Wissel Lakes region. The size of the nuptial asperities may be larger in the males from the Vogelkop. Three specimens from there have about four or five asperities per square mm., whereas among 25 from the Wissel Lakes region the average is 14, range nine to 20. The elaborate throat pattern described above is typical of frogs from the Wissel Lakes area, and the more simple pattern is seen in frogs from the Vogelkop. Analysis of the significance of these differences must await the gathering of additional samples of the species.

EARLY STAGES: The egg and larva have not been described. Brongersma (1958, p. 41) remarked "In the Wissel Lakes area, in the central mountains, the larvae of a species of the genus *Lechriodus* are made into a stew eaten by the Papuans."

COMPARISON WITH OTHER SPECIES: Comparisons with *Lechriodus fletcheri* and *L. melanopyga* additional to those in the diagnoses are not needed. *Lechriodus platyceps* resembles *L. aganoposis* in many respects. It may not always be possible to assign immature individuals or adult females to the correct species, although throat patterns do seem to provide diagnostic characters. On the basis of present information, adult males can invariably be distinguished by the difference in relative size of the individual asperities composing the nuptial pads, and most *aganoposis* are in addition

characterized by melanic pigment on the testes.

The relationship between *L. platyceps* and *L. aganoposis* may prove to be intraspecific. This is hinted at by the apparent difference in nuptial pads between the Vogelkop and Wissel Lakes populations of *platyceps*, suggestive of a clinal change toward the condition seen in *aganoposis*. But in this character as well as in throat pigmentation and testes pigmentation, these two samples are certainly much more similar to each other than they are to *aganoposis*, which retains its diagnostic characteristics unchanged over a distance of at least 480 miles (from the Huon Peninsula to the Star Mountains). I think that the best course is to treat the two entities as species and to review their status when additional evidence of their relationship becomes available.

MATING CALL: No information is available.

ECOLOGICAL NOTES: Nothing has been published relating directly to the ecology of this species. A description of the area near the Idenburg River where specimens were collected by the 1938–1939 Archbold Expedition is in Archbold, Rand, and Brass (1942, pp. 246–250). The area is mountainous (elevation about 5900 ft.), and rain forest of lower elevations merges with beech forest of higher slopes. Rain was a daily occurrence during a three-week period in January.

NOMENCLATURAL HISTORY: The first specimens of *Lechriodus platyceps* were collected within a few years of when *L. melanopyga* was described in 1874, but Peters and Doria (1878), Boulenger (1882a), and all subsequent authors prior to Parker (1940) misidentified the species as *melanopyga*. Parker (1940) was the first to recognize *platyceps* as a species distinct from *melanopyga*, but even he misidentified a juvenile *melanopyga* (Upper Tor River) as *platyceps*, and in accepting literature records as representing this species, erroneously attributed to the species a distribution from one tip of New Guinea to the other. No new information regarding *platyceps* has appeared in the literature since Parker wrote, and no taxonomic complications have appeared.

DISTRIBUTION AND SPECIMENS EXAMINED: I have examined 97 specimens of *Lechriodus platyceps*. All specimens examined come from moderatley high elevations on the Vogelkop Peninsula or in the central mountain chain of West Irian (fig. 2). A record for Mansiman, an island on the northeast corner of the Vogelkop Peninsula (van Kampen, 1923, p. 18), may represent only a shipping point or may represent *L. melanopyga* (I have not seen the specimen).

West Irian: Mt. Bantjiet, Tamrau Mountains, *ca.* 6000 ft. (1830 m.) (AMNH 74177–74180 [+ skull of last], MZB [2 specimens]); Hatam, Arfak Mountains (MSNG 29737 [2 specimens]); Mt. Arfak (BMNH

1947.2.18.63; holotype of *Lechriodus platyceps*); "New Guinea" (BMNH 1947.2.18.64, paratype of *L. platyceps*); south of Geelvink Bay, 3700 ft. (1130 m.) (BMNH 1947.2.18.65, 1947.2.18.66; paratypes of *L. platyceps*); "Northern New Guinea" (MZB 225); 15 km. SW Bernhard Camp, Idenburg River, 1800 m. (5900 ft.) (AMNH 49615, 49616); east side of Lake Paniai, Wissel Lakes (RMNH 16941); Ara River, Wissel Lakes region, 1750 m. (5740 ft.) (RMNH 16942–16945, 16946 [2 specimens], 16958, 16960, 16969, 16971, 16998 [2 specimens]); environs of Lake Paniai, Wissel Lakes (RMNH 16947 [6 specimens], 16948–16950, 16952–16957, 16959, 16961–16968, 16972–16975, 16979–16981, 16983–16986, 16991, 16997, 16999–17002 [16 specimens]); Enarotali, east side of Lake Paniai (RMNH 16951, 16970, 16976–16978, 16982, 16987–16990, 16992–16996, 17013).

INTERSPECIFIC RELATIONSHIPS

Satisfactory interpretation of interspecific relationships requires knowledge (or reasonable assumptions) of which of the characters that differ among related species are primitive and which are derived. Species of *Lechriodus* differ in relatively few aspects of morphology (the only usable characters available), and I find little cogent argument for the proposition that any particular character-state is more primitive than another. The principal ways in which the species differ are these: size small (*fletcheri* and *melanopyga*) or large (*aganoposis* and *platyceps*); dorsal skin folds prominent (*aganoposis* and *platyceps*) or reduced (*fletcheri* and *melanopyga*); male nuptial pads coarse (*platyceps*) or fine-grained (remaining three species); hands with (*melanopyga*) or without (other three species) tubercles at bases of fingers; testes unpigmented (*platyceps*) or pigmented (other three species).

Lechriodus platyceps is the only species with two unique characters, coarse nuptial pads and unpigmented testes. This species shares large size and well-developed skin folds with *L. aganoposis*. The two small species, *L. fletcheri* and *L. melanopyga*, differ in the possession by the latter of a tubercle at the base of each finger, a character unique to *melanopyga*. Considered in terms of shared character-states, *platyceps* is most like *aganoposis*, whereas *aganoposis* shares equally with *platyceps* and *fletcheri*, and *melanopyga* is most like *fletcheri*. Therefore, a parsimonious phylogenetic arrangement should place *platyceps* and *aganoposis* together, should reflect the close similarity of *fletcheri* and *melanopyga*, and should separate the two most different species, *platyceps* and *melanopyga*.

I present here (fig. 12) only one of several possible phylogenetic arrangements of the four species. This arrangement assumes that the character-states seen in *L. fletcheri* (see bottom of diagram) are the more primitive and

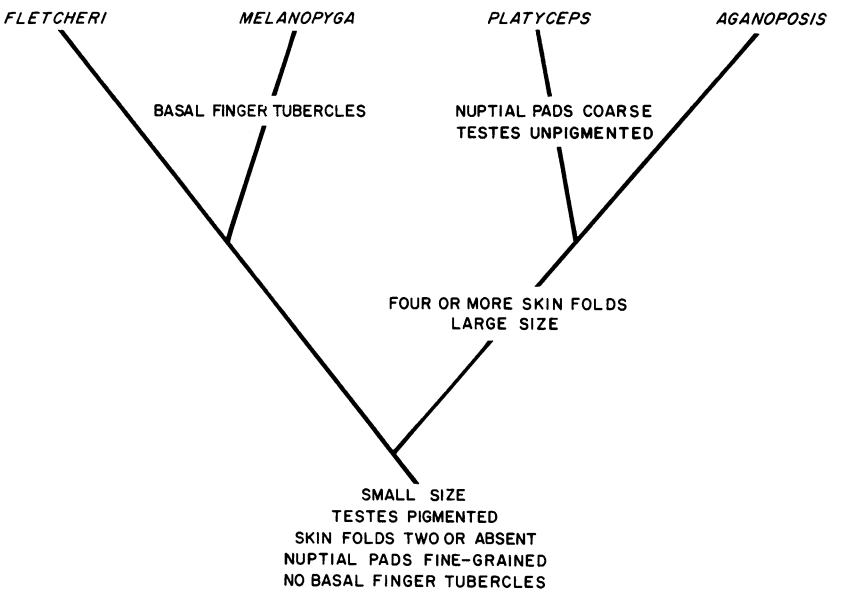

FIG. 12. Suggested phylogenetic arrangement of the species of *Lechriodus*. Characters listed at the base of the diagram all persist in *fletcheri* but differ as indicated in the other species.

that the major dichotomy was between the smaller, relatively smooth-skinned line and the larger frogs with prominent skin folds. This arrangement has some merit in that the presumably primitive species *fletcheri* occurs in the leptodactylid-rich continent of Australia rather than in New Guinea, and the derived species *platyceps* and *aganoposis* occur in the possibly more recent montane habitats of New Guinea.

LEPTODACTYLID FROGS IN NEW GUINEA

The Australian frog fauna is composed more than 60 percent of species of the Leptodactylidae. In marked contrast, there are only five species of this family known to occur in New Guinea in a fauna of more than 160 species. *Lechriodus*, with three species endemic to the New Guinea region and with a wide geographic distribution, is the only genus to have more than a peripheral foothold.

Limnodynastes convexiusculus (Macleay) is a species of northern Australia that has been recorded from only a few localities in southern New Guinea opposite Cape York Peninsula (Katow, Fredrick Hendrik Island, Merauke [Parker, 1940]; Boze [AMNH 82282], Wipim [AMNH 83082, fig. 13]).

Roux (1920) reported *Crinia signifera* Girard from the region of Merauke, and Parker (1940) referred the record to *C. s. signifera*. There are no other published records for *Crinia* in New Guinea, but Fred Parker (personal commun.) has collected specimens in the Western District of Papua. Analysis of mating calls and breeding experiments have shown that Australian *Crinia signifera* of earlier authors is a complex of several sibling

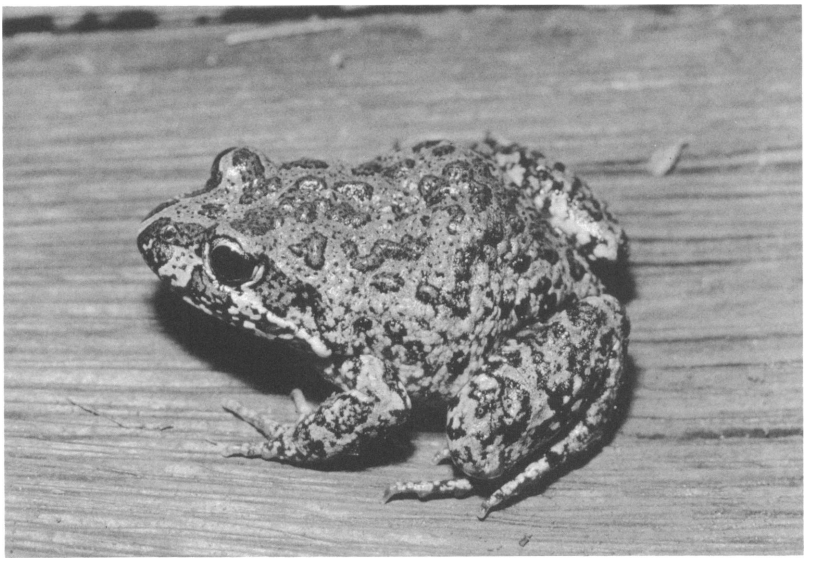

FIG. 13. *Limnodynastes convexiusculus*, AMNH 83082, from Wipim, Western District, Territory of Papua, SV 46 mm.

species scarcely if at all distinguishable by morphology of preserved specimens. Mr. Parker, who has heard the mating calls of the Papuan form and of the *Crinia* on the nearby Cape York Peninsula of Australia, considers that each of these populations represents an undescribed species.

It is evident that leptodactylid frogs have had little success in colonizing New Guinea, although presumably land connections were present during glacial periods when the sea-level was lower. I think that this lack of success reflects the adaptation of most Australian leptodactylids to less mesic conditions than prevail over most of New Guinea. The successful genus, *Lechriodus*, occurs in Australia in rain forest. The two genera with limited distributions appear to be restricted to the part of New Guinea where rainfall is not only less annually than throughout most of the island, but is markedly seasonal (Brookfield and Hart, 1966, maps 5 and 9).

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