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ABSTRACT

The *arfakiana* group of the hylid genus *Litoria* includes three species: *Litoria arfakiana* (Peters and Doria); *Litoria wollastoni* (Boulenger), a new combination for a specific name removed from the synonymy of *arfakiana*; and *Litoria oenicolen*, new species. The first two species cannot be distinguished morphologically (although there is an average size difference), but they differ from each other and from the new species in their mating calls. The new species is highly similar to the other two in most respects of morphology, but is slightly smaller in average size and has one distinct aspect of pigmentation.

Both previously described species evidently are widespread although essentially allopatric in hill and mountain country above the coastal plains of New Guinea, but precise information is scanty because of the need for information on the calls in identifying the species. The new species is known from only one locality, where it is sympatric with *L. wollastoni*. The latter species and *L. arfakiana* have not been captured at the same locality, but occur within 10 miles of each other. The haploid chromosome number of $n = 13$ is known for *wollastoni*.

INTRODUCTION

Tyler's (1968) monograph of Papuan *Litoria* greatly enhanced understanding of the systematics of that frog genus in New Guinea (for the use of *Litoria*, rather than *Hyla*, see Tyler, 1971). Tyler recognized the widespread species *Hyla arfakiana* Peters and Doria. In the course of field work carried out independently of each other, we discovered that *arfakiana* of earlier authors included three partly sympatric species that are virtually indistinguishable in morphology, but differ conspicuously in mating calls, and differ somewhat in habitats. We have pooled our information and here present accounts of the three species that we recognize as comprising the *Litoria arfakiana* group. One we describe as a

new species, for another, we resurrect a name from synonymy, and the third is *Litoria arfakiana*, *sensu stricto*.

We have collected frogs of this group in many parts of Papua New Guinea, and have examined numerous other specimens labeled "*arfakiana*" in museums in Europe and America. Few of the latter can we confidently refer to any one of our three species. It will be apparent that this work is only a first step toward understanding the species complex. Knowledge of all aspects of the biology of the species can only advance slowly so long as the species can be distinguished with certainty by mating calls alone.

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Institution of Oceanography, funded by the National Science Foundation).

MATERIALS AND METHODS

We have examined approximately 400 specimens of the *Litoria arfakiana* group, some 200 of which we collected. Included are the type-specimens of all species. Abbreviations for institutions are: AMNH (the American Museum of Natural History, New York); BMNH (British Museum, Natural History, London); MSNG (Museo Civico di Storia Naturale, Genoa); RMNH (Rijksmuseum van Natuurlijke Historie, Leiden); UPNG (University of Papua New Guinea, Port Moresby).

Abbreviations and methods of making measurements are:

SV, length from snout to vent (upper margin of cloacal opening)

HW, head width measured at midtympanic level

HL, head length, snout tip to posterior margin of the tympanic membrane

IN, internarial distance between dorsal margins of the nostrils

TD, tympanic diameter, measured horizontally

E-N, shortest distance from the anterior edge of the eye opening to posterior edge of the nostril

ED, eye diameter, anterior to posterior corner

TL, external measurement of the tibial section of the limb held with the joints at right angles

Conventional procedures are used to describe body proportions as ratios of the parameters noted above. Measurements are of adult frogs.

LITORIA ARFAKIANA SPECIES GROUP

Tyler (1968, pp. 21-24, 39, 40) defined *Litoria arfakiana* as having the following combination of characters (paraphrased here): medium-size frogs, SV of males approximately 35 to 45 mm., of females 45 to 65 mm.; snout prominent, pointed; canthus rostralis sharp, straight or slightly curved; a conspicuous straight dermal fold from posterior corner of eye running dorsal to tympanic membrane; widely-spaced nostrils, E-N/IN 0.60-0.76; head longer than broad, HL/HW greater than 1.01; fingers with scarcely any webbing; hind limbs moderate to long, TL/SV 0.55-0.71; each heel with a conical tubercle, and tubercles on eyelids.

Our specimens (of all three species) conform essentially to this definition, with the exception of slightly greater size range of adult males (31-47 mm. SV), lower E-N/IN ratio (to 0.47, see table 1), and occasionally wider heads (to 0.95). Thus, we do not repeat some of the basic descriptive material in the individual species accounts that follow.

Frogs of this species group are more widely distributed in New Guinea than might be inferred from an examination of our distribution maps (figs. 2 and 4). Because individuals can be positively identified only if the mating call is known, the many references in the literature to localities for "*arfakiana*" are of little use. Similarly, we

have numerous unpublished records from museum specimens examined but these only verify that at least one of the siblings occurs at a given locality. Blank areas on our maps in which *arfakiana*-group frogs occur include the north coast ranges of Papua New Guinea, the D'Entrecasteaux Islands at the eastern end of New Guinea, and the central mountainous region of West Irian.

Litoria arfakiana (Peters and Doria)

Hyla (*Litoria*) *arfakiana* Peters and Doria, 1878, p. 421 (part; type-locality, Hatam, Arfak Mountains, Vogelkop Peninsula, West Irian; lectotype, MSNG 29723A, collected by L. M. D'Albertis in 1872, designated by Capocaccia [1957, p. 213]).

Litoria arfakiana: Tyler, 1971, p. 352 (part).

Diagnosis. A species of the *Litoria arfakiana* species group (see foregoing definition) in which the adult males range from 33.5 to 47.3 mm. SV (mean 40.2 ± 0.74 , $n = 30$), the posterior surfaces of the thighs are blotched or spotted but not uniformly colored, and whose breeding call consists of notes 0.1 sec or less in length pulsed at 104-160 pulses per second (table 2, fig. 8). The largest of 10 female specimens that we refer to *arfakiana* is UPNG 4497, which measures 57.4 mm. SV. Probably literature records of up to 65 mm. refer to this species.

Morphological difference from *Litoria wollastoni* seems to be limited to the slightly larger size of *arfakiana* (males rarely as large as 43 mm. SV in *wollastoni*). *Litoria oenicolen* is both smaller than *arfakiana* (males to 40 mm. SV, females not known) and has uniformly colored thighs. Differences among the species in mating calls are discussed in a separate section.

Color in Life. The dorsum is generally some shade of brown, from pale ochre to dark brown with darker brown irregular spots but with no definite pattern except for an hourglass mark in some individuals. The dorsal surface of the snout is brown in some individuals, green in others. Some individuals are entirely green dorsally. The anterior and posterior surfaces of the thighs are generally dark brown with lighter flecks, although they may be cherry red with minute white spots (specimens from the northern part of the Western District of Papua New Guinea).

TABLE 1
BODY PROPORTIONS IN THREE SPECIES OF *LITORIA*

Species	N	TL/SV		HL/HW		HL/SV	
		Mean \pm σ m	Range	Mean \pm σ m	Range	Mean \pm σ m	Range
<i>L. arfakiana</i>	35 ^a	0.65 \pm 0.007	(0.60 - 0.70)	1.03 \pm 0.007	(0.95 - 1.09)	0.35 \pm 0.003	(0.32 - 0.38)
<i>L. wollastoni</i>	66 ^b	0.66 \pm 0.005	(0.57 - 0.71)	1.04 \pm 0.005	(0.96 - 1.11)	0.35 \pm 0.001	(0.32 - 0.38)
<i>L. oenicolean</i>	16 ^c	0.66 \pm 0.007	(0.60 - 0.70)	1.04 \pm 0.013	(0.97 - 1.13)	0.36 \pm 0.005	(0.31 - 0.38)
		E-N/IN		TD/ED		ED/HL	
		Mean \pm σ m	Range	Mean \pm σ m	Range	Mean \pm σ m	Range
<i>L. arfakiana</i>	35 ^a	0.65 \pm 0.012	(0.53 - 0.73)	0.40 \pm 0.017	(0.26 - 0.64)	0.31 \pm 0.005	(0.26 - 0.34)
<i>L. wollastoni</i>	66 ^b	0.60 \pm 0.006	(0.47 - 0.71)	0.38 \pm 0.007	(0.28 - 0.58)	0.33 \pm 0.004	(0.25 - 0.35)
<i>L. oenicolen</i>	16 ^c	0.60 \pm 0.015	(0.48 - 0.64)	0.42 \pm 0.013	(0.32 - 0.48)	0.29 \pm 0.010	(0.23 - 0.34)

^a30 males, 5 females.

^b65 males, 1 female.

^call males.

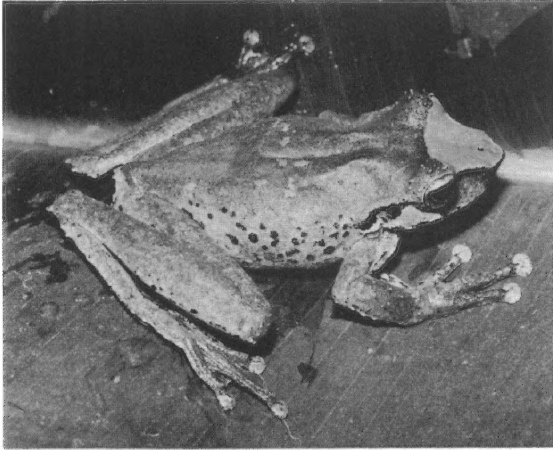


FIG. 1. *Litoria arfakiana*, AMNH 82562, adult female (SV 54 mm.), 4 mi. SE Wau, Morobe District.

The ventral surfaces are grayish white, more or less heavily spotted with brown, especially on the throat. The webbing of the feet and hands is gray.

The individual shown in figure 1 had a light brown dorsum with light green flecks centrally. The small spots on the sides were dark brown, and the light area anteriorly in the groin was light green. The snout area, sharply demarcated on a line between the eyes, was bright green, as was the light area beneath and behind the eye.

Ecological Notes. Specimens collected by Menzies were found in tall *Phragmites* reeds or on shrubs by the banks of fast-running rivers where calling males attracted attention. In contrast, Zweifel captured individuals on shrubby vegetation beneath tree canopy by a small, rocky creek.

Distribution and Specimens Examined. As identification of *Litoria arfakiana* can be verified only by analysis of recorded mating calls, information on distribution is as yet sparse. Such records as are available, however, indicate a wide distribution at moderately high elevations (1250-1710 m., fig. 2).¹

West Irian: Hatam, Arfak Mountains, Vogel-

kop Peninsula (MSNG 29723A [lectotype], 29723B [several paralectotypes], RMNH 12241 [4 paralectotypes]).

Papua New Guinea: Madang District: Kaironk Valley, 1710 m. (UPNG). Eastern Highlands District: Wonenara, 1530 m. (UPNG 1234, 1235). Western Highlands District: Kulkim River near Imegibip, 1240 m. (UPNG 1478-1482); Talil River, Bultem area, 1380 m. (UPNG 4490-4495, 4497, 4498, 4613); Duwin River, Bultem area, 1700 m. (UPNG 4499-4501). Southern Highlands District: Tari, 1500 m. (UPNG 3088). Morobe District: 4 mi. SE Wau, 1400 m. (AMNH 80739-80742, 82558-82562).

Discussion. Our decision to use the name *Litoria arfakiana* for the form with the mating call described is somewhat arbitrary and expedient. Peters and Doria's original description gives no ecological details and no mention of the mating call, nor is it possible, by reading D'Albertis's account of his travels (1880) or Vink's (1965) description of exploration in the Arfak Mountains to guess at what kind of place the frogs were collected. The type-locality "Hatam" does not appear to be a place at all but a group of people, and D'Albertis spent many days in their area ascending from a base camp at approximately 1000 m. to the peak "Hatam Vero" at 1520 m. The type series (which contains numerous specimens) may therefore have been collected at any altitude over 1000 m.

Our assignment of the name *arfakiana* rather than *wollastoni* (see following) is based only on the type series of *arfakiana* probably having been collected at a fairly high altitude and, in our experience, this species typically is found at higher elevations than is *wollastoni*. This admittedly is unsatisfactory, but the problem cannot be resolved without retracing D'Albertis's route through the Arfak Mountains and attempting to collect and tape-record topotypic material, a solution that is presently impossible.

This is, perhaps, the place to comment on the type material of *L. arfakiana*. Peters and Doria (1878) did not designate a holotype, but gave measurements of one specimen from among "una grande serie d'individui" collected in two differ-

¹ Since this paper went to press Menzies tape-recorded and collected *Litoria arfakiana* at Agaun, Milne Bay District, Papua New Guinea, at an elevation of about 1100 m. This extends the distribution of

arfakiana onto the southeastern tail of New Guinea and increased both the known geographic overlap and altitudinal overlap of the species with *L. wollastoni*.

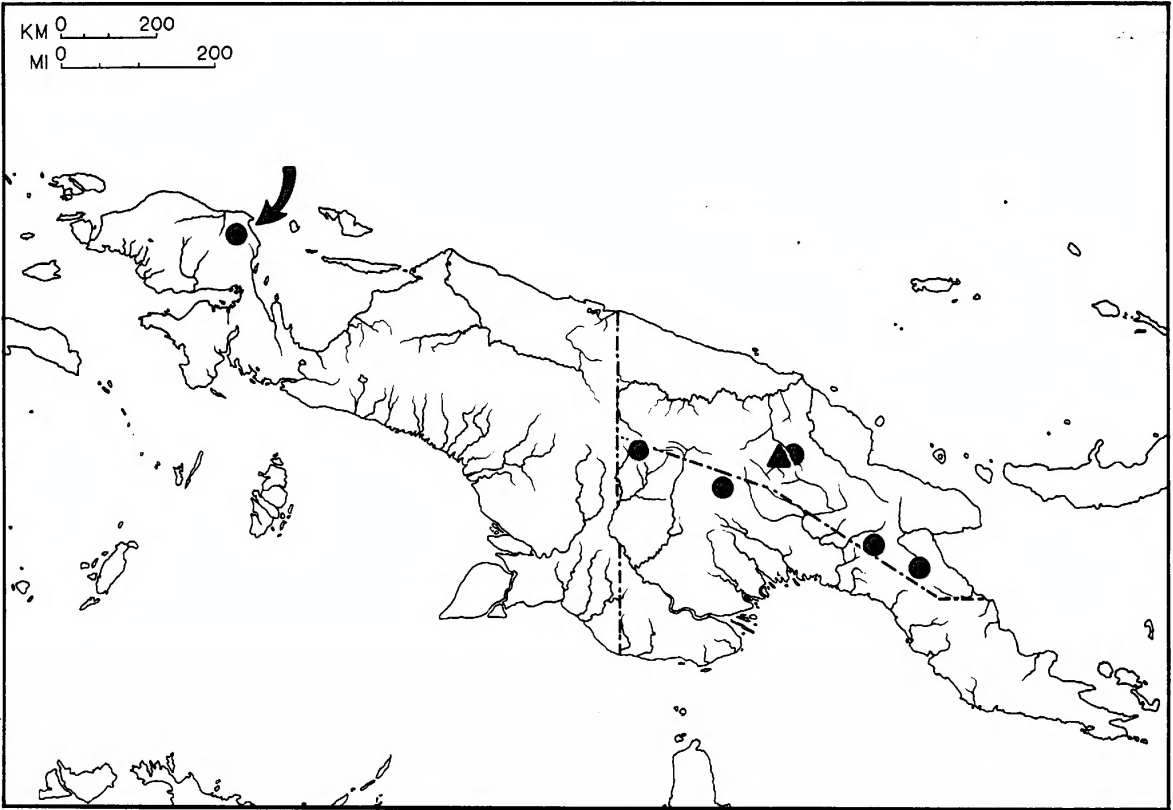


FIG. 2. Distribution of *Litoria arfakiana* (spots) and *L. oenicolen* (triangle) in New Guinea; arrow indicates type-locality of *arfakiana*.

ent years by D'Albertis and Beccari. Capocaccia (1957) designated MSNG 29723A as lectotype and listed nine "paratypes" (paralectotypes). The lectotype, the largest specimen in the series, now measures approximately 56 mm. SV and may well be the same individual for which Peters and Doria gave a total length of 60 mm. Four frogs in the Rijksmuseum, Leiden (RMNH 12241) labeled "Beccari, Hatam, 1900 m., 1875 ex Genoa," although evidently sent to Leiden prior to the publication of *arfakiana*, almost certainly were part of the series studied by Peters and Doria, and so are paralectotypes.

In addition to the lectotype and nine paralectotypes mentioned by Capocaccia (which Zweifel examined in 1968), there is in Genoa a museum jar stuffed with specimens that may represent the remainder of Peters and Doria's "grande serie." The restricted syntype series of *arfakiana* considered by Capocaccia includes representatives of

at least two and probably more species. For example, there are individuals with half-webbed fingers in the series (*arfakiana* shows less webbing), and an adult male (vocal sac and thumb pads present) with such webbing measures only 25 mm. SV, well below the minimum size for adults of either *L. arfakiana* or *L. wollastoni*.

Litoria wollastoni (Boulenger),
new combination

Hyla wollastoni Boulenger, 1914, p. 248 (type-locality, camp 6, Utaskwa [= Octakwa] River, 2500 ft. [760 m.], West Irian; holotype, BMNH 1947.2.23.59 [formerly 1913.11.1.-151], collected in 1913 [inferred from Wollaston, 1916] on the Wollaston Expedition).

Hyla arfakiana: Tyler, 1968, p. 39 (in part).

Litoria arfakiana: Tyler, 1971, p. 355 (in part).

Diagnosis. A species of the *Litoria arfakiana*

species group (see foregoing definition) in which adult males range from 32.3 to 42.7 mm. SV (mean 37.5 ± 0.36 , $n = 65$), the posterior surfaces of the thighs are blotched or spotted but not uniformly colored, and whose breeding call is a buzzing note 0.1 to 0.6 sec in length, pulsed at 105 to 154 pulses per second and typically followed by one or more brief "pips" of sound (table 2, fig. 8). A female from Garaina, where only *wollastoni* is known to occur, measures 49 mm. SV. Female specimens from the Huon Peninsula measure up to 56 mm. SV, but we cannot be certain that this is not a mixed sample of *wollastoni* and *arfakiana*.

Litoria arfakiana and *L. wollastoni* are not distinguishable on the basis of morphology, although the latter has an average smaller size. *Litoria oenicolen* is smaller on the average than *wollastoni* (males to 40 mm. SV) and has the posterior surfaces of the thighs uniformly colored. Differences among the species in mating calls are discussed in a separate section.

Color in Life. This species exhibits great variety in its color pattern. The dorsal ground color may be green or any shade of brown from pale ochre to dark blackish brown. Usually there is a sharp line of demarcation running across the eyelids that separates the relatively light color of the snout region (brown or green) from that of the back. In many individuals this line is the anterior edge of an hourglass-shaped pattern of dark brown that occupies much of the back. In others a definite pattern does not exist, although the interocular line remains (fig. 3). Occasional frogs are nearly all green with scarcely any pattern on the back. Generally the area below the canthus rostralis is brown, and in some frogs a brown streak follows the supratympanic fold. Many brown frogs have a broad streak of light green low on the side of the body that extends back into the groin.

The parts of the thighs concealed at rest are either yellow or brown, spotted with white, tan or green or blotched with yellow but never uniformly colored. The ventral surfaces are grayish white, more or less heavily spotted with brown. The iris is gold, slightly darker below the horizontal pupil.

Chromosome Number. Squash preparations from testes of UPNG 3664 (Baiyer River), 3570,



FIG. 3. *Litoria wollastoni*, AMNH 80735, adult male (SV 37 mm.), Clearwater Creek, N Wau, Morobe District.

and 3571 (Ma-u River) reveal a haploid chromosome number of $n = 13$ as in the majority of other Papuan *Litoria* examined. Duellman (1967, p. 42) reported a haploid number of $n = 13$ for "*H. arfakiana* (AMNH 74666)," which is a specimen collected by Zweifel on the Huon Peninsula. *Litoria wollastoni* was tape-recorded at this locality, so it is possible that the specimen is that species rather than *arfakiana*.

Ecological Notes. All specimens collected by the authors were found in forest close to small, fast-running creeks. Males call from vegetation up to 5 or 6 m. above the ground, but commonly no higher than 2 m. The calling site may be over the water, but may also be 100 m. or more from the stream bank, as at Ma-u River. The considerable altitudinal range (at least from 300 to 1500 m.) reflects the distribution of the preferred habitat—hill forest with fast-running streams.

Distribution and Specimens Examined. If the specimens we group under *L. wollastoni* are indeed the same species (see below), this species has a wide range in New Guinea, from the Octakwa River in West Irian to Mt. Suckling (Ma-u River) on the eastern tail of the island (fig. 4). Almost certainly, the distribution is even broader than is now apparent. Except for the type-locality, all records here are for localities where the characteristic mating call of *wollastoni* was tape-recorded.

West Irian: Octakwa River, 760 m. (BMNH 1947.2.23.59, holotype).

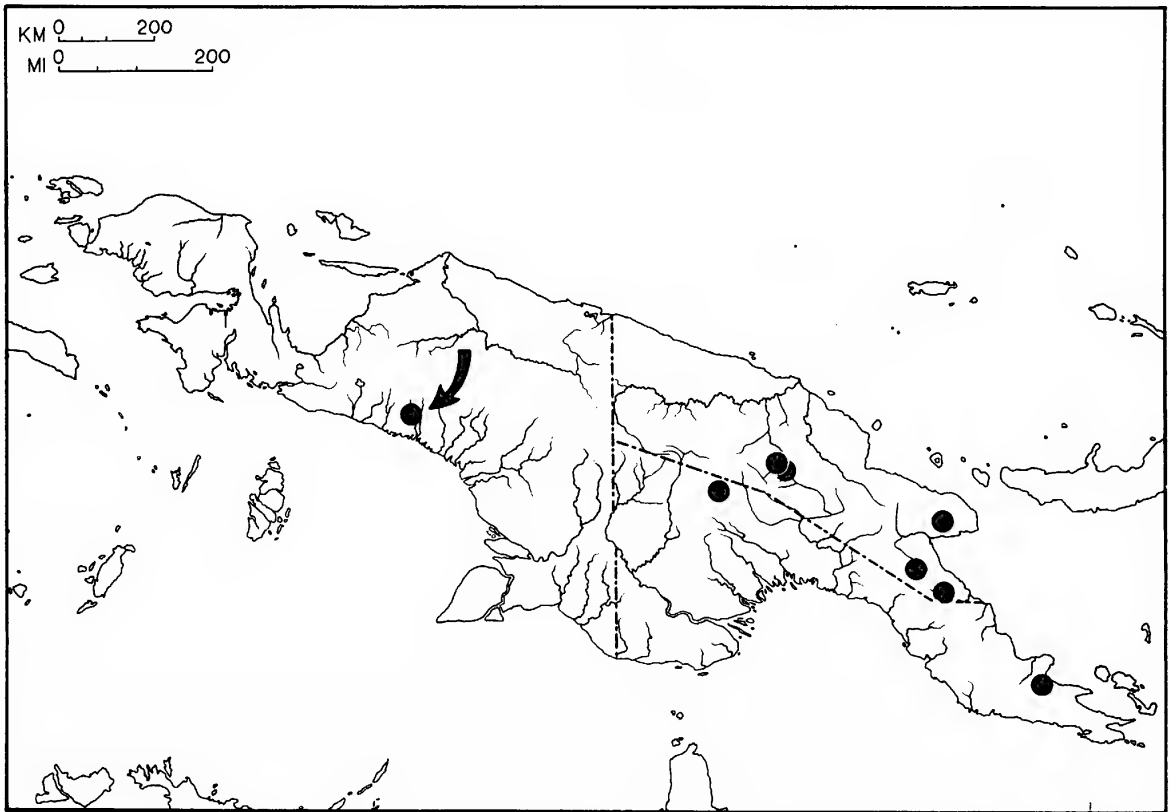


FIG. 4. Distribution of *Litoria wollastoni* in New Guinea; arrow indicates type-locality.

Papua New Guinea: Southern Highlands District: Piwa River, Tari, 1500 m. (UPNG 3070-3087, AMNH 87923). Western Highlands District: Tigi Plantation, 1340 m., 20 mi. N Mt. Hagen (town) (AMNH 80733); Baiyer River Wildlife Sanctuary, 1200 m. (UPNG 3664, 3775, 3776, AMNH 80730-80732). Morobe District: Gang Creek, Mt. Rawlinson, 1340 m. (AMNH 74662-74665, 75849-75897 + 18 untagged); Garaina, 700 m. (AMNH 80743-80766, UPNG 1395-1402); Clearwater Creek, N Wau, 1070 m. (AMNH 80734-80737); Kulolo Creek, N Wau, 1000 m. (AMNH 80738). Northern District: Ma-u River, 300 m., NE face of Mt. Suckling (UPNG 3564-3580, 3772-3774).

Discussion. We are faced with deciding whether this species should be referred to *Litoria arfakiana*, to *L. wollastoni*, or to neither. Boulenger (1914) gave the elevation of the type-locality of *wollastoni* as 2100 feet (640 m.), whereas the records in the British Museum state 2500 feet

(760 m.). Wollaston's (1916) account of the expedition on which the holotype was collected is of no help on this specific point. Of the three species we recognize as comprising the *arfakiana* species group, the one we refer to *wollastoni* has the lowest known lower altitudinal range limit, 300 m. We have not recorded *arfakiana* (in the restricted sense) below 1400 m., and it is likely that the holotype was collected at a relatively high elevation (see discussion under *L. arfakiana*). Therefore, we prefer to use the available name *wollastoni* for the species discussed here rather than coin a new name. The validity of this decision can only be verified in the unlikely event that someone can revisit the type-locality and tape-record the species found there.

We regard the differences in the mating calls of *L. arfakiana* and *L. wollastoni* as prima facie evidence that the two, despite their morphological similarity, are different species. The two forms have been found within a few miles of

each other (as in the vicinity of Wau and near Tari), but not at the same locality. It would be surprising, however, if there were not some overlap in their distribution along streams at an elevation of about 1400 m.

***Litoria oenicolen*, new species**

Holotype. AMNH 87922, an adult male collected beside the Trauna River (a tributary of the Baiyer River) at the Baiyer River Wildlife Sanctuary (141°11' E, 5°29' S), Western Highlands District, Papua New Guinea, elevation 1200 m., on September 19, 1970, by J. Menzies.

Paratypes. Fifteen adult males from the type-locality: UPNG 2068-2073, 2075-2079, collected by J. Menzies; AMNH 80903-80906, collected by R. G. Zweifel, July 7 and 9, 1968.

Diagnosis. A member of the *Litoria arfakiana* species group (see foregoing definition) with the parts of the thighs that are concealed at rest uniform reddish purple (not speckled with lighter or mottled with darker colors), maximum size of adult males (there are no female specimens) about 40 mm. SV (30.8-40.3 mm., mean 33.2±0.67, $n = 15$), and a mating call consisting of a harsh chirp or buzz 0.16 to 0.21 sec in length, pulsed at 82 to 97 pulses per second (table 2, fig. 8).

Litoria oenicolen, so far as present information goes, is distinguishable from its two virtual siblings, *L. arfakiana* and *L. wollastoni*, by the color and pattern of the thighs. The purple of *oenicolen* fades in preservative to a pale, yellowish brown, whereas in the other two species the same area remains darker and clearly patterned. The maximum known male size in *oenicolen* (40 mm. SV) is less than that recorded for *arfakiana* and *wollastoni* (43 and 47 mm.). Mating calls are compared in a following section.

Description of Holotype. Head longer than broad (HL/HW 1.02), slightly more than one-third of body length (HL/SV 0.38); snout pointed and projecting obtusely from above and acute in profile; nostrils prominent, lateral, very widely spaced (E-N/IN 0.54); canthus rostralis sharp, concave; lores sloping, concave; tympanic membrane small but raised and clearly defined (TD/ED 0.31); vomerine teeth absent (but present in paratypes); choanae circular.

Fingers long with fairly prominent discs, outer finger slightly more than one-third webbed; toes, in decreasing order of length, 4>5>3>2>1; web extending almost to the base of the discs on digits 3 and 5, leaving one phalanx free on digit 4; inner metatarsal tubercle well developed, a small outer one present, subarticular tubercles weak.

Dorsal and lateral skin generally warty, warts especially prominent on upper eyelids, snout, forearms, and lower legs; a prominent skin fold from posterior corner of eye, passing over upper edge of tympanic membrane, ending behind insertion of forelimb; no skin folds, lappets, or crenulations on limbs but a rather inconspicuous line of tubercles running down posterior sides of forelimbs and lower hind limbs; a small pointed tubercle on each heel and several conspicuous white warts around cloacal opening; ventral skin granular and, on throat, rather loose due to large vocal sac.

Measurements (in Mm.). SV 31.1; TL 18.6; HL 10.6; HW 10.4; E-N 2.2; IN 4.2; ED 3.5; TD 1.6.

In life, the holotype had dull brown dorsal coloration that merged into the ventral color with a perceptible boundary. The parts of the thighs concealed at rest were plain reddish purple. The ventral surfaces were whitish, speckled with brown. The throat was translucent. The iris was gray-brown. In preservative the colors remain much the same except that the concealed parts of the thighs are now dull yellow.

Variation. Comparative body ratios are set out in table 1.

The following field notes on color in life describe three of the paratypes (AMNH 80903-80905): "In light phase the body is tan with little trace of dark markings, only a slightly darker area between the eyes. The anterior and posterior surfaces of the thighs are deep port wine color, solid, without any other markings. The dorsal surfaces of the fore and hind limbs are colored as is the body. The limbs are not cross-banded or otherwise marked. The side of the body bears small blue to green flecks. The underside of the tibia is colored the same as the anterior and posterior surfaces of the thigh and groin. The ventral surfaces are white with gray flecking on the chest and belly. The throat may be immaculate or marked with the same gray flecking.



FIG. 5. *Litoria oenicolen*, AMNH 80905, adult male (SV 34 mm.), Baiyer River Wildlife Sanctuary, Western Highlands District.

The finger and hand webbing is not distinctively colored. The loreal region is slightly darker than the top of the head, but there is no very contrasting face mask effect. The iris is light gray-brown, the pupil horizontal. In the dark color phase [fig. 5] . . . the ground color is dark brown and the darker brown irregular dorsal blotches become more evident. The spotting on the sides seems to be more green than blue in the dark phase."

Ecological Notes. The type series was collected in a relatively small area on the banks of the Trauna River, a wide, shallow tributary of the Baiyer River. Males were calling from tall reeds or shrubs a few meters from the river. This species is partly sympatric with *L. wollastoni*, several examples of which were collected in the same general area (the two species may be heard on the same tape-recording). However, that species appears to prefer the forested banks of the small creeks running into the Trauna rather than the open banks of that river.

Etymology. The trivial name is a noun derived from the Greek *oenos* (wine) and *colen* (thigh), in reference to the species' principal diagnostic feature of coloration.

Discussion. Both the lectotype of *Litoria arfakiana* and the holotype of *L. wollastoni* have the posterior surface of the thigh speckled, so cannot represent the species diagnosed here. So far as we have been able to determine, *L. oenicolen* is not represented by any name currently in the synonymy of another species of Papuan *Litoria*.

Distribution and Specimens Examined. The holotype and paratypes, listed in a foregoing section, are the only specimens we know of, and all are from the same locality (fig. 2). With such limited information, there is little basis for speculation on the distribution of the species. The general area of the type-locality, the southern drainage of the Sepik River, is poorly known herpetologically, and *Litoria oenicolen* may be widespread though yet undetected elsewhere.

Larval Stages

The species of the *arfakiana* group are among those in which the tadpoles are peculiarly adapted to life in fast-flowing water. This is established on the basis of a larva captured at Garaina. It was in a late stage of metamorphosis when captured but still retained remnants of the large, ventrally-directed, sucker-like mouthparts of the stream-adapted hylids (fig. 6). It completed metamorphosis and was readily identified as *L. wollastoni*, the only species of the group known to occur at Garaina. Although it is certain that the larva of *Litoria wollastoni* is one of the stream-adapted sort, it is not yet possible to identify beyond question the larva of this species or of *L. arfakiana*, and nothing at all is known of *L. oenicolen*.

Collections made at Garaina include two distinct types of stream-adapted tadpoles that differ basically as follows: type A has tooth rows 2/3, the upper beak keratinized in two parts and the lower beak also keratinized in two parts except in the largest tadpoles where the parts fuse to form a single beak; type B has tooth rows 2/4 and more heavily keratinized beaks, with both upper and lower parts as single units even in small tadpoles. We known of three species native to Garaina that presumably have tadpoles of the general sort described: *Litoria wollastoni*, *Nyctimystes cheesmani* Tyler, and *N. semipalmata* Parker.

Tyler (1963) described and illustrated a tadpole from the Wahgi-Sepik Divide with type A mouthparts and attributed it to *Hyla angularis* (a junior synonym of *Litoria angiana* [Boulenger]), but later (1968, p. 42) he reidentified it as *Hyla arfakiana*. Parker (1936) described tadpoles from Kokoda that closely resemble our type B and



FIG. 6. Metamorphosing individual of *Litoria wollastoni* from Garaina, Morobe District, showing delayed resorption of sucker-like mouthparts (left) and same individual a few days later (right).

considered them apparently referable to *Nyctimystes montana* Parker (= *N. cheesmani*). He also described a tadpole and metamorphosing froglet from Kokoda and provisionally referred them to *N. semipalmata*. This tadpole also had tooth rows 2/4, but the four posterior rows were much shorter than the two anterior, in contrast to his "montana" (and our type B), in which all rows are of about the same length.

Probably our tadpoles from Garaina with type A mouthparts are those of *L. wollastoni*, whereas those with type B mouthparts are *N. cheesmani*, but evidence is circumstantial. If Parker's identification of *N. semipalmata* tadpoles is correct, this species is not represented among our tadpoles from Garaina.

Tadpoles with type A mouthparts have been collected at several places where frogs of the *arfakiana* species group occur: Masba Creek (Huon Peninsula) and Garaina, Morobe District; Mt. Dayman, Milne Bay District; Banz, Kaironk River and Mt. Pipening (Wahgi-Sepik Divide), Western Highlands District; 4 km. SW Bernhard Camp, Idenburg River, West Irian. Tyler's specimens from the Wahgi-Sepik Divide came from an elevation of 6500 feet (1980 m.), which is somewhat higher than *L. wollastoni* is known to range. Thus, they may represent *L. arfakiana*. There are no differences among our type A tadpoles that suggest to us a division of the sample into *wollastoni* and *arfakiana*, although almost certainly both are present. It may be that the larvae of

these species are as similar as are the adults. Two presumed *arfakiana*-group larvae are illustrated in figure 7. Some specimens have one to three vertical white bars on the tails (fig. 7, upper), whereas others lack these (7, lower). Both patterns are found in the sample from Garaina, where only *wollastoni* has been found, so this pattern difference probably is not a specific one.

Notable in these tadpoles is the persistence of the sucker-like mouthparts until near the end of metamorphosis (fig. 6), an adaptation permitting the froglet to remain in the turbulent waters until metamorphosis is virtually completed.

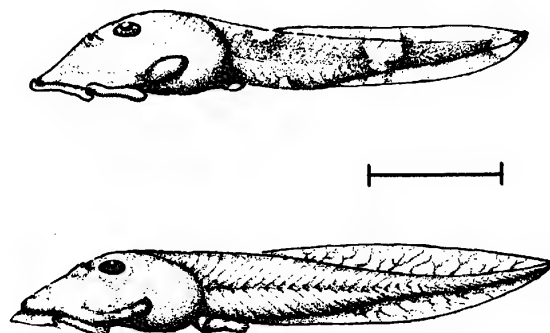


FIG. 7. Tadpoles possibly of *Litoria* in lateral view. Upper, specimen from Kaironk Valley, Madang District, possibly *L. arfakiana* (stage 29 of Gosner, 1960). Lower, specimen from Garaina, Morobe District, possibly *L. wollastoni* (stage 36). Scale line represents 10 mm.

Mating Calls

The calls we discuss are those given by the male frogs from stations in vegetation beside watercourses. We refer to them as "mating calls" on the not-unreasonable assumption that they serve, as has been demonstrated in other hylids, to attract females prepared to breed. That the calls may also serve a territorial function is quite possible but is not pertinent to our purpose of differentiating the species.

The tape-recorded calls were analyzed with the aid of a Kay Elemetrics Company Sona-

Graph, model 6061A. Pulse rates and call lengths were measured on wide-band (300 Hz) spectrograms. Typical calls are displayed in figure 8 and data are tabulated in table 2.

Litoria arfakiana. The call consists of short notes each about 0.05 to 0.10 sec in length, which may occur in series separated by intervals of from 0.3 to 1.5 sec, or may be uttered singly with long intervals between notes. Of the several harmonics emphasized, the second, at about 2300-2600 Hz but with an increase in frequency through the note, is the most prominent in the spectrograms. The pulsed nature of the call is evi-

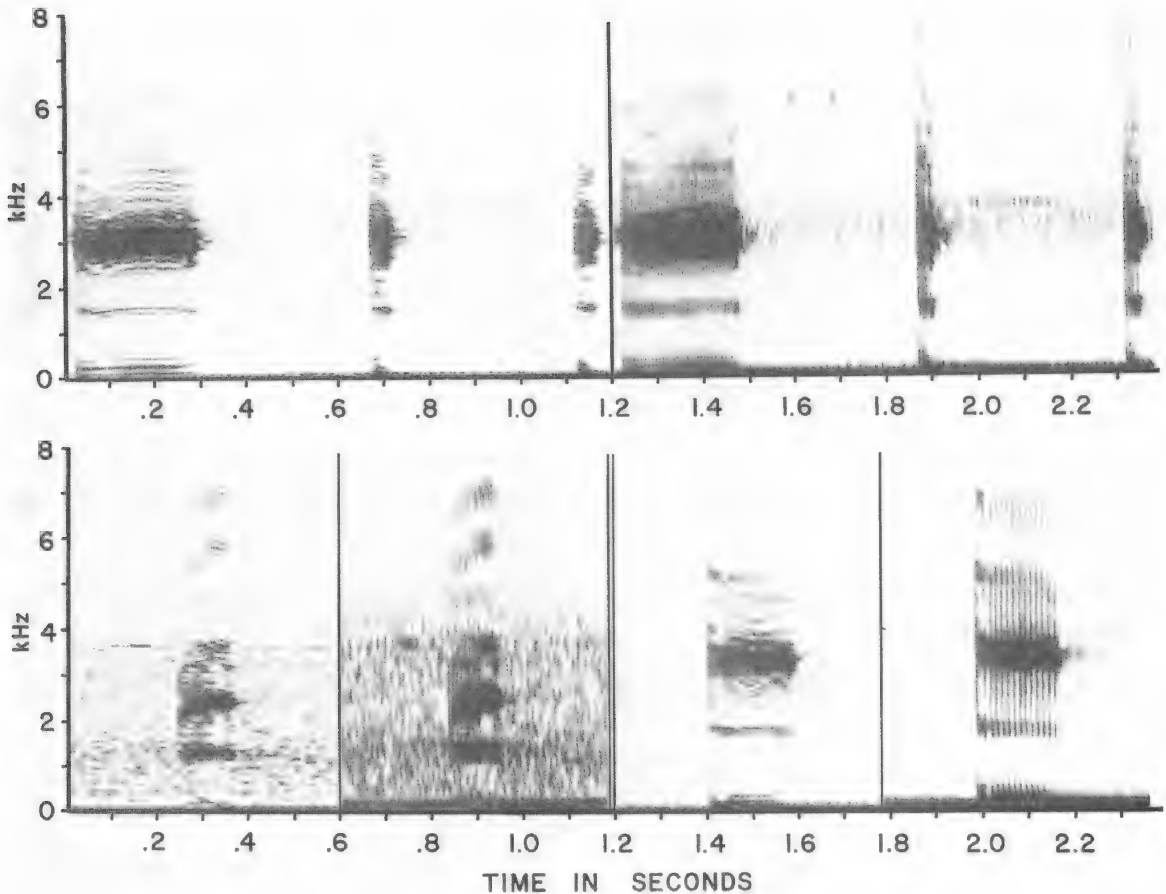


FIG. 8. Audiospectrograms of mating calls of the frogs of the *Litoria arfakiana* species group. Upper pair, call of *L. wollastoni*, AMNH 80738, recorded July 21, 1968, at Kulolo Creek near Wau, Morobe District, air temperature 20.8°C. Lower left pair, call of *L. arfakiana*, AMNH 82558, recorded September 5, 1969, 4 mi. SE Wau, Morobe District, body temperature 18.7°C. Lower right pair, call of *L. oenicolen*, AMNH 80904, recorded July 7, 1968, at Baiyer River Wildlife Sanctuary, air temperature 19.6°C. Each call is displayed twice—on the left graphed with the 45 Hz filter and on the right with the 300 Hz filter.

dent in the wide-band spectrogram; the mean pulse rate ranges from 104 to 160 pulses per second in the small sample available.

Litoria wollastoni. The call of this species is best described as a buzz usually followed by one or more brief pips. The "buzz" part of the call may be as short as 0.1 sec or as long as 0.6 sec. It has an average pulse rate of from 105 to 154 pulses per second in our sample and a strongly dominant frequency band in the region of 2400 to 3500 Hz (evidently varying with temperature and among individuals). The "pips" are short bursts of sound less than 0.05 sec in length. Up to at least six pips may be given, although generally the number is fewer. The first pip comes at about 0.25 to 0.45 sec after the end of the buzz, and additional pips follow at similar intervals. Calling is not regular; an individual may call two or more times in a row or periods of several minutes of silence may pass between calls.

Litoria oenicolen. The call note is a simple harsh chirp or buzz, with an average length of 0.16 to 0.21 sec among three individuals recorded. The dominant frequency is at about 3300 to 3500 Hz, and the pulse rate averages from 82 to 97 pulses per second. Notes are uttered singly. A call given by one frog often induces almost immediate calls from nearby frogs, so that two or three notes may occur almost simultaneously, but without overlap. Then several minutes may elapse before the next call or series of calls.

Calls of the Three Species Compared. The three calls are distinctly different to human hearing. The differences evidently hinge largely on the lengths and pulse rates of the notes. Although our data are too few to permit reliable calculations of the effects of temperature on calls, the temperatures at which we recorded calls are sufficiently similar so that differences noted are not attributable to temperature effects.

The call of *L. wollastoni* is both the longest and the most rapidly pulsed of the three. There is no overlap in length between calls of *wollastoni* and *arfakiana*, and that of the former also differs in the frequent addition of "pips" following the initial "buzz." The calls of *wollastoni* and *oenicolen* are more similar in length, although only one of six *wollastoni* gave calls that averaged within (actually, below) the mean range of *oenicolen*. Again, *oenicolen* lacks the "pips" pro-

duced by *wollastoni*, but it is perhaps more significant that there is no overlap between the two species in pulse rates.

The differences in pulse rate between *wollastoni* and *oenicolen* are paralleled by those between *arfakiana* and *oenicolen*; again, there is no overlap in ranges. There is no overlap in length of calls of the last two species, and the dominant frequencies are more than 1000 Hz apart.

Samples of recorded calls are too small to permit analysis of possible geographic variation, but calls of *wollastoni* from such widely separated localities as Tari in the Eastern Highlands, the Huon Peninsula, and the Ma-u River on the eastern tail of New Guinea are closely similar.

Interspecific Relationships

We presume that the three species dealt with in the present paper are clearly closely related because of their extreme morphological similarity. Their high degree of similarity makes it virtually impossible to infer which of the three species may be the more primitive or where the closest interspecific relationships lie. In that *L. arfakiana* and *L. wollastoni* are indistinguishable morphologically (except for average size) and *L. oenicolen* has one character—thigh color pattern—that distinguishes it, the first two may be the more closely related, although this is meager evidence. The mating calls of *arfakiana* and of *wollastoni* are highly similar in pulse rate, although they differ in length, whereas the call of *oenicolen* has a slower pulse rate and is intermediate in length. Thus, if pulse rate is a valid criterion of degree of relationship, *arfakiana* and *wollastoni* are the more closely related, but if length of call is emphasized, then these two are farthest apart.

Certain characteristics of the *arfakiana*-group are shared with other Papuan *Litoria* which may together be described as the "stream-breeding *Litoria*" (they have been referred to as "montane" *Litoria*, but it is reproductive behavior rather than elevation of habitat that distinguishes them and there are some mountain-dwelling *Litoria* that are not stream-breeders). Characteristics of these species are broadly spaced nostrils (E-N/IN often 0.80 or less), unwebbed or sparsely webbed fingers, a warty dorsum, especially the upper eyelids, a variable coloration that

TABLE 2
CHARACTERISTICS OF CALLS OF THREE SPECIES OF *LITORIA*

Species and Locality	Specimen Number	Temperature °C. ^a	Number of Notes Analyzed	Mean Note Length (in Seconds)	Mean Pulses per Second	Dominant Frequency Hz ^b
<i>L. arfakiana</i>						
Tari	UPNG 3088	17.0	4	0.09	104	2500
Vic. Wau	AMNH 82558	18.7 (BT)	7	0.07	132	2400
Kaironk Valley	No specimen	19.0	7	0.05	160	2700
<i>L. oenicolen</i>						
Trauna River	AMNH 80903	19.6	10	0.21	82	3200
Trauna River	AMNH 80904	19.6	3	0.16	84	3500
Trauna River	AMNH 87922 ^c	23.0	9	0.20	97	3300
<i>L. wollastoni</i>						
Gang Creek, Huon Peninsula	No specimen	16.0	10	0.49	105	2800
Tigi Plantation	AMNH 80733	16.9	9	0.33	133	3400
Vic. Wau	AMNH 80738	20.8	10	0.27	128	3400
Tari	AMNH 87923	21.0	2	0.53	120	3000
Garaina	AMNH 80743	22.4	9	0.27	154	3200
Ma-u River	UPNG 3564	23.0	5	0.13	149	3200

^aAir temperature except where body temperature (BT) is indicated.

^bTaken at midpoint of note.

^cHolotype.

is basically some shade of brown with an hour-glass mark, and a white, gray- or brown-spotted ventrum.

Some and probably all of these frogs lay unpigmented eggs with a glutinous jelly that adheres to stones or vegetation in the water. The larvae have extremely wide suctorial mouths by which they cling to stones and so resist being swept away by the current.

The members of the *arfakiana*-group differ from all other stream-breeders by having more acutely projecting snouts and small fleshy spikes on their heels. There is no positive reason to associate this group with any other particular group among the stream-breeders. Nor is there any positive reason to associate any of the stream-breeders with any one of the pond-breeders, even among those living at high altitudes, but it is reasonable to suppose that the specialized stream-breeders are derived from the other group.

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