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Systematics of Microhylid Frogs, Genus *Oreophryne*, Living at High Elevations in New Guinea

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ABSTRACT

Oreophryne known from high elevations (2800–3900 m) in the mountains of New Guinea (Indonesia: Papua, and western Papua New Guinea) comprises six species, five described here as new. They constitute a group, probably but not necessarily monophyletic, characterized by relatively short hind legs, small digital disks, and small hands. We interpret these features as adaptations to a primarily terrestrial mode of life, contrasting to the scansorial/arboreal mode typical of most species of *Oreophryne*. Distinctive advertisement calls characterize four of the six species; calls of the remaining two are unknown. Identification of preserved specimens depends upon average or, less often, complete differences in certain body proportions and is not always possible with certainty.

INTRODUCTION

Oreophryne is the most widespread of the genera of genyophrynine microhylid frogs, ranging from the southern Philippines and Lesser Sunda Islands of Indonesia eastward throughout New Guinea to New Britain. The abundant species of New Guinea—26 are currently recognized—are mostly found in low- to middle-elevation habitats. Only two species of *Oreophryne* have been recorded from high elevations in New Guinea. *Oreophryne anthonyi* (Boulenger, 1897) attains at least 2840 m in the Owen Stanley Range of Papua New Guinea (Zweifel, 1956: 19). It is an arboreal frog, large for an *Oreophryne*, and only remotely related to the terrestrial species we treat here; it is not discussed further. The second species is *Oreophryne brevicauda*. In nearly 50 years since its description (Zweifel, 1956), *O. brevicauda* has received scant attention in the literature. The name appears in checklists (Allison, 1993; Iskandar and Colijn, 2000; Scott et al., 1977; Zweifel, 1985; Zweifel and Tyler, 1982), but information additional to that in the original description is quite limited; brief mentions of distribution (Zweifel, 1985) and habits (Zweifel and Tyler, 1982) appear to constitute the whole.

In 1965, Barry Craig of the South Australian Museum collected a series of *Oreophryne* at a high elevation in the Star Mountains of western Papua New Guinea 290 km east of the type locality of *O. brevicauda* in Indonesia's Papua Province (formerly known as Irian Jaya). These specimens, examined by Zweifel, are similar in morphology to *O. brevicauda* and were responsible for the inclusion of that species in the fauna of Papua

New Guinea by Zweifel and Tyler (1982) and Zweifel (1985).

Species of microhylid frogs are often difficult to distinguish by morphology alone, but the added dimension of vocalization frequently reveals hidden species diversity; Zweifel et al. (2003) provided a recent example in the genus *Oreophryne*. In 1987 Cogger tape-recorded and collected at the same locality as had Barry Craig and found sympatric, morphologically very similar frogs uttering quite different calls. Four years later Richards, working at the same locality, independently made the identical discovery. Our purpose is to review this new material and other previously unstudied specimens from the high mountains with the goal of distinguishing and describing the new species identified.

METHODS

ANATOMY: We made a suite of measurements of most specimens with dial calipers read to the closest 0.1 mm or, if appropriate, using an ocular micrometer in a binocular dissecting microscope and read to the nearest 0.05 mm. Sex of the specimen was apparent if it was a male calling when captured. Otherwise, males were determined by the presence of vocal sac openings or by examination of gonads, and females by examination of gonads. Color descriptions of living frogs are taken from field notes and photographs.

The following abbreviations pertain to measurements made (with some exceptions) on each specimen:

EN	Distance between anterior edge of eye opening and center of external naris
EY	Horizontal diameter of eye opening

FD	Width of disk of third finger measured at a right angle to the axis of the digit with the disk flattened against a glass plate
FT	Length of foot between proximal edge of inner metatarsal elevation and tip of fourth toe (see HD)
HD	Length of hand between proximal edge of inner metacarpal elevation and tip of third finger. Both hand and foot measurements may have reduced accuracy owing to the sometimes indistinct nature of the metacarpal and metatarsal elevations and to the difficulty of properly spreading the hands and feet of indifferently preserved specimens.
HW	Head width at widest point, generally at the level of the tympanum or jaw angle
IN	Distance between centers (not medial edges) of external nares
SVL	Length from snout to vent—from tip of snout to cloacal opening
TD	Width of disk of fourth toe measured at a right angle to the axis of the digit with the disk flattened against a glass plate
TL	Tibia length, between heel and outer surface of flexed knee
TY	Diameter of tympanum, including tympanic ring, measured horizontally. The ear is scarcely apparent externally and hence it is difficult to measure with accuracy.

Relative lengths of fingers and toes were determined by placing them parallel to an adjacent finger or toe; actual lengths were not measured. What may prove to be a fundamental dichotomy within *Oreophryne* is whether the cartilaginous procoracoid extends to the scapula or if there is instead a ligamentous connection between these elements. This is best demonstrated with specimens cleared and stained for bone and cartilage, but in well-preserved specimens the question often may be satisfactorily resolved by dissection and microscopic examination. Judged from the latter mode all the species treated here have the cartilaginous procoracoid reaching the scapula.

Tape recordings of advertisement calls were made on different machines with different microphones over a span of years. Some spurious variation in the recorded calls is thus possible, but the differences among the calls are of a degree that renders any such variation unimportant for present purposes. Audiospectrograms and waveforms were produced on a Kay 5500 DSP Sona-Graph.

Analyses of calls—measurements of rates, note and call durations, dominant frequencies—were made with the aid of the CECIL computerized speech analysis system (Hunt, 1993). Copies of the tape recordings used are archived and cataloged in the Department of Herpetology, American Museum of Natural History.

A list of the institutions that furnished specimens for our examination follows, with institutional abbreviations and names of responsible parties, who have our sincere thanks.

AMNH	American Museum of Natural History, New York; L. Ford
AMS	Australian Museum, Sydney; R. Sadler
BPM	Bishop Museum, Honolulu; A. Allison, C. Kishinami
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden; R. Hoogmoed
SAMA	South Australian Museum, Adelaide; A. Edwards
UPNG	University of Papua New Guinea, Port Moresby; J. Menzies
ZMB	Museum für Naturkunde, Humboldt Universität, Berlin; R. Günther

HABITS AND CHARACTERISTICS OF HIGH MONTANE *OREOPHRYNE*

Most *Oreophryne* in New Guinea live at low to moderate elevations and are scansorial or even largely arboreal. Individuals that spend the daylight hours hidden in leaf litter or other shelter climb into bushes and trees at night. In contrast, the six species from high elevations (2800 m and above) treated here are terrestrial (so far as is known) and live in meadows or exposed alpine grassy habitats. Morphological features associated with this way of life include hind limbs shorter on the average than in other *Oreophryne*, relatively small digital disks (fig. 1), and small hands (*O. brevicrus* is an exception; see figs. 2, 10, 11). Average proportions of $TL/SVL \leq 0.40$ combined with $FD/SVL \leq 0.05$ and $HD/SVL \leq 0.29$ characterize the high montane species. No known scansorial/arboreal species has average proportions in these ranges, although individuals of some species in the two groups may have similar proportions.

One species, *O. minuta*, is unique in lacking digital disks and has relatively short legs

Fig. 1. Average ratios of tibia length and width of third finger disk to snout-vent length in 44 samples of New Guinean *Oreophryne*. Black squares represent the six species treated in this paper: 1, *O. brevicrus*; 2, *O. terrestris*; 3, *O. habbemensis*; 4, *O. geminus*; 5, *O. brevirostris*; 6, *O. alticola*. Open squares represent other samples, including undescribed or otherwise unidentified samples. The arrow identifies *O. minuta*.

(fig. 1). It lives at a middle elevation (2000 m) in thick clumps of moss on boulders or low tree branches (Richards and Iskandar, 2000). Thus, its microhabitat is perhaps more similar to that of the high montane species than that of the arboreal/scansorial forms.

Similarities among the high montane species render morphological diagnoses difficult, but advertisement calls of four of the six species we recognize are available and confirm the distinctiveness of these species at least. Resort to careful measurements and calculations of ratios are needed to identify preserved specimens, and even then there may be specimens of questionable identity.

Whether the six highland species constitute a monophyletic group within *Oreophryne* remains to be seen. Their considerable morphological similarity suggests this may be true, particularly as their differences in proportions (but not in the pectoral girdle) from other *Oreophryne* can be considered derived characters. However, similar adaptations to a secretive, terrestrial existence have accrued to distantly related microhylid species, so there is no assurance that the high-

Fig. 2. Average ratios of tibia length and hand length to snout-vent length in 34 samples of New Guinean *Oreophryne*. Black symbols represent the six species treated in this paper: 1, *O. brevicrus*; 2, *O. terrestris*; 3, *O. habbemensis*; 4, *O. geminus*; 5, *O. brevirostris*; 6, *O. alticola*. Open symbols represent other species samples as well as undescribed or otherwise unidentified samples.

land species of *Oreophryne* do not owe their similarity to adaptive convergence in different phyletic lines.

SPECIES ACCOUNTS

Oreophryne alticola, new species

Figure 3

HOLOTYPE: UPNG 9520 (field no. Blum 1979-5) collected in June 1979 by J. Paul Blum at a pass, elevation 3900 m, in the central ranges of Papua, Indonesia, about 70 km east and 35 km south of Angguruk, and 20 km west-southwest of Bime.

PARATYPES: UPNG 9521 and 9522 (field nos. Blum 1979-6, -7) bearing the same data as the holotype.

TYPE SPECIMENS: The three specimens upon which the description of this new species is based were found to have been destroyed when one of us (SJR) sought in April 2004 to retrieve them for photography at the University of Papua New Guinea. In view of this unfortunate circumstance, figure 3 must serve as holotype by proxy (see International Commission on Zoological Nomenclature, 1999: art. 73.1.4). Eventual rediscovery of

Fig. 3. *Oreophryne alticola* paratype, UPNG 9522, SVL 18.7 mm, male.

the species may warrant designation of a neotype if the qualifying conditions of Article 75.3 are satisfied.

ETYMOLOGY: The name is an adjective deriving from the Latin *altus* (high) + the suffix *-colus* (dwelling in), in reference to the alpine habitat of the species (see Remarks).

DIAGNOSIS: Small eyes ($EY/SVL \leq 0.113$) and a short EN span ($EN/SVL 0.64\text{--}0.65$) are the principal diagnostic features of *O. alticola*. There is overlap in both ratios considered together only with *O. brevirostris*, but this overlap is a function of the size of the individual frogs: the largest *brevirostris* have the relatively smallest eyes. When eye diameter is regressed against snout-vent length, the distinction between *O. alticola* and *O. brevirostris* in the same SVL range is clear (fig. 4). See Comparisons with Other Species for additional species. The advertisement call is diagnostic insofar as calls of other *Oreophryne* are known.

DESCRIPTION OF HOLOTYPE: Adult male (vocal slits present) with the following measurements and proportions: SVL 19.1, TL 6.5, HW 7.0, EY 2.15, EN 1.25, IN 1.6, HD 4.3, FT 6.6, FD 0.6 (penultimate phalanx 0.5), TD 0.5 (0.5); TL/SVL 0.340, HW/SVL 0.366, EY/SVL 0.113, EN/SVL 0.065, IN/

Fig. 4. Regression of eye diameter on snout-vent length in *Oreophryne brevirostris* (squares) and *Oreophryne alticola* (crosses). Regression lines calculated as power curves of the form $Y = a \times b^x$: *brevirostris* alpha = 0.576, beta = 0.476, $r = 0.911$; *alticola* alpha = 0.513, beta = 0.475, $r = 0.850$.

SVL 0.084, HD/SVL 0.225, FT/SVL 0.346, FD/SVL 0.031, TD/SVL 0.026.

This is a chunky bodied frog with short legs, a blunt snout, and small eyes; canthus rostralis rounded, loreal region nearly vertical, sloping slightly outward. Relative length of fingers $3 > 2 \approx 4 > 1$, the first about one-half the length of the second; tips of second to fourth fingers disklike and grooved but only slightly expanded, that of the first not expanded; low subarticular and inner metatarsal elevations scarcely evident. Relative lengths of toes $4 > 3 > 5 > 2 > 1$, the third only a little longer than fifth; toe tips disklike and grooved, but not broader than penultimate phalanges. Neither fingers nor toes are webbed. The procoracoid-scapula connection is cartilaginous.

In preservative, the dorsum is brown with a faint light vertebral hairline, the sides paler with irregular, large dark spots. The facial area is dark, slightly darker below the canthus rostralis. A diagonal light area bordered above and below with dark streaks passes across the tympanum. The throat is pale with coarse, darker mottling; chest and abdomen are mostly dark with large, irregular white

TABLE 1
Body Proportions in High Montane *Oreophryne*

	HW/SVL			TL/SVL		
	Mean $\pm$ σ_m	Range	<i>N</i>	Mean $\pm$ σ_m	Range	<i>N</i>
<i>alticola</i>	0.369 $\pm$ 0.006	0.361–0.380	3	0.350 $\pm$ 0.015	0.330–0.380	3
<i>brevicrus</i> ^a	0.381 $\pm$ 0.009	0.352–0.408	5	0.401 $\pm$ 0.009	0.375–0.418	5
<i>brevicrus</i> ^b	0.393 $\pm$ 0.004	0.379–0.415	9	0.375 $\pm$ 0.006	0.357–0.414	10
<i>brevicrus</i> ^c	0.389 $\pm$ 0.004	0.352–0.415	14	0.384 $\pm$ 0.006	0.357–0.418	15
<i>brevirostris</i> ^d	0.379 $\pm$ 0.006	0.361–0.400	6	0.345 $\pm$ 0.005	0.330–0.357	6
<i>brevirostris</i> ^e	0.384 $\pm$ 0.008	0.349–0.429	11	0.340 $\pm$ 0.007	0.299–0.378	11
<i>brevirostris</i> ^f	0.383 $\pm$ 0.005	0.349–0.429	17	0.342 $\pm$ 0.005	0.299–0.378	17
<i>geminus</i>	0.390 $\pm$ 0.003	0.375–0.421	15	0.355 $\pm$ 0.004	0.325–0.387	15
<i>habbemensis</i>	0.364 $\pm$ 0.009	0.343–0.388	4	0.359 $\pm$ 0.008	0.331–0.377	4
<i>terrestris</i>	0.373 $\pm$ 0.004	0.337–0.405	22	0.390 $\pm$ 0.005	0.339–0.442	22

	EY/SVL			EN/SVL		
	Mean $\pm$ σ_m	Range	<i>N</i>	Mean $\pm$ σ_m	Range	<i>N</i>
<i>alticola</i>	0.106 $\pm$ 0.003	0.099–0.133	3	0.064 $\pm$ 0.005	0.064–0.065	3
<i>brevicrus</i> ^a	0.129 $\pm$ 0.004	0.119–0.138	5	0.085 $\pm$ 0.004	0.072–0.094	5
<i>brevicrus</i> ^b	0.121 $\pm$ 0.004	0.104–0.136	8	0.076 $\pm$ 0.002	0.068–0.084	9
<i>brevicrus</i> ^c	0.124 $\pm$ 0.003	0.104–0.138	13	0.079 $\pm$ 0.002	0.068–0.094	14
<i>brevirostris</i> ^d	0.125 $\pm$ 0.002	0.121–0.135	6	0.067 $\pm$ 0.002	0.063–0.074	6
<i>brevirostris</i> ^e	0.121 $\pm$ 0.005	0.094–0.143	11	0.067 $\pm$ 0.001	0.059–0.071	11
<i>brevirostris</i> ^f	0.122 $\pm$ 0.003	0.094–0.143	17	0.067 $\pm$ 0.001	0.059–0.074	17
<i>geminus</i>	0.126 $\pm$ 0.002	0.113–0.143	15	0.078 $\pm$ 0.001	0.070–0.082	15
<i>habbemensis</i>	0.125 $\pm$ 0.004	0.117–0.135	4	0.078 $\pm$ 0.002	0.073–0.081	4
<i>terrestris</i>	0.131 $\pm$ 0.002	0.118–0.151	22	0.080 $\pm$ 0.001	0.070–0.092	22

blotches centrally. Undersides of the thighs are obscurely spotted and mottled in no clear pattern.

VARIATION IN TYPE SERIES: The two paratypes are a male of 18.7 mm SVL, and a gravid female of 22.7 mm. See table 1 for proportions. The paratypes have a light area across the tympanum as seen in the holotype, one has a pale vertebral hairline, and both have a pale interocular bar. Ventral surfaces are similar to those of the holotype.

ADVERTISEMENT CALL: The call,⁴ recorded by Dr. Blum in June 1979, is a series of four to seven (mean 5.0) notes given at an average rate of 1.9 per sec (1.6–2.2), with 2–23 (mean 11.5) pulses per note. Call duration averages 2.4 sec (1.6–4.0), and note duration 0.293 sec (0.099–0.378). The notes are pulsed slow enough that the human ear perceives each note as a series of rapid clicks

(fig. 6, table 2). The dominant frequency is 2800–3250 Hz, though within any one call the span is less. Two male specimens were taken at the type locality, UPNG 9520 and 9522; presumably one of these uttered the call displayed in figure 6.

Dr. Blum obtained one of the nine recorded calls of this species at the 3500 m locality where he recorded and collected *O. brevicrus* and possibly *O. habbemensis* (see account of the latter species). Unfortunately, none of the specimens from the 3500 m site is *O. alticola*, so the locality is without a physical voucher.

COMPARISONS WITH OTHER SPECIES: *Oreophryne alticola* differs from *O. brevicrus* most conspicuously in its smaller hands and smaller digital disks; there is no overlap between these species in the ranges of these characters (table 1). The smaller eyes and shorter eye-naris span of *alticola* distinguish it from *O. habbemensis*, *O. terrestris*, and *O. geminus* (table 1).

⁴ Archived on AMNH Herpetology Department tape cassette no. 241.

TABLE 1
(Continued)

	IN/SVL			HD/SVL		
	Mean $\pm \sigma_m$	Range	N	Mean $\pm \sigma_m$	Range	N
<i>alticola</i>	0.084 $\pm$ 0.003	0.079–0.088	3	0.231 $\pm$ 0.004	0.225–0.238	3
<i>brevicrus</i> ^a	0.089 $\pm$ 0.002	0.086–0.094	5	0.279 $\pm$ 0.005	0.270–0.291	5
<i>brevicrus</i> ^b	0.092 $\pm$ 0.003	0.074–0.107	9	0.271 $\pm$ 0.003	0.257–0.289	10
<i>brevicrus</i> ^c	0.091 $\pm$ 0.002	0.074–0.107	14	0.274 $\pm$ 0.003	0.257–0.291	15
<i>brevirostris</i> ^d	0.094 $\pm$ 0.002	0.088–0.103	6	0.237 $\pm$ 0.006	0.220–0.256	6
<i>brevirostris</i> ^e	0.094 $\pm$ 0.002	0.082–0.106	11	0.231 $\pm$ 0.004	0.206–0.250	11
<i>brevirostris</i> ^f	0.094 $\pm$ 0.002	0.082–0.106	17	0.233 $\pm$ 0.003	0.206–0.256	17
<i>geminus</i>	0.101 $\pm$ 0.001	0.093–0.111	15	0.244 $\pm$ 0.003	0.213–0.263	15
<i>habbemensis</i>	0.085 $\pm$ 0.001	0.082–0.089	4	0.237 $\pm$ 0.006	0.233–0.247	4
<i>terrestris</i>	0.109 $\pm$ 0.001	0.099–0.122	22	0.242 $\pm$ 0.003	0.217–0.274	22

	FD/SVL			TD/SVL		
	Mean $\pm \sigma_m$	Range	N	Mean $\pm \sigma_m$	Range	N
<i>alticola</i>	0.034 $\pm$ 0.003	0.031–0.040	3	0.030 $\pm$ 0.002	0.026–0.033	3
<i>brevicrus</i> ^a	0.051 $\pm$ 0.003	0.042–0.057	5	0.043 $\pm$ 0.003	0.035–0.049	5
<i>brevicrus</i> ^b	0.049 $\pm$ 0.001	0.044–0.055	10	0.045 $\pm$ 0.002	0.038–0.055	10
<i>brevicrus</i> ^c	0.050 $\pm$ 0.001	0.042–0.057	15	0.044 $\pm$ 0.001	0.035–0.055	15
<i>brevirostris</i> ^d	0.033 $\pm$ 0.002	0.028–0.040	6	0.031 $\pm$ 0.001	0.028–0.036	6
<i>brevirostris</i> ^e	0.034 $\pm$ 0.001	0.030–0.038	11	0.030 $\pm$ 0.001	0.025–0.033	11
<i>brevirostris</i> ^f	0.034 $\pm$ 0.001	0.028–0.040	17	0.030 $\pm$ 0.001	0.025–0.036	17
<i>geminus</i>	0.036 $\pm$ 0.001	0.030–0.041	15	0.032 $\pm$ 0.001	0.025–0.039	15
<i>habbemensis</i>	0.039 $\pm$ 0.002	0.034–0.044	4	0.036 $\pm$ 0.001	0.034–0.038	4
<i>terrestris</i>	0.037 $\pm$ 0.001	0.031–0.042	22	0.033 $\pm$ 0.001	0.024–0.042	22

^a Type series.^b Specimens from 3500 m.^c All *O. brevicrus*.^d Specimens from Mt. Elit.^e Specimens from Gunung Mandala.^f All *O. brevirostris*.

HABITAT AND HABITS: Nothing is on record, although subalpine grassland may be inferred from the elevation of the type locality.

DISTRIBUTION: Known from the type locality and, on the basis of a tape recording of the call, from: Indonesia, Papua, central mountain range south of Serabum, ca. 30 km S, 65 km E of Angguruk, 3500 m, ca. 4°31'S, 140°00'E (see fig. 9).

REMARKS: The type locality is one of the highest sites in New Guinea known to be inhabited by frogs. Another microhylid, *Oxydactyla stenodactyla*, lives even higher at 4000 m on Mt. Wilhelm, Papua New Guinea (Zweifel, 2000: 87).

Oreophryne brevicrus Zweifel Figure 5

Oreophryne brevicrus Zweifel, 1956: 23 (type locality, "at an elevation of 2800 meters, 9 kilometers northeast of Lake Habbema, Netherlands New Guinea [Indonesia: Papua]", holotype AMNH A-43699,⁵ collected by W.B. Richardson on the Third Archbold Expedition [Indisch-Amerikansche Expeditie] on October 15, 1938).

DIAGNOSIS: *Oreophryne brevicrus* differs from the other montane species in having relatively long legs (TL/SVL $\geq$ 0.350) and relatively broad finger disks (FD/SVL $\geq$

⁵ Erroneously given as A-43669 in the original description.

Fig. 5. *Oreophryne brevicrus*, UPNG 9525, SVL 27.6 MM, male.

0.042). Used together, these traits will separate most *brevicrus* from the other five montane species. See Comparisons with Other Species.

MORPHOLOGY: Head slightly narrower than body, snout subacute to slightly rounded in dorsal view, truncate in profile; canthus rostralis rounded, loreal region sloping outward, barely convex, nares just visible from above; eyes lateral, corneal outline visible from below, interorbital space wider than eyelid. Tympanum small, indistinct. Fingers unwebbed, relative lengths $3 > 4 > 2 > 1$, first well developed, one-half length of second or slightly greater and with a small disk, disks of other fingers broader than penultimate phalanges. Legs short, maximum TL/SVL 0.418; toes unwebbed,⁶ relative lengths $4 > 3 \approx 5 > 2 > 1$, or the fifth slightly longer than the third, all with disks broader than terminal phalanges. Subarticular elevations of hands and feet low and rounded. Dorsum slightly rugose, a weak postorbital-supratympanic fold. The connection be-

tween scapula and procoracoid is cartilaginous in three of the UPNG specimens examined (but see Remarks).

COLOR AND PATTERN: In preservative these frogs are various shades of brown. The dorsal region, defined by weak scapular folds, may be darker or lighter than the flanks and usually has obscure darker spots, as do the flanks. The top of the head may be uniform brown, or the area anterior to the midocular region abruptly paler, or there may be a pale interocular bar. The loreal region may be paler or darker than the top of the snout. A short, dark postocular line may define a lighter region below it. The ventral surfaces may show an even scattering of melanophores on a pale background or may be uniformly spotted or mottled with the chin either the same or more densely pigmented. The groin and anterior and posterior surfaces of the thighs may be uniformly pale or vaguely mottled. In short, there is nothing distinctive in the color pattern of preserved specimens.

Notes taken from color photographs and referring to the series RMNH 25191–24199 (Valentý Mtns.) mention “one golden brown with darker loreal region, vertebral light line; another black with tiny yellow spots all over dorsal surfaces.”

VARIATION IN SIZE AND PROPORTIONS: Specimens in the type series are 15.9–24.4 mm SVL, with two males being 19.6 and 22.0 mm. The other specimens of this group are in poor condition and were not sexed. The UPNG specimens include adult males of 21.1–29.3 mm and a 24.9 mm female. A decision as to whether the average difference in body size of the two samples is meaningful must await larger samples.

Average proportions in the two samples (table 1) are similar and ranges overlap greatly. Given larger sample sizes, slight differences (for example, TL/SVL) might well be reduced. Regression lines for these samples are closely similar.

ADVERTISEMENT CALL: The call⁷ is a series of 18–23 short, harsh-sounding notes uttered at a mean rate of 4.6 notes per sec (range 4.0–4.9) over a span of about 4–5 sec. The notes average 0.082 sec in duration (0.077–

⁶ The original description (Zweifel, 1956: 24) stated “toes with a basal web”. We now regard the toes as essentially unwebbed.

⁷ Archived on AMNH Herpetology Department tape cassette no. 241.

0.087) and comprise 4–11 (mean 8.5) discrete pulses (table 2, fig. 6). A dominant frequency is not well resolved, but varies in the range of 1600–2200 Hz. The initial note of a call is the shortest in all five calls analyzed, accounting for much of the variation in note duration and number of pulses in a note. We have no information on frequency of calling or on temperatures of the frogs recorded. Recordings were made by Dr. J. Paul Blum in June 1979 south of Serabum, Papua. No vouchers were identified, but presumably they are among the specimens from that locality (see Locality Records and Specimens Examined).

COMPARISONS WITH OTHER SPECIES: The TL/SVL ratios of *Oreophryne terrestris* and *O. brevircus* overlap completely, and in a scatter diagram combining TL/SVL and FD/SVL the arrays for the two species are separate but the plots for FD/SVL abut closely. Most questionable specimens of these species may be diagnosed by comparing IN/SVL ratios: <0.100 in *brevircus*, >0.100 in *terrestris*. The advertisement calls are distinctly different. The other species treated here are readily distinguished from *brevircus* by the characters given in the diagnosis.

HABITAT AND HABITS: Archbold et al. (1942: 263) described the type locality as “heavily forested country consisting of parallel spur ridges and very narrow valleys or ravines.” There are no specifics as to exact habitat of frogs in the type series.

Dr. J. Paul Blum collected and tape recorded this species in montane rainforest at an elevation of 3500 m. This was “a rocky area where water was running down a wide and long rock . . . the edge of the rock-plateau was covered with moss and low vegetation and there I caught the frogs which were sitting under moss” (personal commun.). Similarly J.M. Mangen, the collector of RMNH 24192, recorded the habitat as “grass tussocks on bare rock, 3350 m.” (notes accompanying specimen).

DISTRIBUTION: High elevations (2800–3500 m) in the central ranges of eastern Papua from the vicinity of Lake Habbema eastward to about 70 km southeast of Angguruk (see fig. 9).

LOCALITY RECORDS AND SPECIMENS EXAMINED: Indonesia, Papua: 9 km NE of Lake

TABLE 2
Advertisement Calls of Four Species of *Oreophryne*
(Call duration and note duration are given in seconds)

Species	Call duration		N ^a	Notes per call		Notes per sec		Note duration		Pulses per note		Dominant Hz
	Mean	Range		Mean	Range	Mean	Range	Mean	Range	Mean	Range	
<i>alticola</i>	2.41	1.59–4.03	9	5.0	4–7	1.9	1.6–2.2	0.293	0.225–0.344	11.5	2–23	2800–3300
<i>brevircus</i>	4.45	3.98–4.83	5	20.8	18–23	4.6	4.4–4.9	0.082	0.077–0.087	8.5	4–11	1600–2200
<i>terrestris</i>	1.83	1.47–2.98	7	13.8	12–16	7.9	6.3–8.4	0.048	0.033–0.060	5.5	2–15	3200–3400
<i>geminus</i>	9.30	8.17–12.27	12	24.9	20–28	2.2	1.4–2.7	0.205	0.152–0.299	13.7	9–21	2600–3300
Unknown ^b	2.35	—	1	10	—	4.1	—	0.107	0.085–0.118	0	—	2100–2150

^a Number of calls analyzed except for call duration of *geminus*, where $N = 10$.

Fig. 6. Waveforms and audiospectrograms of advertisement calls of two species of *Oreophryne*. **Top:** four successive notes of *O. alticola* (the last incomplete) graphed with 59- and 300-Hz filters. **Bottom:** nine successive notes of *O. brevicrus* graphed with 59- and 300-Hz filters. See species accounts for pertinent data.

Habbema, 2800 m (AMNH A-43697, 43699–43702); central mountain range south of Serabum, ca. 30 km S, 65 km E of Angguruk, 3500 m, ca. 4°31'S, 140°00'E (UPNG 9517–9519, 9523–9528)⁸; southern slopes of Valentyn Mountains, 3350 m (RMNH 24192⁹).

REMARKS: The poor condition of the specimens in the type series interferes with determination of sex and confirmation of the nature of the procoracoid-scapula connection, and makes other morphological assessment less than optimal. On the basis of in-

formation available at present, assignment of the samples from 3350 and 3500 m to *brevicrus* is reasonable. Fresh material and recordings of vocalizations from the type locality are needed to confirm this tentative conclusion.

The type series included a specimen, AMNH A-43694, from Lake Habbema, Papua. It now appears that a different species occurs at Lake Habbema (see account of *O. habbemensis*), and it is likely that AMNH A-43694 represents that species. Unfortunately, the specimen is in too poor condition to allow the measurements critical for specific assignment to be made.

It seems ironic that this, the first high-mountain species to be described, was initially distinguished by its short legs and narrow digital disks, whereas with respect to leg length and disk size it now is seen to occupy

⁸ All the UPNG specimens of *O. brevicrus* except UPNG 9524 were destroyed. See Type Material in the account of *O. alticola*.

⁹ Nine specimens collected along with RMNH 24192 (RMNH 14191, 24193–24199) probably are *O. brevicrus* but their condition does not permit measurements to be made with the precision necessary for identification.

Fig. 7. *Oreophryne brevirostris* holotype, ZMB 65110, SVL 28.1 mm.

a position in the spectrum of montane species closest to the more typical *Oreophryne*.

***Oreophryne brevirostris*, new species**
Figure 7

HOLOTYPE: ZMB 65110, collected by M. Balke on September 16–17, 1993, in Papua, Indonesia, on Gunung Mandala (formerly Mt. Juliana), 140°20'E, 4°40'S, at an elevation of 3400–3500 m.

PARATYPES: ZMB 65111–65120, same data as holotype; ZMB 65125–65130, collected by M. Balke on October 10, 1993, in Papua, Indonesia, on Mt. Elit, 139°12'E, 4°12'S, at an elevation of 3500 m.

ETYMOLOGY: The name is an adjective derived from the Latin *brevis* (short) + the suffix *-rostris*, referring to the species' distinctive morphology.

DIAGNOSIS: The principal distinguishing feature of *O. brevirostris* is its relatively short snout, an attribute it shares with *O. alticola* (see diagnosis of that species). The mean EN/SVL of 0.067 is less than the minimum for the other four species but there is some overlap in ranges down to about 0.070. Most other proportions broadly overlap those of the other four species (see Comparisons with Other Species).

DESCRIPTION OF HOLOTYPE: Adult female (gravid) with the following measurements and proportions: SVL 28.1, HW 9.8, TL 8.5, EY 2.65, EN 1.65, IN 2.3, HD 6.1, FT 9.5, FD 0.95 (penultimate phalanx 0.6), TD 0.7 (0.6); HW/SVL 0.349, TL/SVL 0.302, EY/SVL 0.094, EN/SVL 0.059, IN/SVL 0.082, HD/SVL 0.217, FT/SVL 0.338, FD/SVL 0.034, TD/SVL 0.025.

Head relatively broad but narrower than the rotund body; snout blunt, slightly rounded in profile but scarcely projecting beyond lower jaw; canthus rostralis rounded, loreal region sloping only slightly outward; nares slightly visible from above; eyelid narrower than interorbital space (2.0 vs. 2.6 mm); tympanic annulus scarcely visible, about 1 mm in diameter. Legs short. Fingers unwebbed, relative lengths $3 > 4 > 2 > 1$, first about one-half length of second, all with terminal disks, those of fingers 2–4 slightly broader than penultimate phalanx, subarticular and inner metacarpal elevations very low and rounded. Toes unwebbed, relative lengths $4 > 5 > 3 > 2 > 1$, fifth little longer than third, first reaches to base of disk of second, subarticular and inner metatarsal elevations low and rounded, the latter elongate. Terminal disks of all toes narrow, scarcely broader than penultimate phalanx. Body lacking any conspicuous tubercles or ridges.

In preservative the general appearance is pale yellowish tan with a few darker markings. The dorsal ground color of the body (posterior to the eyes) and limbs is yellowish tan. Two brown dorsolateral stripes begin on the nape and converge slightly before spreading apart and becoming indistinct in the lumbar region. There are indistinct darker areas on the body and limbs. The eyelids and upper surface of the snout have a pale yellow ground color overlain with gray splotches. The nostrils are ringed with yellow and there

Fig. 8. *Oreophryne geminus* holotype, AMS R144521, SVL 18.5 mm, male; Cogger photos.

is a dark gray area between nostril and eye. The upper lip is pale yellow and the area between lip and eye a darker yellowish tan. A diagonal pale yellow swath, bordered above and below by brown, starts by the posterior corner of the eye, spreads and passes over the tympanum before fading out near the arm insertion. The groin is pale with darker spots. The anterior surface of the thigh is light brown with darker spots, the posterior side light brown with faint darker spots. The palms are pale yellow and unmarked, the soles light brown. The ventral surfaces are pale yellowish white with faint indication of a darker pattern and no regional differentiation.

VARIATION IN TYPE SERIES: The largest specimens are two females from the type locality measuring 28.0 and 28.1 mm. The largest in the smaller Mt. Elit series is an adult female of 21.5 mm. The largest males in the two samples are 20.3 mm (Mt. Juliana) and 19.1 mm (Mt. Elit). Body proportions in the two samples are closely similar (table 1), and individual measurements adhere closely to common regression lines.

ADVERTISEMENT CALL: Not known.

COMPARISONS WITH OTHER SPECIES: An EN/SVL ratio of 0.073 or greater distinguishes the four type series specimens of *O. habbemensis* from all but one *O. brevirostris*. Similarly, EN/SVL $\leq$ 0.070 separates 14 of 17 *O. brevirostris* from all 22 *O. terrestris*,

and EN/SVL $\geq$ 0.072 separates 13 of 15 *O. geminus* from 16 of 17 *O. brevirostris*. An EN/SVL $\geq$ 0.072 distinguishes 12 of 14 *O. brevicrus* from 16 of 17 *O. brevirostris*. In the case of the last pair, the broader finger disks of *brevicrus*, FD/SVL $\geq$ 0.042, provide complete separation.

HABITAT AND HABITS: The specimens were taken in montane grassland at elevations of 3400–3500 m.

DISTRIBUTION: Known from the type locality, Gunung Mandala (Mt. Juliana) in eastern Papua and from Mt. Elit, 140 km to west-northwest (see fig. 9).

Oreophryne geminus, new species
Figure 8

HOLOTYPE: AMS R144521 (field no. AMH 33941), collected by Harold Cogger on April 3, 1987, in West Sepik Province, Papua New Guinea, at Dokfuma Meadow south of Mt. Capella, Star Mountains, 05°01'S, 141°06'E, elevation 3080 m.

PARATYPES: JCUNQ 5597, AMS R138846–138851, collected by S.J. Richards and G.R. Johnston on November 17, 1991 at the type locality; AMS R144522–144527, collected by H.G. Cogger on April 3 and 4, 1987, at the type locality.

ETYMOLOGY: The Latin *geminus*, a twin, is a noun in apposition referring to the close

Fig. 9. Distribution of high montane *Oreophryne* in Papua and western Papua New Guinea. Areas above 3400 m are in black; contour line approximates 2800 m. Numbered circles mark localities for *Oreophryne*: *O. alticola* (4 and 5, Central Ranges); *O. brevicrus* (1, NE of Lake Habbema; 4, Central Ranges); *O. brevirostris* (3, Mt. Elit; 6, Gunung Mandala [Mt. Juliana]); *O. habbemensis* (2, Lake Habbema); *O. terrestris* and *O. geminus* (8, Dokfuma, Star Mtns.); *Oreophryne* sp. (7, Mt. Antares, Star Mtns.). The broken north-south line marks the boundary between Papua (west) and Papua New Guinea (east).

Fig. 10. Plantar and palmar views of hand and foot of (A) *Oreophryne geminus* and (B) *Oreophryne terrestris*.

similarity of this species to a sympatric congener, *O. terrestris*.

DIAGNOSIS: The morphology of *O. geminus* is typical of that of most high-elevation *Oreophryne*, with no features that set it uniquely apart. Its distinction from *O. brevicrus*, *O. alticola*, and *O. terrestris* is based primarily on differences among the advertisement calls. In addition, *O. brevicrus* has larger hands (minimum HD/SVL 0.257 vs. *O. geminus* maximum 0.263) and larger finger disks (minimum FD/SVL 0.042 vs. maximum 0.041). Smaller eye size, shorter eye-naris span, and narrower internarial span all distinguish *O. alticola* from *O. geminus* (table 1). *O. terrestris* and *O. geminus* cannot

be distinguished by morphology (see account of *terrestris*). See Comparisons with Other Species for *O. habbemensis* and *O. brevirostris*.

DESCRIPTION OF HOLOTYPE: Adult male (vocal slits present, calling when captured) with the following measurements and proportions: SVL 18.5, HW 7.4, TL 6.4, EY 2.65, EN 1.5, IN 1.75, HD 4.4, FT 6.8, FD 0.65 (penultimate phalanx 0.45), TD 0.5 (0.4); HW/SVL 0.400, TL/SVL 0.346, EY/SVL 0.143, EN/SVL 0.081, IN/SVL 0.095, HD/SVL 0.238, FT/SVL 0.368, FD/SVL 0.035, TD/SVL 0.027.

Head slightly narrower than body, snout bluntly rounded seen from above, nearly ver-

Fig. 11. Plantar and palmar views of hand and foot of (A) *Oreophryne habbemensis* and (B) *Oreophryne brevirostris*.

tical in profile; nares lateral, barely visible from above; canthus rostralis rounded, loreal region steep, shallowly concave; eyelid narrower than interorbital space (1.5 vs. 2.0 mm); tympanic annulus indistinct, ca. 1.0 mm. Fingers unwebbed, relative lengths $3 > 4 > 2 > 1$, first about one-half length of second; all with grooved terminal disks scarcely broader than penultimate phalanges; subarticular elevations low, rounded, scarcely evident. Toes unwebbed, relative lengths $4 > 3 = 5 > 2 > 1$, disks scarcely broader than penultimate phalanx, terminal grooves present, subarticular elevations scarcely evident. Body with some low longitudinal ridges most prominent on the sides and some slight tuberculosity on the limbs.

In preservative the general appearance is medium brown with darker brown markings. A narrow, pale stripe passes from the snout tip to the posterior end of the body. Dorsal and lateral body surfaces have poorly defined short, dark bars and spots. The facial region is dark brown; a pale diagonal streak bordered above and below by dark brown passes over the tympanum. Upper surfaces of the limbs have indistinct darker markings on a pale background. The groin and anterior surface of the thigh are pale with a few small, brown flecks. The posterior surface of the thigh is darker but without definite pattern, becoming much paler and unmarked distally. This paleness continues beneath the tibia. Soles and palms are light brown, fingers and toes largely pale beneath but with moderately well-defined crossbands above. The chin, throat, chest, and abdomen show a fine brown reticulum on a pale background.

In life the dorsal surfaces were brown slightly mottled with tan. The middorsal stripe was yellow, and the top of head from middle of eyelids to snout tip yellowish, paler than body, with obscure darker markings. The venter had a fine gray-brown maculation that contrasted only slightly with the more yellowish ground color. The chin had less intense dark maculation and appeared paler than the chest and abdomen.

VARIATION IN TYPE SERIES: Adult males measure 18.0–21.0 mm SVL; the only gravid female among the paratypes is 21.2 mm. (See Remarks in the account of *O. terrestris* for the assignment of the last specimen to this

species.) However, three female specimens among those collected by Barry Craig (see Remarks under *O. terrestris*) that we cannot positively identify to species have IN/SVL and TL/SVL ratios that in combination could ally them with *O. geminus* rather than *O. terrestris*. They measure 22.1, 23.5, and 25.0 mm SVL. Proportions of the holotype and paratypes are summarized in table 1. See figure 10 for the hand and foot proportions of *O. geminus*.

Only 2 of the 15 specimens resemble the commonest dorsal pattern type seen in *O. terrestris*, and in these the paravertebral band is broken. The infrequent variant in *O. terrestris* having a linear pattern with heavy spotting in the pale dorsolateral field is more common in *O. geminus* (8 specimens). Two specimens lack a vertebral stripe and have irregular dark spotting between the dark lateral fields. The pattern of the ventral surfaces varies individually from a fine, weak reticulum to a much bolder scattering of larger dark spots. Generally the chin, chest, and abdomen are patterned much alike.

ADVERTISEMENT CALL: The call¹⁰ is a train of brief, pulsed notes: call duration 8.2–12.3 sec (mean 9.3); notes per call 20–28 (mean 24.9); rate of calling 1.4–2.7 notes per sec (mean 2.23); note duration 0.109–0.347 sec (mean 0.205); pulses per note 9–21 (mean 13.7); dominant frequency typically within the range of 2600–2900 Hz, though one individual persistently called at 3200–3300 Hz. SJR recorded two of the calls on November 17, 1991, at an air temperature of 9.0°C, HGC the remainder on April 3, 1987, at 11.6°C.

This assessment is based on 10 to 12 calls (table 2), only 2 of which could be attributed to particular specimens, one being the holotype. It is likely that fewer than 12 individual frogs were involved.

COMPARISONS WITH OTHER SPECIES: The two species for which we have no recordings of advertisement calls and rely upon morphology for comparison with *O. geminus* are *O. brevirostris* and *O. habbemensis*. The mean eye-naris span of *brevirostris* is significantly shorter than that of *geminus* (table 1).

¹⁰ Archived on AMNH Herpetology Department tape cassette no. 291.

Fig. 12. Habitat of *Oreophryne geminus* and *O. terrestris*, Dokfuma Meadow, Western Province, Papua New Guinea, November 1991; Richards photo.

A dividing line set at $EN/SVL = 0.070$ correctly places 14 of 17 *brevirostris* and 14 of 15 *geminus*. *O. habbemensis* is even more like *O. geminus* in proportions. The internarial span of *habbemensis* averages shorter; a regression plot (fig. 16) separates *habbemensis* from *geminus* with no overlap. A similar difference appears in the plot of finger disk size.

HABITAT AND HABITS: The Dokfuma site (fig. 12) is a subalpine meadow in karst terrain where moss forest clothes the higher elevations (ridgetops and steep upper slopes). Many of the valleys and lower slopes are open herb fields or fern fields of ferns, mosses, and scattered tussock grasses. Sparse to very dense stands of cycadlike tree ferns (*Cyathea* sp.) dominate the open areas (fig. 13). Large moss mounds, averaging about 1 m in height and usually 1–2 m in diameter, are scattered across the landscape, usually in close proximity to the forest edges. Small streams dissect the area, many disappearing into sinkholes in the limestone rock.

Both HGC and SJR noted that *O. geminus*

nearly always called from elevated sites—usually moss mounds—and sometimes climbed partway up a fern frond or grass stalk. In contrast, *O. terrestris* usually called from open ground.

DISTRIBUTION: Known only from the type locality (fig. 9).

***Oreophryne habbemensis*, new species**
Figure 14

HOLOTYPE: ZMB 65123, collected by M. Balke on September 16–17, 1993, at Lake Habbema, 3000–3500 m, ca. 4 km S, and 32 km W of Wamena, Papua, Indonesia.

PARATYPES: ZMB 65121, 65122, and 65124 with the same data as the holotype.

ETYMOLOGY: The name is an adjective based on the type locality.

DIAGNOSIS: This species has no unique morphological features, but for the most part it differs from the other high-montane *Oreophryne* in average proportions that, taken collectively, differ significantly from those of the other four species: TL/SVL 0.359, $EY/$

Fig. 13. Habitat of *Oreophryne geminus* and *O. terrestris*, Dokfuma Meadow, Western Province, Papua New Guinea, April 1987; Cogger photo.

SVL 0.125, EN/SVL 0.078, IN/SVL 0.085, HD/SVL 0.237, FD/SVL 0.039 (see Comparisons with Other Species).

DESCRIPTION OF HOLOTYPE: Male, presumably adult from its size, with the following measurements and proportions: SVL 20.6, HW 8.0, TL 7.5, EY 2.65, EN 1.6, IN 1.7, HD 4.8, FT 7.9, FD 0.9 (penultimate phalanx 0.55), TD 0.7 (0.6); HW/SVL 0.388, TL/SVL 0.364, EY/SVL 0.129, EN/SVL 0.078, IN/SVL 0.083, HD/SVL 0.233, FD/SVL 0.044, TD/SVL 0.034.

Head a little narrower than body; snout rounded, scarcely projecting in profile; nares barely visible from above; lores steep, slightly concave; canthus rostralis rounded; eyelid narrower than interorbital space (2.0 vs. 2.5 mm); tympanum scarcely visible, about 1 mm in diameter. Fingers not webbed, relative lengths $3 > 4 > 2 > 1$, first about one-half length of second, disks scarcely broader than penultimate phalanges, terminal grooves present, subarticular elevations scarcely evident. Toes not webbed, relative lengths $4 > 3 > 5$

$> 2 > 1$, first more than one-half length of second with a narrow but distinct terminal disk.

In preservative the middorsal area is brown with some darker spotting. Irregular, somewhat broken dark dorsolateral lines converge slightly in the scapular region and then diverge. A middorsal light line is present but no lumbar ocelli. Lateral body surfaces are pale with some darker spotting. The snout and eyelids are yellowish white with a sparse melanic stipple, lores and region below eyes brown. A pale, broad, diagonal postocular yellow swath is bordered above by a dark streak and by a weaker one below. The groin and anterior of the thighs are pale with no distinct spots, the posterior and top of the thighs brown. The venter is pale yellowish with no distinct markings.

VARIATION IN TYPE SERIES: Two males measure 20.4 and 20.6 mm and two females 23.1 and 24.8 mm. There is little variation in proportions (table 1). ZMB 65122 has a cartilaginous procoracoid-scapula connection.

Fig. 14. *Oreophryne habbemensis* holotype, ZMB 65123, SVL 20.6 mm.

Color and pattern in the topotypic specimens vary only slightly. One lacks a mid-dorsal line. The top of the snout varies from much paler than the postocular dorsum to only slightly so.

ADVERTISEMENT CALL: Not known, but see Remarks below.

COMPARISONS WITH OTHER SPECIES: Smaller hands ($HD/SVL \leq 0.025$) and narrower finger disks ($FD/SVL \leq 0.034$) distinguish *O. habbemensis* from *O. brevicrus* (table 1). The FD/SVL ratios of these two species

Fig. 15. Regression of third finger disk width on snout-vent length in *Oreophryne brevicrus* (□) and *O. habbemensis* (X).

overlap slightly; but regression comparisons provide some distinction (fig. 15). Larger eyes ($EY/SVL \geq 0.115$) and greater eye-naris span ($EN/SVL \geq 0.070$) separate *O. habbemensis* from *O. alticola*. The ranges of EN/SVL ratios of *O. brevirostris* and *O. habbemensis* overlap slightly, but EN/SVL of ≤ 0.072 for *brevirostris* and ≥ 0.075 for *habbemensis* leaves only 1 of 17 of the former and one of four of the latter unidentified. In most respects of morphology *O. habbemensis* and *O. terrestris* are similar if not identical. However, their internarial spans differ markedly, with the mean IN/SVL for *terrestris* (0.109) greater than that of *habbemensis* (0.085) and with no overlap in the ranges. *O. geminus* is also quite similar in proportions to *O. habbemensis*. Again, *habbemensis* has the narrower internarial span (mean IN/SVL 0.085 vs. 0.101) and there is no overlap in the ranges. Regression comparison illustrates the distinction (fig. 16). *O. habbemensis* may be a larger species, but there are no female specimens of *geminus* for comparison.

HABITAT AND HABITS: The collector noted "grassland". Archbold et al. (1942: 266) described the "major topographic features" of the vicinity of Lake Habbema as "timbered ridges" and "nearly flat broad grassy valleys". These authors determined the elevation of Lake Habbema as 3225 m.

Fig. 16. Regression of internarial span on snout-vent length in *Oreophryne geminus* (□) and *O. habbemensis* (X).

Fig. 17. *Oreophryne* sp., UPNG 9516, SVL 23.6 mm, not sexed.

DISTRIBUTION: Known from two localities: the type locality and provisionally from a site ca. 30 km S, 65 km E of Angguruk, 3500 m, Papua, Indonesia (fig. 9); but see Remarks.

REMARKS: A specimen (UPNG 9516, fig. 17) that Dr. Blum collected along with 9 *O. brevicrus* at 3500 m in the central ranges south of Serabum differs from all 14 *brevicrus* in several respects. The legs are shorter than in *brevicrus* (TL/SVL 0.342 vs. minimum 0.357), the third finger disk narrower (FD/SVL 0.038 vs. 0.042), and the hands only slightly larger than the minimum seen in *brevicrus* (HD/SVL 0.263 vs. minimum 0.257). Eye size, eye-naris span, and internarial span are all within *brevicrus* ranges but are all below the averages. Hence, this does not appear to be a specimen of *brevicrus*. However, UPNG 9516 does not fit comfortably in any other of the five species we recognize.

Oreophryne alticola has somewhat smaller eyes, a much shorter eye-naris span, and much smaller hands. The EY and EN ratios of UPNG 9516 are within the ranges of *O. brevirostris* but are low, while IN is minimal, HD high (out of range), and FD larger than average. The sum of these differences suggests that UPNG 9516 is not a specimen of *O. brevirostris*. The minimal EY and IN ra-

tios for *O. terrestris* are higher than those of UPNG 9516. Similarly, the EY of UPNG 9516 is at the minimum for *O. geminus* and the IN is below the minimum.

In most respects UPNG 9516 is similar to *O. habbemensis*: TL, EY, and IN are at the minima for *O. habbemensis* while EN and FD are well within range. Only HD is substantially different (HD/SVL 0.263 vs. a maximum of 0.247). The ventral surfaces of UPNG 9516 are distinctly mottled whereas the other specimens show only a hint of pattern. We provisionally refer this specimen to *O. habbemensis* but exclude it from paratype status and from the statistical summaries.

At the same locality where he recorded calls of *O. brevicrus* Dr. Blum recorded one distinctive call not associated with a particular specimen (see fig. 18 and "unknown" in table 2). In its various parameters the call does not fit well with any of the calls of any of the other species. In particular the call is not pulsed. The association of this call with the locality where UPNG 9516 was collected may be coincidental, but deserves consideration.

A specimen from Lake Habbema (AMNH A-43694) was part of the type series of *Oreophryne brevicrus* (Zweifel, 1956). It now appears more likely that the specimen is *O.*

Fig. 18. Waveform and audiospectrogram of advertisement call of an unidentified and unvouchered frog, presumably an *Oreophryne*. See Remarks under *O. habbemensis* and in table 2. Modulation in the initial note is presumably caused by a change in tape speed.

habbemensis, but its condition precludes a positive identification.

***Oreophryne terrestris*, new species**

Figure 19

HOLOTYPE: AMS R145378 (field no. AMH 33942), collected by Harold Cogger on April 4, 1987, in West Sepik Province, Papua New Guinea, at Dokfuma Meadow south of Mt. Capella, Star Mountains, 05°01'S, 141°06'E, elevation 3080 m.

PARATYPES: SAMA R59082, AMS R138843–138845, collected by S.J. Richards and G.R. Johnston on November 17, 1991, at the type locality; AMS R145379–145395, collected by H.G. Cogger on April 3 and 4, 1987, at the type locality.

TYPE LOCALITY: The type locality is not identified on any map that we have seen. Barry Craig, who collected there on the Star Mountains Expedition in 1965, informed us that Dokfuma in the local language means

“place where dog was cooked” (personal commun.).

ETYMOLOGY: The Latin adjective *terrestris* alludes to the close association of this species with the ground.

DIAGNOSIS: Insofar as montane *Oreophryne* are concerned, the morphology of *O. terrestris* is average, with standard ratios overlapping those of the other species in most instances. The principal distinguishing feature is a broad internarial span with the mean IN/SVL (0.109) exceeding the maxima of that of all other species except *O. geminus*. See Comparisons with Other Species for specific diagnostic information. The advertisement call is diagnostic among the four montane species whose calls are known.

DESCRIPTION OF HOLOTYPE: Adult male (vocal slits present, calling when captured) with the following measurements and proportions: SVL 17.9, HW 6.5, TL 6.7, EY 2.35, EN 1.4, IN 1.9, HD 4.0, FT 6.7, disk

Fig. 19. *Oreophryne terrestris* holotype, AMS R145378, SVL 17.9 mm, male; Cogger photos.

of third finger 0.55 (penultimate phalanx 0.4), disk of fourth toe 0.55 (0.45); HW/SVL 0.363, TL/SVL 0.374, EY/SVL 0.131, EN/SVL 0.078, IN/SVL 0.106, HD/SVL 0.224, FT/SVL 0.374, FD/SVL 0.031, TD/SVL 0.031.

Head slightly narrower than body, snout bluntly rounded seen from above, similar in profile; nares lateral, barely visible from above; canthus rostralis rounded, loreal region steep, shallowly concave; eyelid narrower than interorbital space (1.4 vs. 1.9 mm); tympanic annulus indistinct, ca. 1.0 mm. Fingers not webbed, relative lengths $3 > 4 > 2 > 1$, first about one-half length of second; disks scarcely broader than penultimate phalanx, terminal grooves present; subarticular elevations scarcely evident. Toes not webbed, relative lengths $4 > 3 = 5 > 2 > 1$, disks scarcely broader than penultimate phalanx, terminal grooves present, subarticular elevations scarcely evident. There are no prominent dorsal skin folds. Tuberculosity is more evident on the dorsal surfaces of the hind legs than on the body.

In preservative the dorsal ground color is light brown with darker markings that form a ragged paravertebral streak bordering a thin middorsal light line. Dark irregular spots and mottling dominate the light dorsolateral fields, bordered below by a dark lateral streak. The top of the snout is brown with

indistinct darker markings, followed by a pale midocular bar. The facial area—lores, beneath eye and lip—is dusky. A pale diagonal bar extends from immediately behind the eye to the arm, passing through the tympanum. The arms and hands are pale brown above with darker spots. The groin and anterior surface of the thigh are dusky without dark markings. The posterior of the thigh is dusky with dark spots around the cloacal opening. The tibia is pale dorsally with darker spots. The chin, throat, chest, and abdomen have a dull yellow ground color with moderately large and well separated, irregular dark spots that are more distinct on the abdomen than anteriorly.

In life the dorsal surfaces were dark brown with some paler mottling. The narrow, dark edged, middorsal stripe was yellow, as was the postorbital stripe. The chest and abdomen were pale yellow with heavy black maculation, the chin less heavily marked.

VARIATION IN TYPE SERIES: Adult males measure 16.8–19.7 mm SVL; three gravid females are 19.0–19.1 mm (but see Remarks). See table 1 for proportions. See figure 10 for proportions of fingers and toes.

The dorsal color pattern is variable. Most specimens have a narrow, pale vertebral stripe bordered by fairly regular dark paravertebral bands; a pale, largely unspotted dorsolateral band, darker than the vertebral

Fig. 20. Waveforms and audiospectrograms of advertisement calls of two species of *Oreophryne*. **Top:** five successive notes of *O. geminus* graphed with 59- and 300-Hz filters. **Bottom:** 15 successive notes of *O. terrestris* graphed with 59- and 300-Hz filters. See species accounts for pertinent data.

stripe; a narrower, dark lateral stripe (12 specimens). A minor variant differs in having the paravertebral band variously broken and mottled (8 specimens), whereas in others the pale dorsolateral band has heavy dark spotting (three specimens). In one specimen the dark paravertebral and lateral areas are broken. Only two specimens lack a pale vertebral stripe. In these the region between the lateral dark areas has irregular dark spots and lacks any hint of linearity.

In 17 specimens the abdomen has clusters of dark, irregular spots, with the size and number of spots being quite variable. The throat may be similar to the abdomen but often has a lower density and smaller size of spots. Five specimens have scarcely any dark spots.

ADVERTISEMENT CALL: The call¹¹ is a train

of brief, pulsed notes. The following summary is based on seven calls recorded by HGC on the evening of April 3, 1987 at an air temperature of 10.8°C, and one call recorded by SJR on November 16, 1991, air 9.6°C: call duration 1.47–2.98 sec (mean 1.71); notes per call 12–16 (mean 13.9); rate of call 6.6–8.4 notes per sec (mean 7.9); note duration 0.013–0.070 sec (mean 0.048 sec); pulses per note 2–7 (mean 5.4); dominant frequency 3200–3400 Hz. Calls occasionally begin with an abbreviated note, accounting for the wide range in note duration. The call of the holotype is included in this sample. See table 2 and figure 20.

COMPARISONS WITH OTHER SPECIES: *Oreophryne alticola* has smaller eyes, shorter eyenaris span, and a narrower internaris span than does *O. terrestris*, with no overlap in any of these ratios (table 1). The hand size of *O. brevicrus* averages greater than that of

¹¹ Archived on AMNH Herpetology Department tape cassette no. 291.

O. terrestris and the internarial span is narrower. A plot combining IN/SVL and HD/SVL correctly places all but 2 of 36 specimens (fig. 21, left). No single proportion distinguishes *O. terrestris* from *O. brevirostris*, but a plot combining the IN/SVL and EN/SVL ratios provides satisfactory separation (fig. 21, right). *O. habbemensis* has a much narrower internarial span, not overlapping that of *O. terrestris* (table 1). *O. terrestris* and *O. geminus* are essentially identical in all proportions except for internarial span and tibia length (table 1), but there is much overlap and superimposed plots of IN/SVL and TL/SVL for the two species (fig. 22) give inadequate resolution. Advertisement calls provide the only reliable means of identification. One of us (HGC) noted in the field that these two species differed in that *terrestris* had a tubercular dorsum and patterned venter, whereas *geminus* had a smoother back and little dark pigment on the venter (see figs. 8 and 19). Unfortunately, any such differences are largely obscured in the preserved specimens.

HABITAT AND HABITS: See the account of *O. geminus*.

DISTRIBUTION: Known only from the type locality (fig. 9).

REMARKS: Our inability to distinguish with confidence between preserved specimens of the two Dokfuma species dictates that the specimens collected by Barry Craig in 1965 must remain unassigned to species: SAMA R6463, 6469, 6470, 12630–12664. Our reference to female specimens of *O. terrestris* and *O. geminus* to their respective species accounts is based on their assignment to species in life by HGC (see above).

PROBLEMATIC SPECIMENS

A specimen (RMNH 17012) from an elevation of 3400 m on Mt. Antares in extreme eastern Papua is not readily identified with any of the other species treated here. It shares morphological features with other high montane species in being small (17 mm SVL) with short legs, small hands, and small digital disks. The collector noted "colour red-brown, thin yellow stripe on back".

Coming from the same massif (Star Mountains), and from a locality only about 27 km

from the site where *Oreophryne terrestris* and *O. geminus* are found, the Antares specimen might be expected to belong to one of those species. In several body proportions, however its measurements fall slightly outside of or barely within those seen in the relatively large samples of *terrestris* and *geminus*. Moreover, the differences assort in such a way that they do not suggest a closer similarity to one or other of these species. In fact, there is at least as much similarity to *Oreophryne brevirostris* from Mt. Mandala 65 km to the northwest. More specimens from Mt. Antares are needed to establish the systematic position of the population; recordings of the call should be given high priority.

A specimen (BPBM 4180) from "Star Mountains, 10,500 ft." (presumably West Sepik Province, PNG) bears no more specific locality data; its identity cannot be resolved.

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Fig. 21. **Left:** Comparison of hand and internarial ratios in *Oreophryne brevicrus* (□) and *O. terrestris* (X). **Right:** Comparison of internarial and eye-naris ratios in *Oreophryne brevirostris* (□) and *O. terrestris* (X).

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Fig. 22. Comparison of internarial and tibia length ratios in *O. terrestris* (X) and *O. geminus* (□).

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