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## New Species of Microhylid Frogs from the Owen Stanley Mountains of Papua New Guinea and Resurrection of the Genus *Aphantophryne*

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### ABSTRACT

Three new species of genyophrynine frogs are described from southeastern New Guinea: *Aphantophryne minuta*, *A. sabini*, and *Cophixalus verecundus*. Two of these, one possibly the smallest species of microhylid, are assigned to the resurrected genus *Aphantophryne* Fry, which among

other features is characterized by the possession of seven rather than eight presacral vertebrae. The new species of *Cophixalus* is without obvious close relationships to other New Guinean or Australian species of the genus.

### INTRODUCTION

The Owen Stanley Mountains form the backbone of southeastern New Guinea, with peaks rising to 4000 m within 80 km of the sea. The variety of habitats implied by such a range in elevation in a tropical region is realized in seasonal, relatively arid foothills with savanna vegetation, rainforested montane slopes, and grassland above tree line. Some of the earliest publications on the herpetology of Papua New Guinea dealt with collections from this region (e.g., Boulenger, 1897, 1898), and revealed a diverse fauna,

but like most of New Guinea, the Owen Stanley Mountains are inadequately known from a herpetological standpoint. This is true in particular of secretive, cryptic species of frogs such as those that are the subject of this paper.

In August 1987 the authors and Mr. Laurence Penny spent 5 days at the Myola Guest House located at 2080 m elevation on the northern drainage of the mountains on a line between Port Moresby and Popondetta. Under conditions that evidently were somewhat

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dryer than usual, we collected only nine species of frogs, but these included the three new species described here. Description of the new forms has necessitated a reconsideration of the status of the genus *Aphantophryne* Fry 1917, currently referred to the synonymy of *Cophixalus*.

#### METHODS

Measurements used in generating ratios and calculating regressions are: body length, from snout to vent (SV); length of tibia, from heel to outer side of flexed knee (TL); length of foot, distance between proximal edge of inner metatarsal elevation and tip of fourth toe (FT); length of hand, distance between proximal edge of inner metacarpal elevation and tip of third finger (HD); distance from anterior edge (corner) of eye opening to center of naris (EN); internarial distance, between centers of external nares (IN); head width, at jaw articulation (HW); diameter of orbit, measured between anterior and posterior edges of eye opening (EY). The tips of the digits were measured at a right angle to the digital axis with the tip of the digit held against a flat surface.

Recordings of frog calls were made with a Sony TC-150 cassette recorder modified to permit manual gain control and using a TEAC ME-120 Electrec condenser microphone. Test tones from a TEAC TO-122A test tone oscillator provided frequency control. Audio-spectrographic analyses were done with a Kay Elemetrics Corporation Digital Sona-Graph model no. 7800.

#### ACKNOWLEDGMENTS

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field, Mr. Peter Lambley for the loan of UPNG specimens, and Mr. James Menzies for numerous courtesies, not the least of which was suggesting that we include Myola in our itinerary. Technical assistance of Norma Feinberg (radiographs), Carol Townsend (clearing and staining), and Joan Whelan (SEM photographs) is gratefully acknowledged. Frances W. Zweifel contributed her artistic talents to figures 2-5 and 12. Drs. Robert F. Inger and Linda Trueb read a late draft of the manuscript. Their suggestions clarify and improve the presentation, and we appreciate their efforts. Mr. Karol M. Kiso-kau, Secretary, Papua New Guinea Department of Environment and Conservation, kindly provided export permits for our collection. Fieldwork in Papua New Guinea was made possible by a grant from the Sabin Conservation Fund.

#### The Genus *Aphantophryne*

The genus *Aphantophryne* has had an unsettled taxonomic history. Fry (1917) described the new genus and species *A. pansa* based on specimens from an elevation of 3700 m on Mt. Scratchley in the Owen Stanley Range. When he revised the Microhylidae, Parker (1934) lacked specimens of *A. pansa* and relied on Fry's thorough description. The morphological features Parker used to distinguish *Aphantophryne* from other spheno-phrynine (= genyophrynine) genera were the absence of clavicles and procoracoids and presence of only a vestigial sternum. The last character in particular differentiated *Aphantophryne* from *Cophixalus*. Loveridge (1948) confused a species of asterophryine microhylid with *A. pansa* and synonymized *Aphantophryne* with *Asterophrys* to accommodate this confusion.

With new material available, Zweifel (1956) demonstrated that *A. pansa* did, in fact, possess a moderately well-developed sternum, and thus did not differ from *Cophixalus* in the ways critical to Parker's diagnosis. Zweifel noted that *pansa* lacked digital disks (a character brought out in Fry's original description), and also differed from *Cophixalus* in its more squat, toadlike body form, but he thought it inadvisable to reestablish a monotypic genus on these grounds alone. Hence,

he referred *Aphantophryne* to the synonymy of *Cophixalus*.

The discovery of a new, montane species that was referable to *Cophixalus* but which lacked expanded digital tips led Zweifel and Allison (1982) to reexamine the status of *Aphantophryne*. The new species appeared to be more closely related to *Cophixalus* other than *pansa*, and these authors found no new justification for segregating *pansa* in a resurrected, monotypic genus.

Our collections made in 1987 require reopening the question of the status of *Aphantophryne*. Not only did we find two new species that resemble *pansa* in external morphology, but a trenchant skeletal character previously overlooked in *pansa* proved to be common to the three species. With evidence now in hand of a monophyletic group of three species, we propose to resurrect the genus *Aphantophryne* and to describe the new species.

### *Aphantophryne* Fry, 1917

*Aphantophryne* Fry, 1917: 172 (type species by designation, *A. pansa* Fry). van Kampen, 1923. Parker, 1934.

*Asterophrys*: Loveridge, 1948: 417 (*Aphantophryne* considered a junior synonym of *Asterophrys*).

*Cophixalus*: Zweifel, 1956: 41 (*Aphantophryne* considered a synonym of *Cophixalus*). Zweifel and Allison, 1982.

**DIAGNOSIS:** A genus of genyophrynine (Burton, 1986; Zweifel, 1972, as Sphenophryinae) microhylid frogs that differs from other genera of Genyophryinae in having seven rather than eight presacral vertebrae. Additional distinctive characteristics include short hind legs, digits with rounded tips lacking flattening or terminal grooves (fig. 10; see also Green and Simon, 1986: fig. 2), and absence of clavicles and procoracoid cartilages. Species of *Cophixalus*, a genus which also lacks the clavicles and procoracoids, show a wide range in leg length and expansion of digital tips, but very few have hind legs relatively as short as those of *Aphantophryne* (maximum TL/SV < 0.37), and even those with the least development of digital disks show some flattening and traces of terminal grooves. Members of the genus *Copiula* also

lack clavicles and procoracoids but possess digital disks (Menzies and Tyler, 1977).

**CONTENT:** *Aphantophryne pansa* Fry and two new species described herein, *A. sabini* and *A. minuta*.

**DISTRIBUTION:** Mountains of eastern Papua New Guinea, from Mt. Amungwiwa southwest of Wau, Morobe Province, south-eastward at least to Myola Guest House, Northern Province, northeast of Port Moresby (fig. 1).

**DISCUSSION:** The presence of seven presacral vertebrae noted in *Aphantophryne* is decidedly unusual among genyophrynine microhylids and appears to be unique to this genus as a typical condition. Combining counts made on cleared-and-stained specimens and on radiographs, we find seven vertebrae in all of 11 *A. pansa*, 17 *A. sabini*, and 1 *A. minuta*.

We examined cleared-and-stained specimens and radiographs of 25 species (some undescribed) of Australian and New Guinean *Cophixalus*, 115 specimens in all, and found only seven deviations from the normal count of eight presacrals. The only specimen of *C. crepitans* Zweifel has vertebrae 1 and 2 fused (diapophyses present on the first vertebra) followed by five free presacrals, giving effectively six presacrals.<sup>3</sup> One of 45 *C. ornatus* (Fry) specimens has vertebrae 1 and 2 fused (diapophyses present) and six additional presacrals. Another *ornatus* has asymmetrical sacral diapophyses, that of the ninth vertebra expanded on the left, and the tenth on the right. A specimen of *C. tagulensis* Zweifel has seven presacrals. Apparently this resulted from an abnormal fusion of vertebrae five and six, as the fifth vertebra bears paired diapophyses on one side. One of eight *C. verrucosus* (Boulenger) has seven normal-looking presacrals, the atlas without diapophyses. One of six *C. darlingtoni* has vertebrae 1 and 2 fused (diapophyses present). One of five specimens of a local sample of the *variegatus* species group has the second and third vertebrae fused. Five other specimens of "*variegatus*" have the normal complement of eight presacrals.

<sup>3</sup> Walker (1973: fig. 1) illustrated a similar vertebral column for a South American microhylid, *Syncope antenori*.

In *Aphantophryne* there is no sign of fusion to indicate the source of the reduction; the atlas is normal, lacking diapophyses. In contrast, most of the reductions in *Cophixalus* are obvious fusions occurring as variants (*crepitans* and *tagulensis* are unique specimens). Only in the case of *C. verrucosus* does the one variant individual (among eight from the same population) duplicate the condition in *Aphantophryne*, with seven normal-looking presacral vertebrae.

Two new species of *Aphantophryne* are described here. For an account of the variation and distribution of *A. pansa*, see Zweifel and Allison (1982). In addition, we take advantage of this opportunity to describe a new *Cophixalus* also found at the same locality.

***Aphantophryne sabini*, new species**

Figure 2

**HOLOTYPE:** AMNH 130298 (field no. RZ 13357), collected by Fred Parker, Richard G. Zweifel, and Laurence T. Penny on August 8, 1987, at Myola Guest House, 2080 m, 7 km south, 6 km west of Mt. Bellamy, Northern Province, Papua New Guinea.

**PARATYPES:** AMNH 130299–130318, 130324–130331, 130335–130339, 130341, 130343–130350, 130354, 130358–130362, 130365–130367, AMS R130065, R130066, BPBM 11562, 11563, CAS 170535, 170536, FMNH 235382, 235383, KU 211057, 211058, MCZ 111142, 111143, SAMA R33505, R33506, UPNG 8151–8154, same collectors and locality as holotype, August 8–9, 1987; AMNH 130368–130372, collected by Fred Parker, August 11, 1987, at "Fern Valley," 2600 m, about 2.0 km east, 2.3 km north of Myola Guest House, also in Northern Province.

**ETYMOLOGY:** This species is named for Mr. Andrew E. Sabin in recognition of his interest in and support of herpetological research and conservation.

**DIAGNOSIS:** *Aphantophryne sabini* is smaller than *pansa* (maximum SV 24.1 vs.

31.6 mm) with nostrils slightly more widely spaced and a much more slowly pulsed advertisement call. Probably *sabini* is diploid, in contrast to the tetraploid *pansa* (see below). No morphological feature will reliably separate these sibling species; size is of limited help, as *pansa* females mature at only a slightly larger size than female *sabini*. For diagnostic comparison with *A. minuta*, see the following description of that species.

**DESCRIPTION OF HOLOTYPE:** Adult female (ova 1.4 mm in diameter, oviducts large) with the following measurements and proportions: SV 22.6, HW 8.4, TL 6.9, EY 2.3, EN 1.45, IN 1.7, HD 4.9, FT 8.0; HW/SV 0.372, TL/SV 0.305, EY/SV 0.102, EN/SV 0.064, IN/SV 0.075, EN/IN 0.853, HD/SV 0.217, FT/SV 0.354.

Head notably narrower than rotund body; snout rounded seen from above, high, slightly rounded, scarcely projecting seen in lateral view; nostrils visible from above, much closer to tip of snout than to eyes; loreal region sloping outward to lip, slightly concave, not steep; canthus rostralis rounded, not well marked; eyes moderately small, corneal outline not or scarcely visible from beneath, upper eyelid slightly narrower than interorbital space; tympanic outline obscure. Relative lengths of fingers  $3 > 4 > 2 > 1$ , first well developed, more than one-half length of second; tips rounded, without dilation or terminal groove; no discrete subarticular or metacarpal elevations (fig. 3B). Hind legs short, toes unwebbed, relative lengths  $4 > 3 > 5 > 2 > 1$ ; tips rounded, not disklike or terminally grooved (fig. 10); subarticular elevations scarcely evident, inner metatarsal elevation low, rounded, elongate. Skin with numerous small, low, smooth elevations above and below, best developed on chin, underside of thigh, and upper surface of hind legs.

A pale, dark-edged vertebral stripe passes from the tip of the snout to the cloacal opening, just anterior to which it intersects a similar stripe that runs along the upper surface of the thigh and the back of the lower leg to the heel. The pale gray-brown ground color lateral to the vertebral stripe is broken by an irregular brown band, below which the flanks are spotted with dark brown. A dark line runs from the tip of the snout through the eye and

<sup>4</sup> Myola is plotted on the Efogi Quadrangle, Papua New Guinea 1:100,000 topographic map series sheet 8479, in Central Province at approximately 9°8'44"S, 147°43'44"E. The Myola Guest House where we collected is in Northern Province, 5.0 km E, 0.5 km S of the mapped position of the village of Myola.

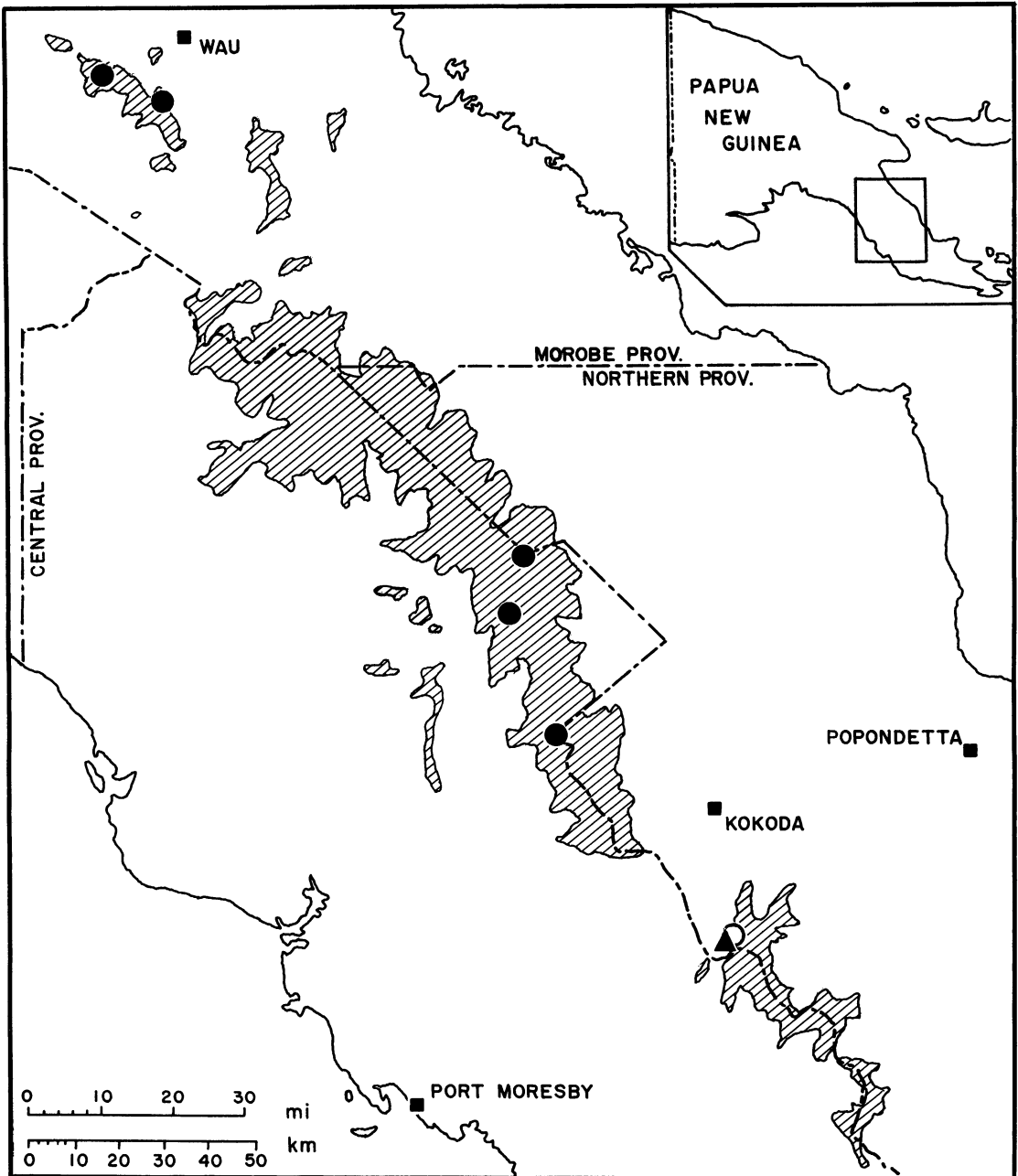


Fig. 1. Portion of southeastern Papua New Guinea, showing localities for *Aphantophryne pansa* (●), *A. sabini* (▲, ○), *A. minuta* (○), and *Cophixalus verecundus* (▲). The shading indicates areas above an elevation of 2400 m.

stops anterior to the arm insertion. The area below the line is pale yellowish brown and almost unmarked. The front legs are pale above with a few dark marks and are unmarked below, the palms similarly pale and

unmarked. The lateral ground color continues into the groin and on the anterior surface of the thigh, where there are a few dark spots. The dorsal surface of the thigh is dark brown, its posterior surface similar and spotted. The

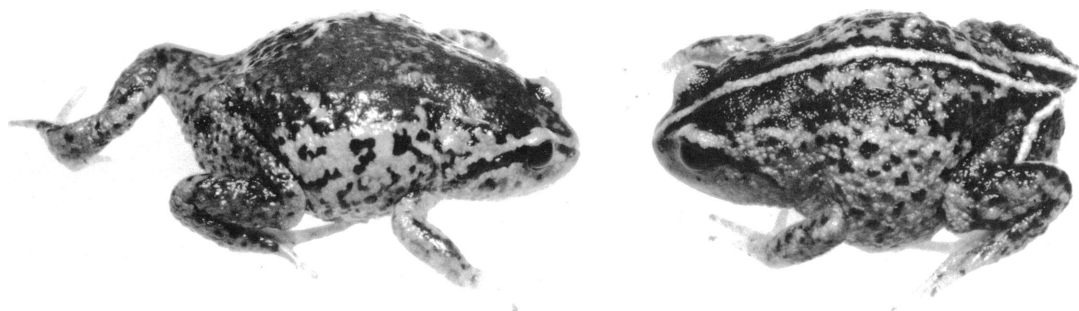


Fig. 2. *Aphantophryne sabini*, new species. Holotype AMNH 130298 right, paratype AMNH 130299 left; both approximately  $2.3\times$  life size.

ventral surfaces are pale and mostly unmarked. There is an ill-defined, pale, mid-ventral stripe beginning at the tip of the chin and fading on the abdomen. A similar inter-brachial line runs out to the underside of the upper arm. Both lines are incompletely edged with black. The abdomen bears clumps of white pigment cells between which the underlying musculature is dimly visible. The hind legs and feet are unpigmented beneath.

In life, the holotype's dorsal ground color was orange-tan, brightest on the hands, feet, and face. The vertebral stripe was white, its borders black, and the other dorsal markings moderate to dark brown.

**VARIATION IN THE TYPE SERIES:** The largest specimen is a female 24.1 mm SV long. Fe-

males in the 17–18 mm range appear to be maturing, and all 19 mm or larger are mature. The largest in the small sample of five males is 16.6 mm SV. Variation in proportions is set forth in tables 1 and 2; regression statistics are in table 3.

As are species of frogs in several families, *Aphantophryne sabini* is polymorphic for the pale vertebral stripe: 13 specimens in our series have the stripe, 59 lack it. Apart from the stripe, the dorsal pattern is basically the same in all specimens (fig. 2). The principal variations involve the dorsal markings being darker or lighter, uniform or splotchy, or with a tendency to darker dorsolateral bands. One dark specimen has lumbar ocelli distinctly outlined, whereas these markings are absent

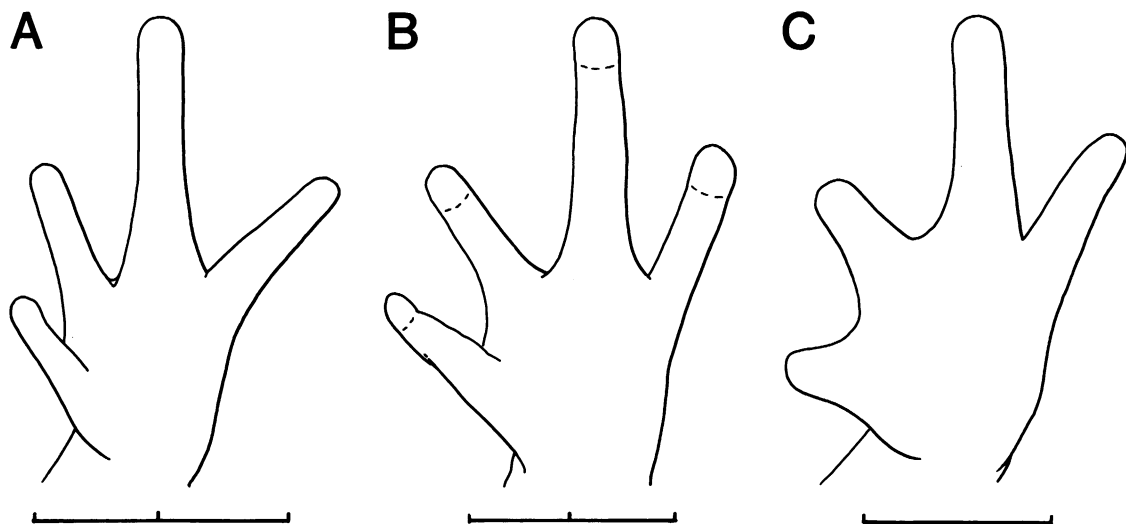


Fig. 3. Left hands of three species in palmar view. A. *Cophixalus verecundus*. B. *Aphantophryne sabini*. C. *A. minuta*. Scale bars calibrated in mm.

TABLE 1  
Body Proportions in Five Samples of the Genera *Aphantophryne* and *Cophixalus*

Sample	N	TL/SV		HW/SV	
		Mean $\pm \sigma_m$	Range	Mean $\pm \sigma_m$	Range
<i>A. pansa</i> <sup>a</sup>	13	0.305 $\pm$ 0.002	(0.292–0.322)	0.396 $\pm$ 0.003	(0.374–0.416)
<i>A. pansa</i> <sup>b</sup>	17	0.309 $\pm$ 0.003	(0.289–0.330)	0.396 $\pm$ 0.004	(0.366–0.427)
<i>A. sabini</i>	24	0.314 $\pm$ 0.003	(0.283–0.345)	0.384 $\pm$ 0.004	(0.352–0.422)
<i>A. minuta</i>	1	0.364 —	—	0.424 —	—
<i>C. verecundus</i>	8	0.374 $\pm$ 0.003	(0.363–0.385)	0.401 $\pm$ 0.005	(0.384–0.416)

Sample	N	HD/SV		FT/SV	
		Mean $\pm \sigma_m$	Range	Mean $\pm \sigma_m$	Range
<i>A. pansa</i> <sup>a</sup>	13	— —	—	— —	—
<i>A. pansa</i> <sup>b</sup>	17	0.226 $\pm$ 0.004	(0.209–0.260)	0.356 $\pm$ 0.005	(0.328–0.392)
<i>A. sabini</i>	24	0.226 $\pm$ 0.002	(0.206–0.248)	0.354 $\pm$ 0.005	(0.312–0.402)
<i>A. minuta</i>	1	0.216 —	—	0.377 —	—
<i>C. verecundus</i>	8	0.224 $\pm$ 0.003	(0.217–0.237)	0.404 $\pm$ 0.006	(0.381–0.428)

<sup>a</sup> Morobe Province.  
<sup>b</sup> Owen Stanley Mountains.

in most or dimly indicated in a few. The ventral surfaces are almost always pale and without dark pigment except for some areas associated with the interbrachial and midventral light lines of striped specimens. A unique striped frog has much dark pigment on all the ventral surfaces, soles and palms included, so that the white pigment cell clumps stand out conspicuously. An occasional specimen has a few random dark spots on the chin, chest, and abdomen.

Owing to color differences, these frogs appear more variable in life than as preserved specimens. The dark central dorsal area varies from reddish brown to dark gray-brown, and the sides range from yellowish tan through duller tan to orange. The chin is orange to yellow, the abdomen a paler shade of orange.

OSTEOLOGY: This description is based on two specimens cleared-and-stained for bone and cartilage, with additional data taken from X-ray photographs of 15 specimens.

TABLE 2  
Body Proportions in Five Samples of the Genera *Aphantophryne* and *Cophixalus*

Sample	N	EY/SV		EN/IN	
		Mean $\pm \sigma_m$	Range	Mean $\pm \sigma_m$	Range
<i>A. pansa</i> <sup>a</sup>	13	0.105 $\pm$ 0.001	(0.098–0.116)	0.818 $\pm$ 0.012	(0.761–0.900)
<i>A. pansa</i> <sup>b</sup>	17	0.102 $\pm$ 0.002	(0.091–0.115)	0.820 $\pm$ 0.020	(0.694–1.000)
<i>A. sabini</i>	24	0.106 $\pm$ 0.002	(0.089–0.118)	0.872 $\pm$ 0.013	(0.735–1.000)
<i>A. minuta</i>	1	0.136 —	—	0.708 —	—
<i>C. verecundus</i>	8	0.116 $\pm$ 0.002	(0.106–0.119)	0.927 $\pm$ 0.018	(0.839–1.000)

Sample	N	EN/SV		IN/SV	
		Mean $\pm \sigma_m$	Range	Mean $\pm \sigma_m$	Range
<i>A. pansa</i> <sup>a</sup>	13	0.067 $\pm$ 0.001	(0.060–0.075)	0.082 $\pm$ 0.001	(0.073–0.090)
<i>A. pansa</i> <sup>b</sup>	17	0.066 $\pm$ 0.001	(0.055–0.072)	0.080 $\pm$ 0.001	(0.072–0.090)
<i>A. sabini</i>	24	0.064 $\pm$ 0.001	(0.057–0.073)	0.074 $\pm$ 0.001	(0.066–0.084)
<i>A. minuta</i>	1	0.072 —	—	0.102 —	—
<i>C. verecundus</i>	8	0.088 $\pm$ 0.001	(0.083–0.094)	0.095 $\pm$ 0.001	(0.090–0.099)

<sup>a</sup> Morobe Province.  
<sup>b</sup> Owen Stanley Mountains.

TABLE 3  
Regression Statistics for Three Samples of *Aphantophryne* and *Cophixalus*

Sample	TL/SV				HW/SV				HD/SV				FT/SV			
	a	b	r <sup>2</sup>	N	a	b	r <sup>2</sup>	N	a	b	r <sup>2</sup>	N	a	b	r <sup>2</sup>	N
<i>A. pansa</i> <sup>a</sup>	.574	.806	.967	30	.469	.949	.961	30	.347	.865	.902	27	.547	.865	.915	27
<i>A. sabini</i>	.647	.763	.917	47	.520	.902	.941	47	.261	.955	.923	47	.534	.864	.900	47
<i>C. verecundus</i>	.679	.790	.969	8	.483	.934	.864	8	.609	.647	.935	8	1.181	.623	.832	8

Sample	EY/SV				EN/SV				IN/SV			
	a	b	r <sup>2</sup>	N	a	b	r <sup>2</sup>	N	a	b	r <sup>2</sup>	N
<i>A. pansa</i> <sup>a</sup>	.351	.609	.787	30	.091	.896	.867	30	.130	.851	.928	30
<i>A. sabini</i>	.257	.709	.827	47	.085	.906	.904	47	.194	.686	.836	47
<i>C. verecundus</i>	.153	.902	.729	8	.080	1.034	.791	8	.143	.855	.791	8

<sup>a</sup> Morobe Province and Owen Stanley Mountains, Central and Northern provinces.

Skull (fig. 4) well ossified; nasals large and in contact; frontoparietals expanded posteriorly, fused prootic and exoccipital well ossified, with extensive fusion with frontoparietals; squamosal zygomatic ramus long and curved, otic ramus with a medially expanded otic plate; strong maxillary-quadratojugal contact, maxillae eleutherognathine, barely overlapping premaxillae, pars palatina of premaxilla deeply indented, pars dorsalis vertical, arising abruptly from premaxilla; tiny, vestigial teeth visible under high magnification on maxillae and premaxillae; vomeropalatine well developed, almost enclosing internal naris, transverse arm reaching shelf of maxilla. Hyoid with pointed, elongate posterolateral processes, shorter and blunter alary processes (fig. 5). Clavicles and coracoids absent, sternal plate cartilaginous. Seven presacral vertebrae (all 17 specimens), mostly nonimbricate, no indication of fusions between presacrals (atlas without diapophyses); diapophyses of second vertebra slightly angled anteriorly, those of other presacrals essentially at right angles to column; sacral diapophyses moderately expanded, bicondylar articulation with coccyx, sacrum and coccyx fused in one of two cleared-and-stained specimens, the other with short, basal diapophyses on the coccyx; coccyx and sacrum possibly fused in three X-rayed specimens, probably not in 12 others; only 2 of 15 X-rayed specimens clearly lacking at least a trace of coccygeal diapophyses. Terminal phalanges rather elongate and T-shaped, crossarm of T relatively short, only about as wide as base of phalange (fig. 6).

CHROMOSOME NUMBER: *Aphantophryne pansa* is unique among microhylids karyotyped so far in being tetraploid (Kuramoto and Allison, 1989). Though direct evidence is lacking on the karyotype of *sabini*, it may be possible to infer level of ploidy from the size of epidermal cells. Green (1980) showed that individual adhesive toe-pad cells of the tetraploid frog *Hyla versicolor* have 1.46 times the surface area (1.77 times the volume) of corresponding cells of its diploid sibling, *H. chrysoscelis*. A report by McAllister and Channing (1983), who found a 1.9× difference in toe-pad cell volume, but no evidence of polyploidy, among specimens of another frog, *Hyperolius marmoratus*, in-



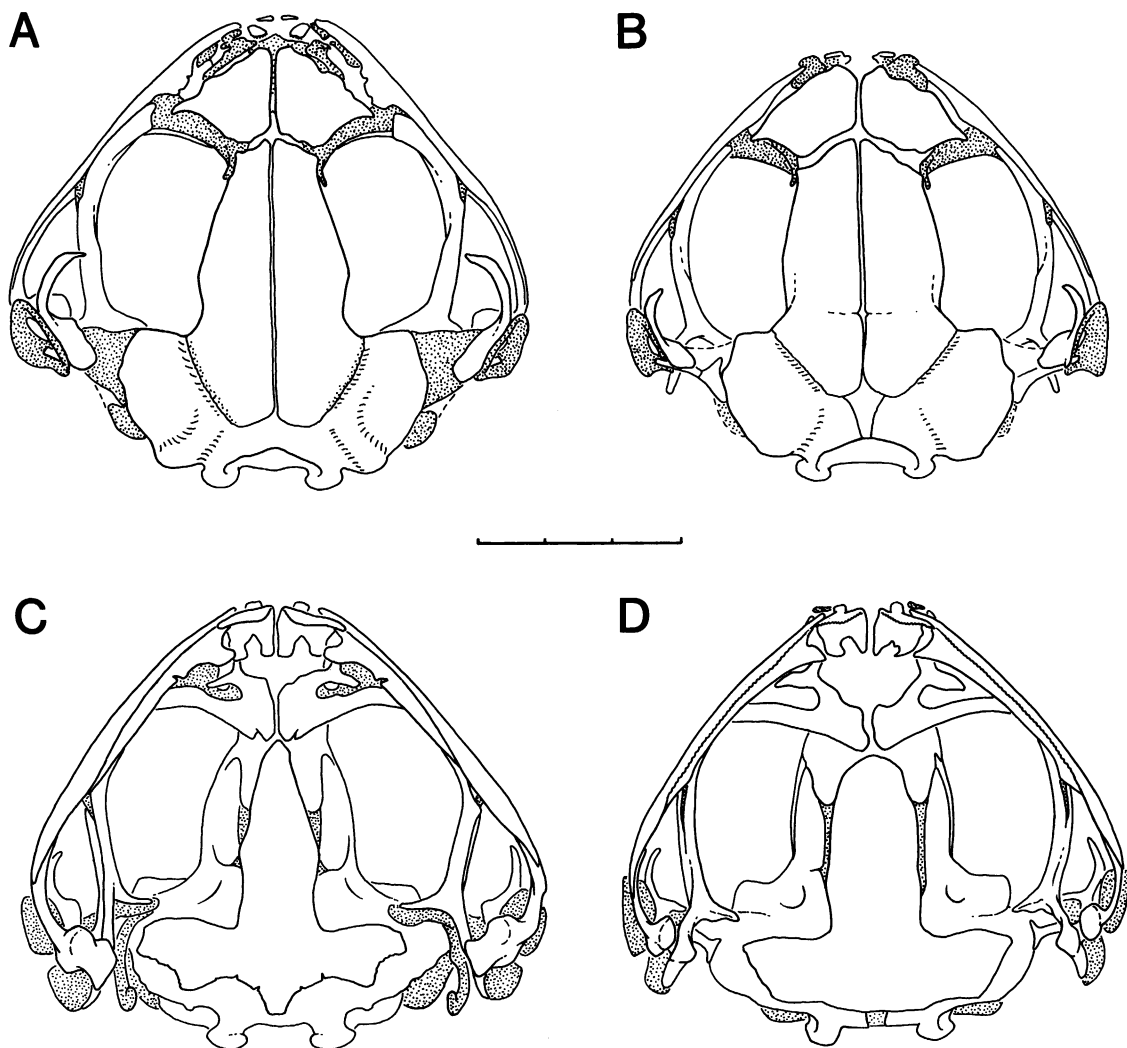


Fig. 4. A. Skull of *Aphantophryne sabini* in dorsal view, AMNH 130329. B. Skull of *Cophixalus verecundus* in dorsal view, AMNH 130409. C, D. Ventral views of above skulls in same order. Stippling indicates cartilage; scale bar calibrated in mm.

spires caution in accepting cell size as evidence of ploidy. Nevertheless, comparison of the subdigital cells of *pansa* and *sabini* (fig. 11) shows that those of *pansa* are indeed distinctly larger than those of *sabini*. It seems likely that *sabini* is diploid, but this needs to be confirmed by direct determination of chromosome number. Green and Simon (1986) commented on the lack of specialization in the digital tips of *A. pansa*, but did not compare cell sizes of *pansa* and other species.

CALL: The advertisement call is a pro-

longed series of soft clicks, fairly evenly spaced but generally speeding up at the end (fig. 12). Four tape-recorded calls, each of two individuals, averaged 17.6 (16.7–18.8) and 16.2 (15.5–17.6) sec long, with click rates of 3.9 and 3.7 per sec at respective air temperatures of 9.5 and 13.6°C. Curiously, the click rate of the presumably warmer frog was slower than that of the other. The call has two energy peaks of similar intensity at about 2700 and 3400 Hz. Several minutes may elapse between calls.

The calls of *sabini* and *pansa* are alike in

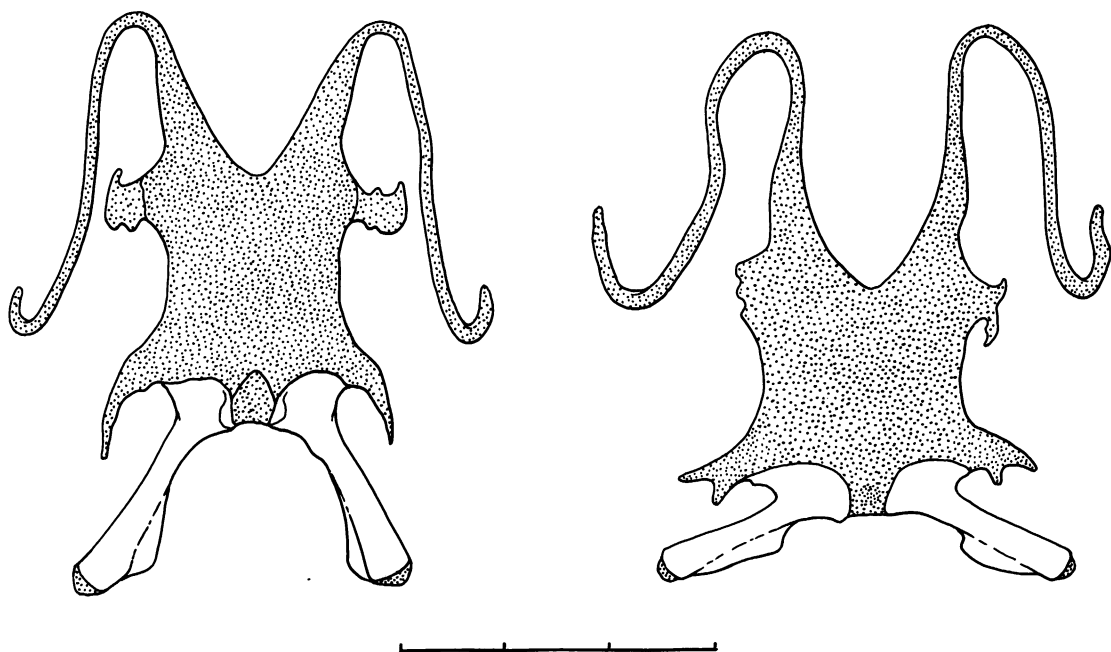


Fig. 5. Hyoids of *Aphantophryne sabini* (left) and *Cophixalus verecundus*, respectively AMNH 130314 and 130409. Proportions of bony posteromedial processes, which pass into the plane of the drawing, are distorted by foreshortening. Scale bar calibrated in mm.

being trains of clicks, but whereas *sabini* utters a long series of clicks at a slow rate, *pansa* gives a much shorter call at a higher click rate (ca. 1.4–2.3 sec long, 18–27 clicks/sec; Zweifel and Allison, 1982).

**COMPARISONS WITH OTHER SPECIES:** This species, with its squat habitus, short legs, small

hands, small eyes, and unexpanded digital tips (fig. 10), resembles other Papuan genyophryne microhylids with similar ground-dwelling habits such as *Oreophryne brevicrus* and *Sphenophryne brevicrus* (the latter a composite of several species). From the systematic standpoint, comparison only with *A. pansa* and *A. minuta* is required. The latter comparison is made in the account of that species.

The most cogent distinction between the *sabini* and *pansa* is in the advertisement call, discussed in the preceding section. The only conspicuous morphological difference between the two is in size: Females of *sabini* attain 24 mm SV, whereas *pansa* reaches 31 mm (Zweifel and Allison, 1982); *pansa* males are up to 22 mm, the largest of the few male *sabini* specimens is less than 17 mm. The two species are remarkably similar in proportions. The maximum difference between the means of all ratios of standard measurements to snout–vent length is only 1.2 percent (tables 1, 2). Only the means of the variable EN/IN comparison are as much as 5.4 percent different, and the ranges overlap greatly.

The ratio comparisons utilize only speci-

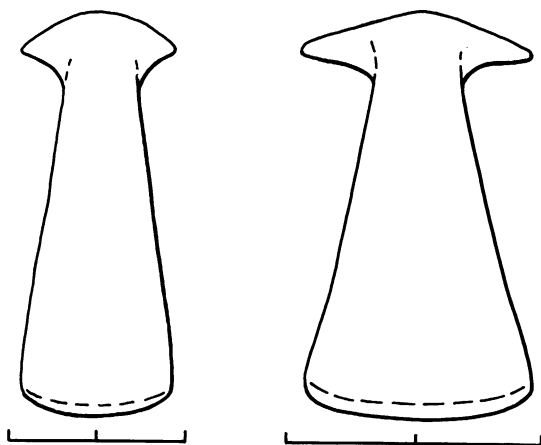


Fig. 6. Terminal phalanges of third fingers of *Aphantophryne sabini* (left) and *Cophixalus verecundus*. Scale bars calibrated in 0.1 mm intervals.



Fig. 7. Edge of meadow at Myola, contrasting the meadow habitat of *Aphantophryne sabini* with the forest habitat of *Cophixalus verecundus*.

mens of adults size. Regression comparisons can reveal different ontogenetic trends (table 3). For most of the standard measurements, the ontogenetic trends of the two species are scarcely distinguished, and the areas occupied by plots of individuals of both species overlap almost completely. The internarial measurement is an exception (fig. 9). Here the curves are moderately separated and divergent, with *sabini* having the lesser rise. However, there is a large area of overlap in

the plots, and this character would not be very useful for identifying individuals to species.

We have had no experience with living *pansa* so cannot compare the colors in life with those of *sabini*. Based on preserved specimens, *pansa* appears to be variable, like *sabini*, but in general is a much darker frog.

**HABITAT AND HABITS:** The habitat of the species at Myola Guest House is a meadow slightly under 2100 m elevation, roughly tri-

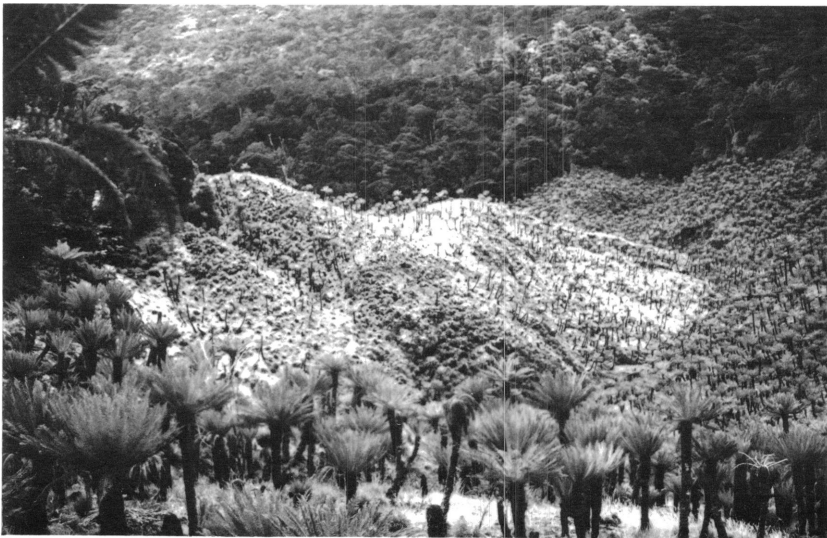


Fig. 8. Treefern-grassland habitat of *Aphantophryne sabini* at 2600 m near Myola.

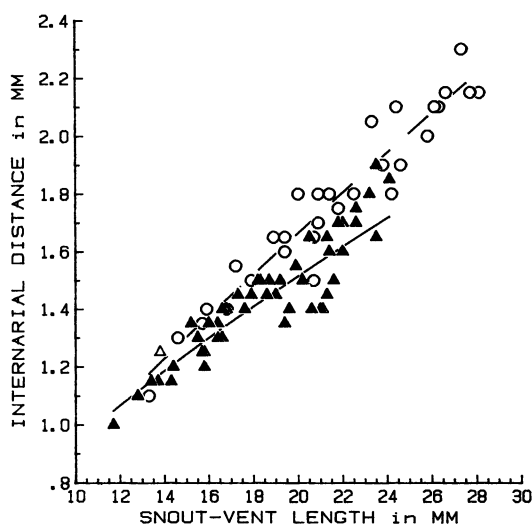


Fig. 9. Regression of internarial distance on snout-vent length in *Aphantophryne pansa* (O) and *A. sabini* (▲), showing different ontogenetic trends but broad overlap of measurements.

angular in shape, about 5 km long, and 2 km in greatest width. Iora Creek crosses the meadow and, somewhat entrenched, meanders northward, leaving at the tip of the triangle; other smaller creeks enter the meadow at several points. Vegetation varies with the local moisture, being grassy with occasional burned cycads, herbaceous, or patchy pit-pit. On the east and south sides of the meadow, there is abrupt transition to heavily mossed rain forest (fig. 7), whereas hillslopes to the west are more open and grassy. During our stay there was little rain, and under more normal conditions the meadow may be much more swampy. We were told that some years earlier, in order to permit an airplane that had made an emergency landing to take off, ditches had been dug to promote drainage.

Our specimens came from beneath cover—logs and other litter—in the meadow and up to the edge of the forest. None was seen or heard in the forest despite searching that yielded several other species of frogs. Judged from the calls, these frogs chiefly inhabit grass clumps.

Along the upper reaches of Iora Creek the species occupies a valley in tree fern grassland habitat at 2600 m elevation, where the terrain is less level (fig. 8).

A female 20.0 mm SV contained 18 ova

1.5 mm in diameter and a 19.4 mm frog held 13 ova 1.2–1.5 mm in diameter.

**DISTRIBUTION:** Known only from the two localities cited for the type series (fig. 1).

*Aphantophryne minuta*, new species

Figure 13

**HOLOTYPE:** AMNH 130297 (field no. RZ 13551), collected by Fred Parker on August 11, 1987, at about 2.0 km north, 1.7 km east of Myola Guest House, 2700 m, Northern Province, Papua New Guinea.

**ETYMOLOGY:** The Latin adjective emphasizes the small size of this species, the smallest in its genus and possibly the smallest species of the family Microhylidae.

**DIAGNOSIS:** This species differs from the other two *Aphantophryne* in its small size, the only known specimen being adult at about 12 mm SV compared to female maturity at about 19 mm in *sabini* and maximum female sizes of about 24 mm in *sabini* and 31 mm in *pansa*. Additionally, these larger species differ in having the first finger relatively longer than in *minuta* (fig. 3).

**DESCRIPTION OF HOLOTYPE:** Adult female (2 ova present, one damaged, the other 0.9 mm in diameter, well-developed oviducts) with the following measurements and proportions: SV 11.8, HW 5.0, TL 4.3, EY 1.6, EN 0.85, IN 1.2, HD 2.55, FT 4.45; HW/SV 0.424, TL/SV 0.364, EY/SV 0.136, EN/SV 0.072, IN/SV 0.102, EN/IN 0.708, HD/SV 0.216, FT/SV 0.377.

Head slightly narrower than body, snout short, rounded in dorsal aspect, rounded verging on truncate and only slightly projecting in lateral profile; nostrils visible from above, closer to tip of snout than to eyes; loreal region flat and rather steeply sloping; canthus rostralis rounded but distinct; eyes moderate in size, corneal outline easily visible from ventral view, upper eyelid about 82 percent of interorbital space; tympanum small, tympanic annulus only partially visible externally. Relative lengths of fingers 3 > 4 > 2 > 1, first short, less than half length of second; tips rounded, not flattened or expanded, lacking terminal groove; no discernable subarticular or metacarpal elevations (fig. 3). Hind legs short, toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, first quite short;

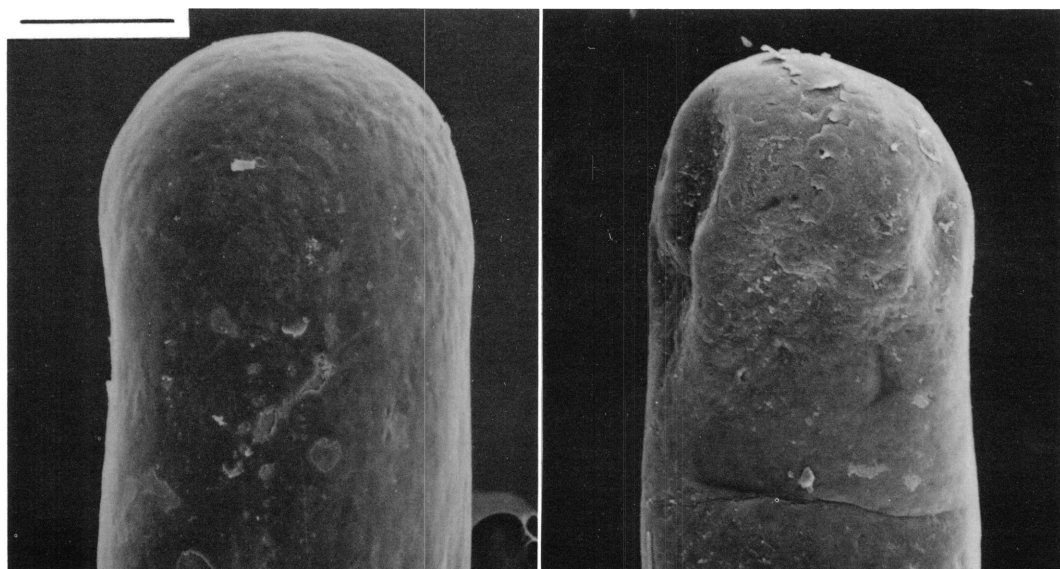


Fig. 10. Tips of undersides of fourth toes of *Aphantophryne pansa* (left) and *A. sabini* showing rounded, unflattened shape and lack of terminal groove. Scale line represents 200  $\mu$ m.

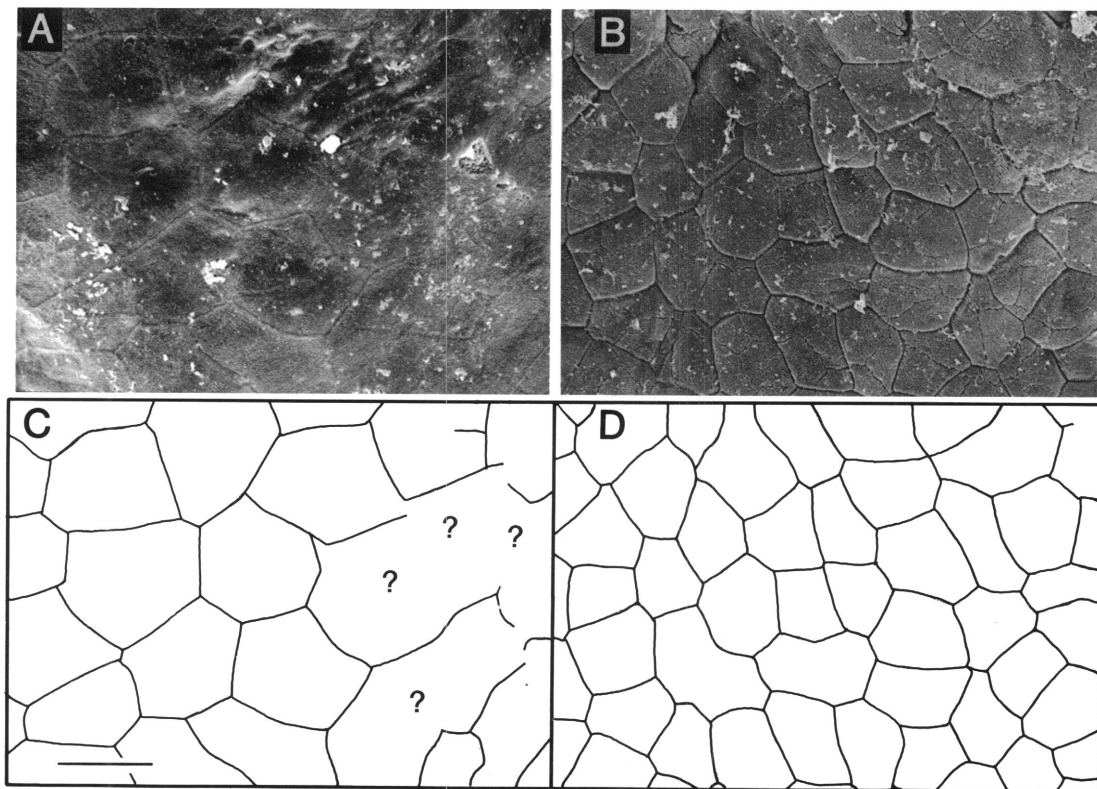


Fig. 11. Lower surfaces of tips of fourth toes of *Aphantophryne pansa* (A, C) and *A. sabini* (B, D). Drawings interpret features in the SEM photographs. Scale line in C represents 20  $\mu$ m and applies to all figures.

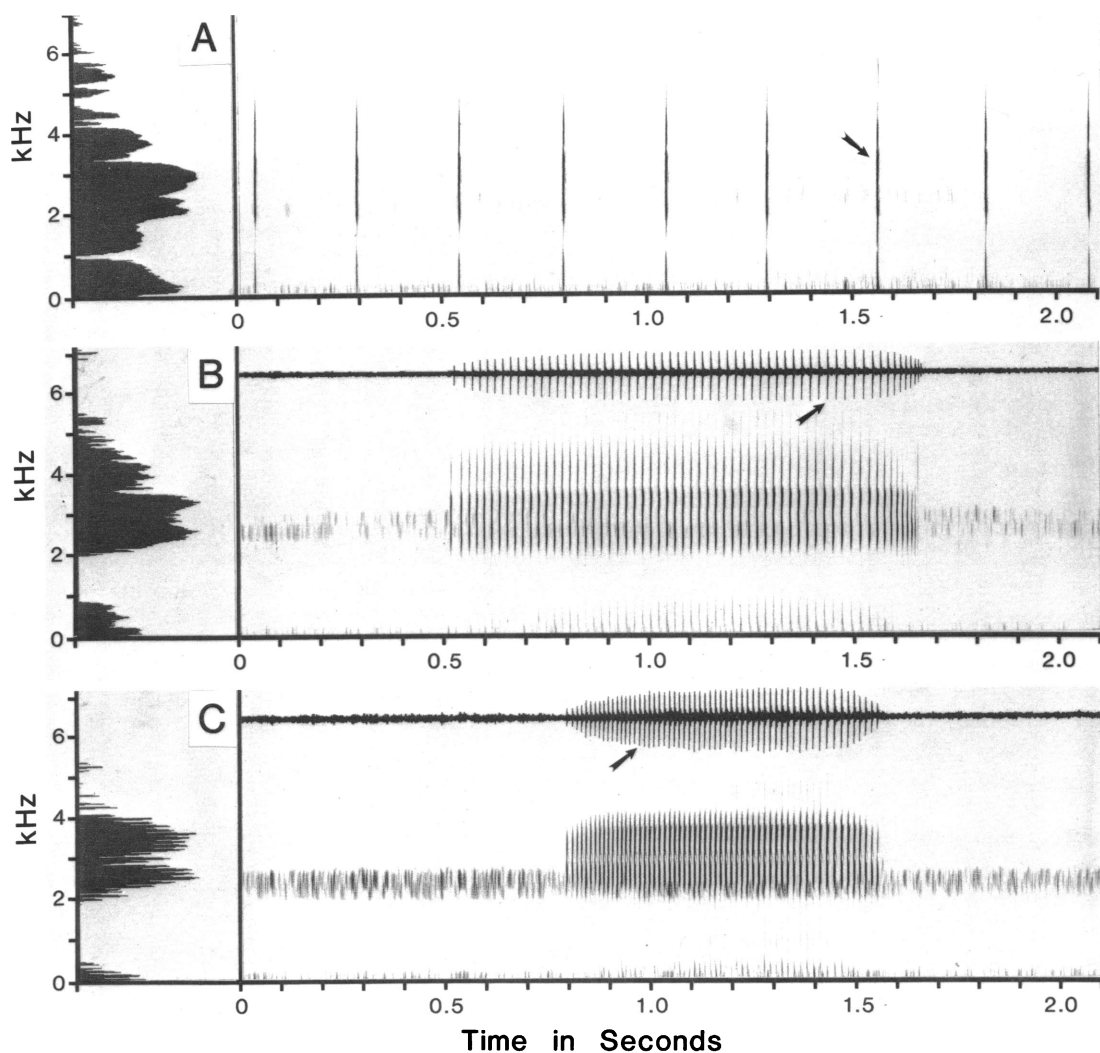


Fig. 12. Audiospectrograms of advertisement calls of frogs from Myola Guest House, Northern Province, Papua New Guinea, August 1987. Power spectra on left; calls on right, graphed with wide band (300 Hz) filter, arrows indicate pulses analyzed in power spectra; wave form displays above B and C. A. *Aphantophryne sabini*, temperature in grass at ground surface 9.5°C, no voucher specimen, AMNH Herpetology tape reel 252. B. *Cophixalus verecundus*, temperature in moss 12.8°C, AMNH 130405 (holotype), AMNH Herpetology tape reel 253. C. (?)*Cophixalus*, 13.2°C, no voucher specimen, AMNH Herpetology tape reel 252.

tips as described for fingers; no distinct subarticular elevations, inner metatarsal elevation low, elongate, rounded, scarcely evident. Most of dorsal surface, arms and legs included, rather warty; moderately conspicuous, convergent scapular folds diverge as rows of warts posteriorly.

We did not note the colors of the holotype in life. In preservative, the top of the snout,

the area between the scapular folds and dorsal wart rows, and a lateral strip bordering the folds and rows are dark brown, contrasting with the paler brown of the flanks. Lumbar ocelli are faintly indicated, and some warts on the side of the body are dark brown. The limbs are brown with darker markings. The ventral ground color is dirty white from chin to tip of abdomen. Small brown markings

edge the jaw, and there are paired irregular dark marks on the chest. There is a general scattering of melanophores, somewhat more concentrated at the posterior end of the abdomen.

**OSTEOLOGY:** The unique specimen has been examined by dissection only to the extent of determining that the pectoral girdle lacks clavicles and procoracoid cartilages. An X-ray photograph confirms the lack of clavicles and reveals seven presacral vertebrae with no indication of fusions. Other features include: 2nd vertebral diapophyses angled slightly forward, 3rd at right angle, 4th and 5th slightly backward, 6th right angle, 7th slightly forward; sacral diapophyses moderately expanded; coccygeal articulation bicondylar; coccyx with a pair of small, blunt diapophyses. Frontoparietal region broad and expanding slightly posteriorly, maxillae eleuthero-gnathine, pars palatina of premaxilla notched, pars dorsalis vertical, arising abruptly.

**COMPARISONS WITH OTHER SPECIES:** We did not distinguish between *Aphantophryne minuta* and *A. sabini* until the specimen was opened and its adult status revealed, which emphasizes the similarity of these species. Apparent differences in the relative sizes of body parts (tables 1, 2) are misleading, as the samples of *sabini* and *pansa*, being restricted to adults, comprise much larger individuals. Estimates of the average ratios of the two larger species at the size of *minuta* (derived from regression data, table 3) indicate that differences from *minuta* are largely due to allometric growth; *pansa* and *sabini* the size of *minuta* would have quite similar proportions. However, such *pansa* and *sabini* may be distinguished by their longer first fingers.

*Aphantophryne minuta* may be the smallest microhylid frog and one of the smallest of all frogs. Among microhylids, there are only two reportedly smaller forms, neither well documented. *Stumpffia madagascariensis* Mocquard is known from a single 9.5 mm specimen, but Guibe (1978) considered this a doubtful species, and the poor state of preservation of the unique specimen prevents adequate study. *Sphenophryne pusillus* (Roux) of the Aru Islands west of New Guinea also is known only from a single specimen, this one "clearly not adult" at 7 mm (Tyler, 1978).

The single specimen of *A. minuta* may be

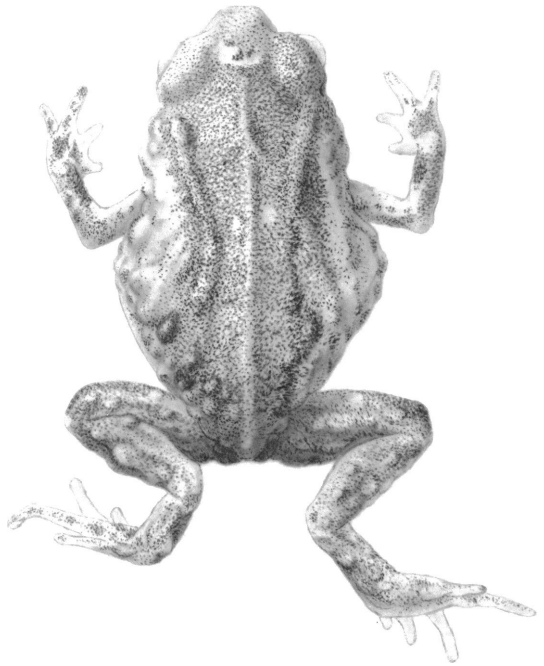


Fig. 13. *Aphantophryne minuta*, new species. Holotype AMNH 130297, dorsal view, 5× life size.

at the small end of the size range for adult females of its species. If this is the case, *minuta* still may be smaller than such tiny species as the Australian *Cophixalus bombiens* Zweifel, *C. crepitans* Zweifel, and *C. hosmeri* Zweifel, females of all of which mature at about 13–14 mm SV (Zweifel, 1985), or smaller than undescribed species related to *C. variegatus* with females adult at 14 mm (Menzies, 1976: 57–58).

**HABITAT AND HABITS:** The unique specimen was found under a small, decayed log lying in leaf litter on a rainforested ridge above the Myola meadow and "Fern Valley."

**DISTRIBUTION:** Known only from the type locality (fig. 1).

#### Relationships of *Aphantophryne*

The genera of the paraphyletic (Burton, 1986) subfamily Genyophryninae have not been sufficiently studied to permit adequate assessment of their relationships. Burton (1986: 415) remarked on a close relationship between the monotypic *Choerophryne* and several species (only two described) currently



Fig. 14. *Cophixalus verecundus*, new species. Holotype AMNH 130405, 3.3× life size.

assigned to *Cophixalus* comprising his “*darlingtoni*-group.” In addition to this distinctive group, the genyophrynine genera include *Aphantophryne*, *Choerophryne*, *Cophixalus* (in a restricted sense), *Copiula*, *Genyophryne*, *Oreophryne*, and *Sphenophryne*.

*Sphenophryne* has a primitive pectoral girdle with cartilaginous procoracoids and well-developed clavicles that extend from the scapula almost to the midline. In *Oreophryne* the clavicles are small and free from scapular articulation, whereas *Genyophryne* lacks clavicles but, like *Oreophryne*, retains the procoracoid cartilages. The remaining genera—*Aphantophryne*, *Choerophryne*, *Cophixalus*, and *Copiula*, as well as the *darlingtoni* group—all lack clavicles and procoracoid cartilages. This clearly derived condition could be taken to indicate monophyly of the four genera and the *darlingtoni* group. *Choerophryne* and the *darlingtoni* group form a sister pair on the basis of synapomorphies other than the condition of the pectoral girdle (Burton, 1986), but the simplified girdle as a character unsupported by other synapomorphies is inadequate to sustain monophyly for the several genera possessing it. This is because identical extensive loss of pectoral elements has taken place independently several times in the Microhylidae (e.g., Zweifel, 1986). The reduced number of presacral vertebrae in *Aphantophryne* establishes its derived position with respect to other genyophrynines, but a comprehensive analysis of all the genera probably will be required to elucidate relationships on a finer level. Burton's (1986) excellent study of the Asteroophryinae could serve as a model for the morphological aspects.

***Cophixalus verecundus*, new species**

Figure 14

**HOLOTYPE:** AMNH 130405 (field no. RZ 13540), collected by Richard G. Zweifel and Laurence T. Penny on August 11, 1987, at Myola Guest House, 2080 m, 7 km south, 6 km west of Mt. Bellamy, Northern Province, Papua New Guinea.

**PARATYPES:** AMNH 130407–130411, UPNG 8151, collected at the type locality by Fred Parker, Zweifel, and Penny on August 10–12, 1987, and UPNG 7088, collected by James I. Menzies on March 17, 1986 at the type locality.

**ETYMOLOGY:** The Latin *verecundus* (shy) refers to the males' habit of calling softly from concealment.

**DIAGNOSIS:** Characters that in combination are diagnostic of the genus *Cophixalus* include: maxillae eleutherognathine, clavicles and coracoids lacking, eight presacral vertebrae, tips of digits flattened and disklike, snout without whitish glandular tip. *Cophixalus verecundus* differs from most other New Guinean species of its genus in combining small size (SV less than 20 mm) with poorly developed digital disks, third toe longer than fifth, and first finger moderately well developed. Comparisons are made in a following section.

**DESCRIPTION OF HOLOTYPE:** Adult male (calling when captured), with the following measurements and proportions: SV 16.1, HW 6.9, TL 6.1, EY 1.9, EN 1.5, IN 1.5, HD 3.6, FT 6.4, disk of 3rd finger 0.45 (penultimate phalange 0.4), disk of 4th toe 0.5 (0.5); TL/SV 0.397, HW/SV 0.429, EY/SV 0.118, EN/SV 0.093, IN/SV 0.093, EN/IN 1.000, HD/SV 0.224, FT/SV 0.398, 3rd finger/SV 0.028, 4th toe/SV 0.031.

Head slightly narrower than body; snout rounded verging on bluntly pointed in dorsal aspect, rounded and slightly projecting in profile; nostrils lateral, scarcely visible from above, much closer to tip of snout than to eye; loreal region flat, steeply sloping, canthus rostralis distinct, slightly curved; eyes moderately small, corneal outline easily visible in ventral view, upper eyelid about 75 percent of interorbital space; tympanic outline scarcely apparent. Relative lengths of fingers



3 > 4 > 2 > 1, first less than half length of second; tips flattened and somewhat disklike, but only third and fourth slightly broader than penultimate phalanges and with indistinct terminal grooves; subarticular and palmar elevations virtually absent. Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1; tips disklike, slightly enlarged, all but first with shallow terminal grooves; subarticular elevations indistinct, inner metatarsal elevation low, rounded, distinguished by paler coloration. An indistinct, curved, postocular-supratympanic fold; dorsal and lateral body surfaces somewhat rugose, more especially so posteriorly and on the hind limbs, warts on the back organized into low paravertebral and W-shaped scapular lines; all undersurfaces regularly pebbled.

In preservative, the dorsal surfaces of body and legs are tan with irregular, small, darker brown markings, and some dark pigment concentrated on the raised paravertebral and scapular lines. The canthal region is slightly darkened, and this is continued posterior to the eye as a more distinct stripe following the postorbital-supratympanic fold. The top of the snout is slightly darker than the general dorsal ground color, and there is a pale interocular line. A lumbar eyespot is moderately well developed. Brown melanin stippling on the chin, chest, and abdomen gives way laterally and posteriorly to a fine melanin network enclosing tiny, irregular light spots. This pattern continues under the legs, feet, and hands, soles and palms included.

In life this was a drab, mostly brown frog with eyelids, middle of back, and snout slightly more reddish than the brown-to-tan sides of the body. The faint lumbar ocelli were tan with a darker brown spot. The undersides were gray with irregular lighter flecks and spots. The iris was gold with a reddish horizontal streak.

**VARIATION IN THE TYPE SERIES:** The largest of eight specimens assigned to this species is a gravid female 18.9 mm SV, and three other gravid females are 17.9, 18.0, and 18.7 mm. A female of 15.6 mm evidently is immature, with small, unyolked ova and narrow, unconvoluted oviducts. Three males are 17.2, 16.1, and 15.2 mm SV; the two smaller ones were calling when taken. Regression data and

proportions are summarized in tables 1–3. Not included in the tables are the following data for digital disks (N = 8): 3rd finger disk/SV, mean  $0.028 \pm 0.001$  (0.022–0.033); 4th toe disk/SV, mean  $0.033 \pm 0.001$  (0.031–0.038). Where X = SV and Y = widths of 3rd finger and 4th toe disks, the following are the power regression formulas: finger,  $Y = 0.082X^{0.622}$ ,  $r^2 = 0.143$ ; toe,  $Y = 0.060X^{0.791}$ ,  $r^2 = 0.406$ . Because of the slight degree of expansion of the disks, the difficulty of measuring them accurately, and the small range of body size, the reliability of these regression data is low. In most instances, the tips of the third fingers and fourth toes are slightly broader than the penultimate phalanges (toe disks slightly larger than those on fingers), and in all specimens, the tips are distinctly flattened and disklike and at least some disks bear terminal grooves.

Variation in dorsal coloration involves mostly relative darkness or lightness of all or part of the pattern. One specimen is much paler than the holotype, with few dark markings; another is much darker except for the area enclosed by the scapular ridges; a third is pale in the scapular and middorsal regions, somewhat darker on the sides, and lacks lumbar ocelli. The ventral surfaces of some specimens are as described for the holotype. In others, the light spotting is better defined against a darker background.

**OSTEOLOGY:** Skull well ossified, nasals large and in contact (fig. 4); frontoparietals broad, expanding slightly posteriorly, fused prootic and exoccipital well ossified; squamosal zygomatic ramus short, slightly curved, otic ramus with a short, medially expanded otic plate; strong quadratojugal-maxillary contact; maxillae eleutherognathine, barely overlapping premaxillae; pars palatina of premaxilla indented, pars dorsalis vertical, arising abruptly; tiny, vestigial maxillary and premaxillary teeth visible under high magnification; vomeropalatine strong, anterior ramus nearly encircling internal naris, transverse ramus reaching maxillary shelf. Hyoid with bifurcate posterolateral processes and short alary processes (fig. 5). Procoracoids and clavicles absent, sternum cartilaginous. Eight nonimbricate presacral vertebrae, transverse processes of 2nd angled slightly forward, 3rd

right angle, 4th and 5th posteriorly, 6th right angle, 7th and 8th slightly forward; sacral diapophyses somewhat expanded, coccyx with short, basal diapophyses and articulating with double condyle. Terminal phalanges short, T-shaped, the expansion as wide as the base of the phalange.

**CALL:** The call is a rapid train of clicklike pulses giving the aural effect of a soft buzz (fig. 12B). Ten tape-recorded calls of each of two individuals had the following means and ranges at air temperatures of 12.8 and 14.5°C, respectively: length 1.13 sec (0.98–1.19), 0.95 (0.88–1.03); pulses/call 61.2 (54–64), 56.0 (52–60); pulses/sec 53.6 (51.6–55.9), 58.3 (57.0–59.9).<sup>5</sup> The call has two energy peaks at about 2500 and 3300 Hz. In one of the two frogs, the calls started with relatively widely spaced pulses, speeded up briefly before reducing to steady slower rate for the bulk of the call, and ended with a few much more closely spaced pulses. Calls of the other individual established a rather steady pulse rate initially, but had the same terminal increase in rate. The first frog initiated calls at a mean interval of 9.65 sec (7.6–12.4, N = 11). The second called less frequently but with similar regularity: 21.2 sec (14.3–24.0, N = 9). The calls show the expected correlations with temperature: shorter duration and higher pulse rate at the higher temperature.

Tiny frogs that call from concealment pose a difficult problem for the person trying to verify the identity of the caller. Initially, we supposed this call came from a species of the *Cophixalus variegatus* sort that we found commonly on low vegetation, though we could not discover one in the act of calling. Eventually we recorded, uncovered, and captured the frog that we are confident was the true caller, and shortly thereafter tracked another calling individual of the same species and found it similarly concealed.

In the course of analyzing what we supposed were three recordings of the same species (only one with a voucher specimen), we found two sets of highly similar calls (fig. 12B; described above), whereas the other (fig. 12C) differed significantly in most ways: length 0.77 sec (0.74–0.82), pulses/call 58.7

(56–63), pulses/sec 77.8 (77.1–80.3); N = 4 calls. At a comparable temperature (air 13.2°C), these calls have a faster pulse rate and shorter length (no overlap in these features), though the number of pulses per call does not differ. The structure of the call differs, beginning with a rapid pulse rate and gradually slowing down. Intercall intervals varied widely (17, 57, 168 sec), though we cannot be sure the unseen frog was undisturbed. Probably the frog that uttered these calls was not the new species we describe, but whether it was the *Cophixalus variegatus* group frog remains to be determined.

**COMPARISONS WITH OTHER SPECIES:** Many species of *Cophixalus*, though small frogs, are larger than *C. verecundus*. Among the 16 recognized New Guinean species, seven are in the same general size range as *verecundus* but none should be confused with it. *Cophixalus variegatus* (van Kampen) and several undescribed related species have the fifth toe longer than the third. *C. tagulensis* Zweifel has toe webbing and relatively well-developed digital disks. *C. ateles* (Boulenger) and *C. daymani* Zweifel have well-developed digital disks, with those of the fingers larger than those of the toes. Three similar and possibly interrelated species have the first finger greatly reduced: *C. pipilans* Zweifel, *C. shellyi* Zweifel, and *C. sphagnicola* Zweifel and Allison. Only the last of these has disks as small as those of *verecundus*; see illustrations in Zweifel (1980) and Zweifel and Allison (1982).

The 11 Australian species of *Cophixalus* include 6 in the size range of *verecundus* (Zweifel, 1985). Among species in this group there are similarities to *verecundus* in several characteristics, including call, but none of the species is enough like *verecundus* in all characteristics that it could be thought conspecific.

*Cophixalus verecundus* is distinct from many New Guinean *Cophixalus* in its small size and from all in having greatly reduced finger and toe disks, while retaining the presumably plesiomorphic condition of a relatively long first finger. We know of no species or set of species within New Guinean *Cophixalus* that appears to be particularly closely allied to *verecundus*. That *verecundus* and *sphagnicola* both lack expanded disks (an apomorphic state in *Cophixalus*) does not es-

<sup>5</sup> The pulse rate is taken over the entire range of each note.

establish monophyly; *sphagnicola* is the most derived of three presumably related species that otherwise have little in common with *verecundus*.

Neither is there evidence of a close affinity of *verecundus* and the Australian *Cophixalus*. It does not ally with the major group of small Australian species (Zweifel, 1985: fig. 59) characterized by reduced hand size, and has no clear synapomorphies with other Australian species, whose own interrelationships are far from clear.

**HABITAT AND HABITS:** Whereas we found *Aphantophryne sabini* in the meadow, *C. verecundus* was captured only in the forest (fig. 7). Males calling at night were concealed in moss: one in a crotch of a broken branch lying a few inches above the ground, the other about a foot above the leaf litter on the root-buttress of a tree. Other specimens were found under surface litter in the daytime.

**DISTRIBUTION:** Known only from the type locality (fig. 1).

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