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Source: Bulletin of the American Museum of Natural History, 2000(253) : 1-130

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0090(2000)253<0001:POTAMF>2.0.CO;2

PARTITION OF THE AUSTRALOPAPUAN MICROHYLID FROG GENUS *SPHENOPHRYNE* WITH DESCRIPTIONS OF NEW SPECIES

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 253, 130 pp., 80 figures, 14 tables
Issued May 22, 2000
Price: $12.00 a copy

ISSN 0003-0090

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ABSTRACT

Parker (1934) distinguished *Sphenophryne* from other genera of the Genyophryninae (Sphenophryninae in his work) by its pectoral girdle having a more nearly complete complement of bony and cartilaginous elements. Otherwise, the species he placed there were a diverse lot, including ones adapted for climbing, for living in or on leaf litter, or for a cryptic, even burrowing existence. The characteristics of the pectoral girdle are primitive compared to those of other genyophrynine genera, which have reduced or lost one or more of the elements. Thus, the common possession of a primitive girdle is inadequate as the sole character defining the genus. In the present work I review species with the supposedly diagnostic character of *Sphenophryne* and recognize four genera: *Sphenophryne* (monotypic), and three removed from synonymy—*Austrochaperina* (23 species), *Liophryne* (6 species), and *Oxydactyla* (5 species). The characters I use to define the genera are for the most part closely tied to the habits of the species and thus are subject to the criticism that homoplasy rather than synapomorphy is demonstrated. Regardless, the probability that the new arrangement identifies four monophyletic lines is considerably greater than that *Sphenophryne,* as it has been constituted, is monophyletic.

Sphenophryne, Liophryne, and *Oxydactyla* are confined to New Guinea. *Austrochaperina* has one species on New Britain, four endemic to northern Australia, one shared between Australia and New Guinea, and 18 on New Guinea and adjacent islands. The genus and species *Microbatrachus pusillus*, based on a hatchling from the Aru Islands, are considered unidentifiable. Of the 35 species recognized, 17 are described as new and one is removed from synonymy.

INTRODUCTION

In his classic monograph of the Microhylidae, Parker (1934) recognized the genus *Sphenophryne* with 10 species found in Australia and New Guinea and considered three genera as synonymous to it.[1] In more than six decades since, the only taxonomic modification at the generic level was the synonymization of *Microbatrachus* (which Parker recognized) with *Sphenophryne* (Tyler, 1978). The number of included species has risen from 10 to 18, mostly through discovery of new species (listed in Zweifel, 1985a, with an additional species in Zweifel, 1985b). Parker's diagnostic feature of the genus within the subfamily Sphenophryninae (Genyophryninae of current authors) was that the pectoral girdle had a more nearly complete set of ventral elements than did the other genera he recognized[2]: coracoids, clavicles that extend from the scapula to near the midline, procoracoid cartilages, and a cartilaginous sternum.

The set of features described for the pectoral girdle is unquestionably primitive compared to the more reduced states in all other genyophrynine genera and thus cannot diagnose a monophyletic clade. Species currently assigned to *Sphenophryne* on the sole basis of girdle structure are a diverse lot morphologically and ecologically, and they include scansorial, riparian, and terrestrial forms. The inevitable impression is that they may not be a monophyletic group. My principal objective has been to examine the suite of genyophrynine species with the primitive pectoral girdle, including several undescribed and synonymized taxa, in order to see if phylogenetic sense can be made and a defensible arrangement can be proposed that does not depend on shared primitive characters. Additional objectives were to identify and describe previously unrecognized species, to assess the status of names in synonymy, and

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[1] Parker (1934: 159) also reported a ''?*Sphenophryne* sp.'' based on embryos ''collected from the pitcher of a Nepenthes at Kuching [Sarawak],'' far from the known range of any genyophrynine microhylid. It is likely that this extralimital record is based on a rhacophorid, possibly *Philautus*, which oviposits in *Nepenthes* and whose larvae may metamorphose prior to hatching; see Dring (1979: 207–208) and Inger and Stuebing (1997: 163).

[2] *Oreophryne, Microbatrachus, Cophixalus,* and *Aphantophryne.*

to describe as far as possible the distribution and ecology of the species.

In a previous paper (Zweifel, 1985b) I reviewed the five Australian species of *Sphenophryne* in detail. Except for one of these that occurs also in New Guinea, they are not treated individually in this account but are considered where pertinent.

ACKNOWLEDGMENTS

Over the many years since initiating this project I have become increasingly in debt to many institutions and to colleagues without whose assistance I could have accomplished little. A list of institutions whose specimens I examined (or if not examined, as cited in the text) follows, with abbreviations and names of responsible parties.

AMNH	American Museum of Natural History, New York; C. Myers, L. Ford
AMS	Australian Museum, Sydney; H. Cogger, A. Greer, R. Sadlier
BMNH	British Museum (Natural History), London; B. Clarke
BPBM	Bishop Museum, Honolulu; Allen Allison, Carla Kishinami
FMNH	Field Museum of Natural History, Chicago; R. Inger
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge; José Rosado, E. Williams, J. Cadle
MNH	National Museum of Hungary, Budapest
MSNG	Museo Civico di Storia Naturale di Genova, Genoa; E. Tortonese, L. Capocaccia-Orsini
MTKD	Staatliches Museum für Tierkunde, Dresden
MZB	Zoological Museum, Bogor, Indonesia; S. Somadikarta, Siti Nuramaliati Prijonok, Curator Mumpuni
NMBA	Basel Natural History Museum, Basel
PNGM	National Museum and Art Gallery, Port Moresby, Papua New Guinea; J. Menzies, I. H. Bigilale
QM	Queensland Museum, Brisbane, Australia
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden; R. Hoogmoed, L. Brongersma
SAMA	South Australian Museum, Adelaide; Adrienne Edwards
UPNG	University of Papua New Guinea, Port Moresby; J. Menzies
YPM	Yale Peabody Museum, New Haven; Fred Sibley
ZMA	Zoological Museum, University of Amsterdam, Amsterdam; S. Daan
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen; Arne Schitz
ZSM	Zoologisches Sammlung des Bayerischen Staates, Munich; Frank Glaw

Fieldwork that permitted me to gain acquaintance with living individuals of certain species studied was supported by the American Museum of Natural History, the National Geographic Society (1968), the National Science Foundation (1964 and Alpha Helix Expedition, 1969), and the Sabin Conservation Fund (1987).

Individual thanks are in order to Linda Ford, for her efficient and prompt replies to my many requests for information and specimens from the AMNH; David Dickey, who produced some of the audiospectrograms; Allen Allison, James Menzies, and Stephen Richards, all of whom provided specimens, photographs, and tape recordings; Carol Townsend for the preparation of cleared and stained specimens; Joan Whelan for SEM photography; Wade Sherbrooke, Director of the AMNH Southwestern Research Station, for providing laboratory space where I carried out much of my work with specimens; and the British Library of Wildlife Sounds and Ian Redmond for the loan of tape recordings. Charles Myers' careful critique of the manuscript improved it significantly in a variety of ways, as did comments from two anonymous referees.

Fred Parker of Townsville, Queensland, Australia, deserves special mention. Not only did I have access to the multitudes of specimens he collected and generously deposited in several museums, but I was privileged to accompany him on patrol in the Eastern Highlands of Papua New Guinea in 1964, and again to share time in the field with him in 1968, 1969, and 1987.

As always, my wife, Frances W. Zweifel, applied her artistic talents to produce many original renderings for this paper in addition

to transforming my crude sketches into realistic drawings.

METHODS

ANATOMY: On most specimens examined I made a suite of measurements with dial calipers read to the closest 0.1 mm or, if appropriate, I used an ocular micrometer in a binocular dissecting microscope read to the nearest 0.05 mm. Sex of the specimen was apparent if the specimen was a male calling when captured. Otherwise, males were determined by the presence of vocal sac openings (absent in two species) or by examination of gonads, females were determined by examination of gonads. With the exception of a few dried preparations, descriptions of osteology derive from cleared and stained specimens (identified as ''C&S'' in lists of specimens examined). Color descriptions of living frogs are from my field notes and photographs, supplemented by notes and photographs provided by other collectors.

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. Distance between anterior and posterior edges of eye opening. It is sometimes necessary to push the eyeball up from within the mouth in order to approximate the condition in life.

FD. Width of disc of third finger measured at a right angle to the axis of the digit with the disc 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, with body flattened if necessary.

TD. Width of disc of fourth toe measured at a right angle to the axis of the digit with the disc 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. In most species 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 the third finger or fourth toe; actual lengths were not measured.

USE OF PROPORTIONS

Species of frogs usually differ in one or more body proportions, and these differences may be employed usefully in discriminating among species. Differences may be evident in comparisons of regressions of the measurements of body parts against body size (SVL), although overlap in ranges may hinder the use of regression data in species discrimination. I routinely calculated and plotted regression data for samples of all species. Ratios comparing body part size to SVL, of course, suffer from the same difficulty; that is, overlap between species ranges of ratios may be so great that the differences in proportions, although statistically and possibly biologically significant, may be largely useless for specific identification of individuals. An effective method of overcoming this problem utilizes two different ratios simultaneously, in each of which the two species being compared show different but overlapping ranges of variation. The statement takes this form or a variant thereof: ''Ratio A less than X *and* ratio B greater than Y, vs. ratio A greater than X *and* ratio B less than Y.'' A graphic presentation allows one to place a given specimen in the spectrum of points. Identifications may be greatly facilitated in this manner.

Ratios present another problem, however. Most proportions—at least those commonly used in systematics studies—change with growth. The degree and direction of change varies not only interspecifically, but also with the body part being considered. By using ratios of adults only, the ranges of variation can often be considerably reduced, leading to less overlap among species and more utility in keying. Ontogenetic change in proportions is discussed under Morphology.

LOCALITY RECORDS

A variety of circumstances hamper, even frustrate, fixing of localities of collection in New Guinea. Even in comparatively recently it has been difficult for field workers remote from towns or the few roads to pinpoint their location. Even as comprehensive maps become available (especially for Papua New Guinea), and with the increasing use of Geographic Positioning System technology, there remains a legacy of politically based and other sources of confusion in museum catalogs and published papers.

IRIAN JAYA: From the 1800s until 1963, the western half of New Guinea was under Dutch control; "Netherlands New Guinea" and "Dutch New Guinea" were the commonly used names. Following the Indonesian assumption of control, the name "Irian Barat" saw some usage (at least as late as 1967). This was followed by "Irian Jaya," as a Province of Indonesia. Quite recently the name was changed again to "Papua Barat" (or West Papua). In the present work I continue to use the more familiar Irian Jaya. Administrative subdivisions of Irian Jaya exist but rarely appear in museum records. Many geographic names established under Dutch governance have been replaced by Indonesian ones. For example, the principal city was Hollandia, then Sukarnapura, then Jayapura, now Port Numbai.

PAPUA NEW GUINEA: The eastern half of New Guinea has had a more complicated political history as well as much more biological collecting activity than has Irian Jaya. The first administrative organization of the northern part was by Germany in 1884 as Kaiser Wilhelmsland. This also included islands to the north and east—Neu Pommern (New Britain), Neu Mecklenburg (New Ireland), and many smaller islands. German New Guinea and Northeast New Guinea are other names often encountered in the literature and in museum records. Australia occupied Kaiser Wilhelmsland in 1914, and in 1920 the League of Nations mandated administrative control of the area to Australia as the Trust Territory of New Guinea.

TABLE 1
Names of Provinces of Papua New Guinea and Their Former District or Provincial Status

Current[a]	Former
East Sepik	Part of Sepik
Eastern Highlands	Eastern Highlands, including Simbu, Western Highlands, Southern Highlands, and Enga
Enga	Part of Eastern Highlands
Gulf	Part of Western
Madang	Madang
Milne Bay	Milne Bay
Morobe	Morobe
Northern (Oro)	Northern
Simbu (Chimbu)	Part of Eastern Highlands
Southern Highlands	Part of Eastern Highlands
West Sepik (Sanduan)	Part of Sepik
Western (Fly River)	Western, including present Gulf
Western Highlands	Part of Eastern Highlands

[a] Alternate names are in parentheses.

The southern part of Papua New Guinea was originally (1888) British New Guinea; in 1906 it was turned over to Australian administration and renamed Papua, later called the Territory of Papua but governed separately from the Territory of New Guinea. Governmental evolution subsequent to World War II produced the combined Territory of Papua New Guinea and then (1975) the independent nation of Papua New Guinea.

The territories of Papua and New Guinea were subdivided into administrative districts that, with nationhood, were redesignated as provinces. Many of these did not long retain their original integrity. New provinces were carved out of old, boundaries were adjusted, provinces were renamed, and alternate spellings were used. Even names used by the provincial and central governments disagree in some instances.

For Papua New Guinea, I have standardized province records according to the names and boundaries shown in King and Ranck (1982: 19). Where alternate (parenthetical) names are given, I have used the primary (older) one unless an alternative is well established (see table 1). In the same publication, another useful map (p. 17) compares province boundaries as of 1950 and 1980.

Many museum records for specimens from Papua New Guinea specify villages that appear only on the most detailed maps. Fortunately, there exists an excellent series of topographic maps for all of Papua New Guinea (Papua New Guinea 1:100,000 survey) upon which, with diligence, many of the more obscure villages can be located. An additional complication, however, is that villages do not always remain on the same spot, sometimes moving with slash and burn agriculture.

I have converted distances and elevations given in miles and feet in original records to kilometers and meters.

RECORDINGS

The tape recordings of frog calls used in this research came from a variety of sources, so differences in tape recorders and changes introduced in copying tapes are potential sources of variation. However, none of the calls compared differ in such subtle ways that these sources of error would be significant.

The audiospectrograms and waveforms illustrated were produced on a Kay 5500 DSP Sona-Graph. I made my analyses of calls—measurements of rates, note and call durations, dominant frequencies—with the aid of the CECIL computerized speech analysis system (Hunt, 1993). Originals or copies of the tape recordings used are, with one exception, stored and cataloged in the Department of Herpetology, American Museum of Natural History (details are in the species accounts or tables).

SYSTEMATICS

GENERA

I have pointed out in the introduction that the genus *Sphenophryne* as defined and diagnosed by Parker (1934) is not a defensible monophyletic group. The sole diagnostic character—the structure of the pectoral girdle—is a primitive state shared by the species Parker recognized as well as by others subsequently described. In my investigation of the species currently assigned to *Sphenophryne* as well as of undescribed species that fit the diagnosis used since Parker (1934), I have found no derived character that serves to unite all these species and validate *Sphenophryne* as a monophyletic clade. The diversity of the assemblage is greater than had been appreciated, but the species still do not fall into trenchant groups, either by criteria of shared derived characters or by traditional methods involving unpolarized similarities. I have, nevertheless, chosen to recognize four genera, for all of which the literature provides names. I think that the arrangement I adopt has a fair likelihood of grouping related species together and thus improves on the current situation. There is no implication, however, that the four genera recognized are more closely related to one another than they are to any other genyophrynine genera.

KEY TO GENERA

The user of this key should first determine whether the specimen in question has elongate clavicles that extend from the scapula to near the midline of the pectoral girdle. If not, the specimen belongs to a genus other than one of those treated here. If the clavicles are as described, it should be verified that there is no bony omosternum. If such is found, the specimen is likely to be a ranid and not a microhylid. Ranids of the genus *Platymantis* are especially likely to be confused with microhylids. This key is intended to apply to adult frogs; juveniles may differ in critical body proportions.

1. A single pointed tubercle on each eyelid; tips of digits (except 1st finger) broadened into flattened discs broader than penultimate phalanges, disc on 3rd finger broader than that on 4th toe .... *Sphenophryne*
   No eyelid tubercle; fingers without terminal discs or if discs present, that on 4th toe broader or rarely equal to that on 3rd finger 2

2. Tips of fingers pointed or rounded but not flattened into discs with distinct terminal grooves .... *Oxydactyla*
   Fingers and toes (except sometimes the 1st digit) with discs usually broader than the penultimate phalanges and with a distinct terminal groove 3
3. Fingers and toes with distinct rather than low, rounded subarticular elevations; legs long, minimum mean TL/SVL = 0.49 *Liophryne*
   Subarticular elevations indistinct to scarcely evident; TL/SVL rarely as large as 0.49 ... . *Austrochaperina*

Genus *Austrochaperina* Fry

Austrochaperina Fry, 1912: 87. Type species by original designation, *Austrochaperina robusta* Fry, 1912.

Sphenophryne: Nieden, 1926: 43 (*Austrochaperina* placed in synonymy of *Sphenophryne*). Parker, 1934: 152.

CONTENT: Twenty-three species; four of them endemic to Australia, one shared between Australia and New Guinea, and 18 endemic to New Guinea (including one in New Britain). The New Guinean species are *Austrochaperina adamantina*, new species; *Austrochaperina aquilonia*, new species; *Austrochaperina archboldi*, new species; *Austrochaperina basipalmata* (van Kampen); *Austrochaperina blumi*, new species; *Austrochaperina brevipes* (Boulenger); *Austrochaperina derongo*, new species; *Austrochaperina gracilipes* Fry; *Austrochaperina guttata*, new species; *Austrochaperina hooglandi* (Zweifel); *Austrochaperina kosarek*, new species; *Austrochaperina macrorhyncha* (van Kampen); *Austrochaperina mehelyi* (Parker); *Austrochaperina novaebritanniae*, new species; *Austrochaperina palmipes* (Zweifel); *Austrochaperina parkeri*, new species; *Austrochaperina polysticta* (Méhelÿ); *Austrochaperina rivularis*, new species; *Austrochaperina yelaensis*, new species. See below for the Australian endemics.

DIAGNOSIS: A genus of genyophrynine microhylid frogs (sensu Zweifel, 1971, and Burton, 1986) with the following combination of morphological characters: clavicles long and slender, reaching from scapula almost to midline of pectoral girdle; tips of fingers and toes (except sometimes the 1st) flattened and disclike with terminal grooves and typically broader than the penultimate phalanx, the disc of the 3rd finger narrower or no broader than that on the 4th toe; subarticular elevations low and rounded, almost undetectable in some species.

MORPHOLOGY: Adults of the several species range in maximum size from about 20 to 50 mm SVL. These are for the most part rather generalized frogs, lacking the adaptations to a semifossorial existence seen in *Oxydactyla* or those fitting *Liophryne* to rapid movement on the surface of the forest floor. Two species have toe-webbing, the only instances of this in any of the four genera treated.

HABITS AND HABITAT: I have only meager information on habits. Six species (two New Guinean and four Australian) are known to call from within leaf-litter on the forest floor, while another calls from exposed positions on grass stems in more open country. None is known to ascend to higher positions in shrubs or trees, and the morphology of most species suggests that the leaf-litter habitat is the common one. However, four species deviate from all other New Guinean microhylids in having riparian habits along small streams.

DISTRIBUTION: Most of New Guinea from near sea level to more than 2000 m, but mostly at middle elevations, with outlying species on Yela Island southeast of mainland New Guinea, on New Britain, and possibly on the Aru Islands of the Sahul Shelf (see Genus and Species inquirenda). In Australia, three species occupy rainforest regions of northern Queensland, and two others occupy seasonally dry regions of the Cape York Peninsula and Northern Territory. McDonald (1992) updated distribution records for three rainforest species.

NEW NAME COMBINATIONS FOR AUSTRALIAN SPECIES

Inasmuch as the four endemic Australian species are not treated in individual species accounts in this paper (see Zweifel, 1985b), it is convenient here to propose formally the new and revived combinations: *Austrochaperina adelphe* (Zweifel, 1985), new combination; *Austrochaperina fryi* (Zweifel, 1962), new combination; *Austrochaperina pluvialis* (Zweifel, 1965), new combination; *Austro-*

chaperina robusta Fry, 1912, revived combination.

Fry (1912) described *Austrochaperina* and three included species, *robusta, ornata,* and *gracilipes,* specifying the first of these as the type species. The second is now in the genus *Cophixalus,* and *gracilipes* (the only microhylid common to Australia and New Guinea) here reverts to its original genus. In the original description, Fry (1912: 91) recognized two ''colour varieties'' of *robusta*: A, to which the type specimen belonged, and B, including a single specimen. Later he reconsidered and (1915) made specimen B the type of a new species, *A. brevipes.* Parker (1934) synonymized this species under *Sphenophryne polysticta* (Méhelÿ), but Zweifel (1962) revived *brevipes* under the new name *fryi,* the change necessitated by the preoccupation of *brevipes* by *Sphenophryne brevipes* (Boulenger, 1897). Here Boulenger's *brevipes* and Zweifel's *fryi* are assigned to *Austrochaperina,* Fry's *brevipes* remaining preoccupied.

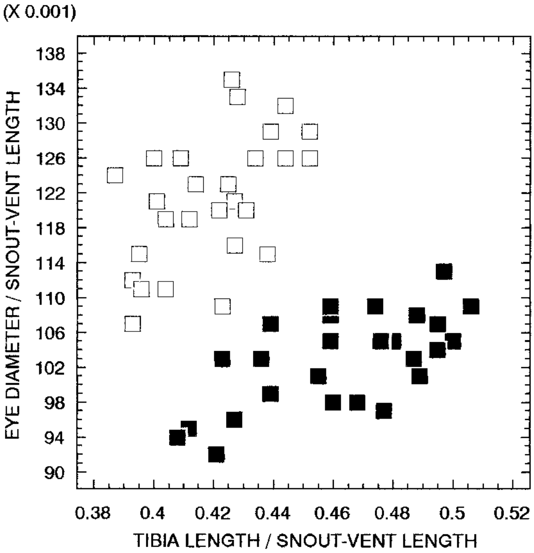

Fig. 1. Comparison of relative tibia length and eye diameter in *Austrochaperina gracilipes* (solid squares) and *A. novaebritanniae.*

KEY TO *AUSTROCHAPERINA*[3]

Inasmuch as four species of *Austrochaperina* are known from only one specimen each and another from just two, the distinctions in this key may be blurred by additional specimens. Geographic considerations may help in puzzling cases. Species are sometimes most readily identified by combinations of ratios; I provide graphs to facilitate keying in these instances. This key is intended to identify adult specimens. *Austrochaperina polysticta,* known only from a single specimen now destroyed, is not keyed (but see species account).

1. Tips of 2nd–4th fingers flattened, disclike, with faint indications of terminal grooves, but only that of the 3rd expanded .... *kosarek*
   Tips of fingers in addition to the 3rd with grooved, expanded terminal discs 2
2. Third finger disc equal in width to or scarcely broader than penultimate phalanx 3
   Third finger disc slightly to much broader than penultimate phalanx 5
3. TL/SVL 0.35–0.44 *and* EN/SVL 0.071–0.087 (fig. 2) .... *brevipes*
   TL/SVL 0.41–0.48 *and* EN/SVL 0.067–0.077 (fig. 2) 4
4. Size smaller, adults 17–21 mm SVL .... *mehelyi*
   Size larger, SVL 23–31 mm (two specimens only) .... *aquilonia*
5. Maximum adult SVL about 26 mm 6
   Adults typically larger than 26 mm SVL 9
6. Adults 22–26 mm SVL, finger discs larger (FD/SVL $\geq$ 0.031) .... *blumi*
   Adults usually $<$22 mm SVL, finger discs smaller (FD/SVL $<$ 0.030) 7
7. EY/SVL $<$ 0.115 *and* TL/SVL $>$ 0.400 (fig. 1) .... *gracilipes*
   EY/SVL $>$ 0.105 *and* TL/SVL $<$ 0.460 .. 8
8. All dorsal surfaces with tiny pale spots, ventral surfaces similar but with larger spots .... *novaebritanniae*
   Spotting absent middorsally, abdomen mottled .... *yelaensis*
9. Toes without webbing 10
   Toes with basal or greater webbing 17
10. FD/SVL $\geq$ 0.035 11
    FD/SVL $<$ 0.035 14
11. Adult at 28 mm SVL (1 female only) .... *adamantina*
    Minimum size of adult females 30 mm SVL, usually much larger 12
12. Dorsum gray-brown with small irregular dark brown spots (fig. 18) .... *guttata*
    Pattern not as described—obscure, or with

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[3] New Guinean species only; see Zweifel (1985b) for a key to the Australian species.

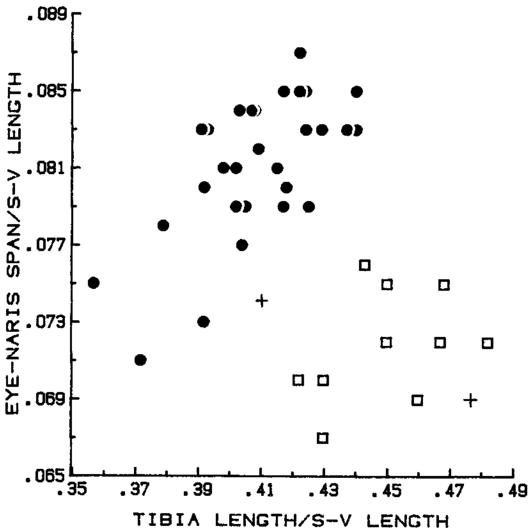

Fig. 2. Comparison of relative eye–naris distance and tibia length in *Austrochaperina brevipes* (circles), *A. mehelyi* (squares), and *A. aquilonia*. Adult individuals only plotted.

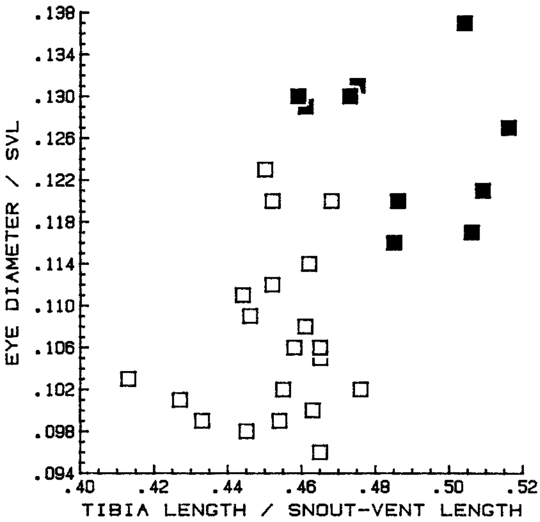

Fig. 3. Comparison of relative tibia length and eye diameter in *Austrochaperina macrorhyncha* (solid squares) and *A. rivularis* from Western Province, Papua New Guinea.

tiny dark flecks or vermiform markings 13

13. TL/SVL ≥ 0.46 *and* EY/SVL ≥ 0.116 (Fig. 3) . . . . *macrorhyncha*

TL/SVL < 0.46 *and* EY/SVL < 0.116 . . . . *rivularis*

14. Dorsal pattern of small, pale spots, more numerous laterally, on darker background; SVL 30.6 mm (1 adult female) . . *parkeri*

Pattern not as described, adult female SVL usually > 32 mm 15

15. IN/SVL > 0.103 *and* EY/SVL ≥ 0.105 . . . . *archboldi*

Proportions not as given 16

16. Middorsal region dark, abruptly differentiated from paler lateral area (fig. 20), groin, anterior and posterior sides of thighs peach color . . . . *hooglandi*

Dorsal region light to dark brown, not sharply distinguished from paler sides (fig. 12), groin and thighs not pink . . . . . *derongo*

17. Toes with well-developed webbing (fig. 56D), usually a prominent spike on each vomer (fig. 65O) . . . . *palmipes*

Toes with basal webbing (fig. 56C), no vomerine spike . . . . *basipalmata*

Austrochaperina adamantina, new species

Figure 4

HOLOTYPE: AMNH A78185, collected by Jared Diamond on July 14, 1966, in West Sepik Province, Papua New Guinea, on Mount Nibo, 9 km N, 15.5 km E of Lumi, at an elevation between 700 and 1550 m.

PARATYPES: There are no paratypes.

ETYMOLOGY: The specific name (Latin, "like a diamond") refers to Jared Diamond, the collector of this and a great many other valuable herpetological specimens from Papua New Guinea.

DIAGNOSIS: A species of moderate size (28 mm SVL, one specimen), lacking toe webbing, with the following diagnostic combination of proportions: eyes large (EY/SVL 0.125), leg length moderate (TL/SVL 0.434), narrow head (HW/SVL 0.338), narrow internarial span (IN/SVL 0.098), and moderately large finger discs (3rd finger disc/SVL 0.041). Eleven New Guinean *Austrochaperina* are eliminated on criteria of size and/or toe webbing alone, and the remaining eight are eliminated on proportions. Differences from the most similar species, *A. macrorhyncha*, are discussed under Comparisons.

DESCRIPTION OF HOLOTYPE: Adult female (gravid) with the following measurements and proportions: SVL 28.1, HW 9.5, TL 12.2, EY 3.5, EN 2.05, IN 2.75, HD 6.3, FT 12.5, third finger disc 1.15 (penultimate phalanx 0.55), fourth toe disc 1.2 (0.65), TY 1.4; HW/SVL 0.338, TL/SVL 0.434, EY/SVL

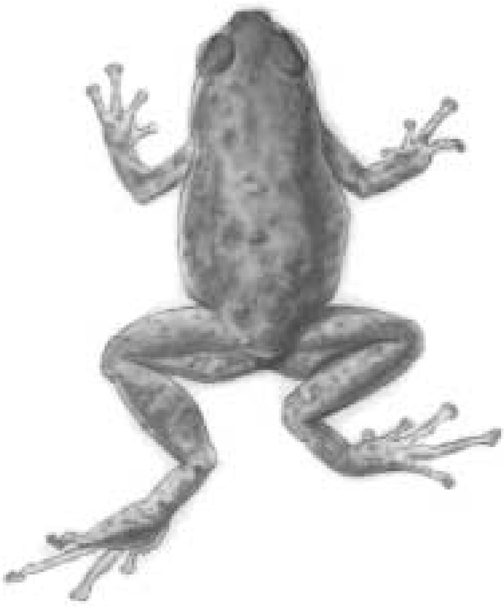

Fig. 4. Holotype of *Austrochaperina adamantina*, AMNH A78185, SVL 28.1 mm.

0.125, EN/SVL 0.073, IN/SVL 0.098, HD/SVL 0.224, FT/SVL 0.445, third finger disc/SVL 0.041, fourth toe disc/SVL 0.043.

Head narrow, snout truncate seen from above, slightly rounded in profile; canthus rostralis rounded but moderately distinct, loreal region nearly vertical, slightly concave, nares not visible from above; eyes (corneal outline) visible from below; eyelid about as wide as interorbital space; tympanic ring scarcely evident externally. Relative lengths of fingers 3 > 4 > 2 > 1, all well developed with broad, grooved discs, that of third finger about 2× penultimate phalanx; subarticular and inner metacarpal elevations low, rounded, scarcely evident (fig. 55E). Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, terminal discs well developed, that of fourth toe slightly broader than that of third finger; subarticular elevations scarcely evident (fig. 55E). Skin smooth dorsally and ventrally except for very slight wartiness on the lower back; a weak, diagonal postocular-supratympanic fold.

Dorsum tan with indistinct darker mottling; side of face and upper lip from just below nostril to tympanic fold abruptly paler than top of snout. Undersides all pale with faint darker mottling, slightly darker on throat and hind legs; posterior of thighs pale with mottling darker than undersides but paler than dorsum and top of thighs.

VARIATION IN TYPE SERIES: Only the single specimen is known.

ILLUSTRATIONS: Hands and feet, fig. 55E.

CALL: The call is unknown.

COMPARISONS WITH OTHER SPECIES: At present only two other species of *Austrochaperina* are known from the Torricelli Mountains: *A. basipalmata* and *A. aquilonia*. The basally webbed toes should immediately distinguish *basipalmata* from *adamantina*. Other characters differentiating *adamantina* from *basipalmata* include smaller size (gravid at 28 mm SVL vs. minimum size at maturity of 33 mm), narrower head (HW/SVL 0.338 vs. minimum of 0.343), and larger eyes (EY/SVL 0.125 vs. maximum of 0.112). See the account of *A. aquilonia* for comparison with that species. The relatively small size of *adamantina* distinguishes it from other species with similar proportions.

HABITAT AND HABITS: Nothing is on record.

DISTRIBUTION: Known only from the type locality in the Torricelli Mountains on the north coast of Papua New Guinea (fig. 7).

Austrochaperina aquilonia, new species

Figure 5

HOLOTYPE: AMNH A78186, collected by Jared Diamond during July 3–8, 1966, in West Sepik Province, Papua New Guinea, on Mount Somoro, 9.5 km N, 10.5 km E of Lumi at an elevation between 730 and 1420 m.

PARATYPE: AMS R130405, collected by Tim Flannery on June 11, 1988, in West Sepik Province, Papua New Guinea, at Wilbeite Village, 3°25′S, 142°07′E (6.5 km N, 10 km E of Lumi, 800 m, on Papua New Guinea Topographic Survey 1:100,000 sheet no. 7391).

ETYMOLOGY: The specific name, a Latin adjective meaning "northern," refers to its habitat in the north coast mountains.

DIAGNOSIS: The following combination of characters distinguishes this species: size moderate, males to 31 mm (no female specimens); toes unwebbed; hands small (HD/

Fig. 5. Holotype of *Austrochaperina aquilonia*, AMNH A78186, SVL 31.0 mm.

SVL 0.22–0.23); finger discs small (3rd finger disc/SVL 0.021–0.026), not or scarcely broader than penultimate phalanges; internarial span broad (IN/SVL 0.111–0.118).

Description of Holotype: Adult male (vocal slits present) with the following measurements and proportions (those of the paratype given in parentheses): SVL 31.0 (23.3), HW 11.2 (9.0), TL 12.7 (11.1), EY 3.4 (3.15), EN 2.3 (1.6), IN 3.45 (2.75), HD 7.1 (5.2), FT 13.6 (11.1), third finger disc 0.8 (penultimate phalanx 0.55) (0.6, phalanx 0.4), fourth toe disc 1.1 (0.6) (1.0, phalanx 0.5), TY 1.7 (1.9); HW/SVL 0.361 (0.386), TL/SVL 0.410 (0.476), EY/SVL 0.110 (0.135), IN/SVL 0.111 (0.118), EN/SVL 0.074 (0.069), EN/IN 0.667 (0.582), HD/SVL 0.229 (0.223), FT/SVL 0.439 (0.476), FD/SVL 0.026 (0.021), TD/SVL 0.035 (0.043).

Body relatively slender, head as wide as body, snout bluntly pointed as seen from above, protruding slightly in lateral view; nares just visible from above; canthus rostralis evident but rounded, loreal region a steep, flat slope; eyelid slightly narrower than interorbit, tympanic ring scarcely visible. Relative lengths of fingers 3 > 4 > 2 > 1, the first half the length of second, all with grooved terminal discs at most only slightly wider than penultimate phalanges, subarticular elevations low, rounded (fig. 55F). Relative lengths of toes 4 > 3 > 5 > 2 > 1, all with grooved terminal discs wider than the penultimate phalanges, that of the fourth toe broadest. Subarticular elevations low, rounded, the inner metatarsal elevation elongate, rounded (fig. 55F). Dorsal skin surface slightly granular; a faint, curved, postorbital-supratympanic fold.

The dorsal ground color is pale gray-brown, dominated by darker brown irregular spotting and mottling. On the limbs the pattern has more the appearance of pale spotting on a dark ground. The snout and face are dark brown with a faint lighter pattern on the upper lips. The anterior and posterior surfaces of the thighs are mottled; the palms and soles are essentially unmarked. The chin and chest are brown with coarse white spotting and mottling; the abdomen is pale with faint indication of darker patterning. The undersides of the hind limbs are pale with a slight darker pattern.

Variation in Type Series: The paratype is an adult male (vocal slits present) whose measurements and proportions are noted above. In color and pattern it closely resembles the holotype except that the patterning is even less distinct.

Illustrations: Hands and feet, fig. 55F.

Call: The call is unknown.

Comparisons with Other Species: Only two other species of *Austrochaperina* are known from the Torricelli Mountains, *A. basipalmata* and *A. adamantina*. Basally webbed toes, narrower internarial distance, and broader finger discs distinguish *basipalmata* from *aquilonia*. *Austrochaperina aquilonia* and *A. adamantina* are similar in most respects but differ strikingly in the larger finger discs of the latter (fig. 55). This does not appear to result from difference in the state of preservation, as the two *aquilonia*, with smaller discs, are well preserved. Confirmation of other possible differences in proportions must await additional specimens.

Habitat and Habits: Nothing is on record.

Distribution: Known only from the type

and paratype localities, about 3 km apart in the Torricelli Mountains of north-coastal Papua New Guinea (fig. 7).

Austrochaperina archboldi, new species

Figure 6

HOLOTYPE: AMNH A66719, collected at Arau, Kratke Mountains, 1400 m, Eastern Highlands Province, Papua New Guinea, October 14–24, 1959 by Hobart M. Van Deusen on the Sixth Archbold Expedition.

PARATYPES: AMNH A66720–66734, bearing the same data as the holotype.

ETYMOLOGY: The patronymic honors Richard Archbold, sponsor and early leader of a series of seven expeditions to New Guinea (1933–1964) that contributed immeasurably to knowledge of the biota of that island. Profitable mining of the collections for material of value to systematic biology will doubtless continue for decades.

DIAGNOSIS: An *Austrochaperina* of moderate size (males to 35, females to 38 mm SVL) with relatively wide internarial spacing (IN/SVL > 0.103), large eyes (EY/SVL ≥ 0.105), and a dorsal pattern of tiny irregular brown markings on a paler background.

DESCRIPTION OF HOLOTYPE: Adult male (vocal slits present) with the following measurements and proportions: SVL 34.7, HW 13.8, TL 16.0, EY 3.7, EN 2.5, IN 3.9, HD 8.0, FT 15.6, disc of third finger 1.1 (penultimate phalanx 0.8), disc of fourth toe 1.6 (0.8); HW/SVL 0.398, TL/SVL 0.461, EY/SVL 0.107, IN/SVL 0.112, EN/SVL 0.072, EN/IN 0.641, HD/SVL 0.231, FT/SVL 0.450, FD/SVL 0.032, TD/SVL 0.046.

Head slightly narrower than body; snout bluntly rounded seen from above, rounded and slightly projecting in lateral view; canthus rostralis rounded; loreal region steeply sloping, shallowly concave; nostrils a little closer to end of snout than to eye, just visible from above. Eyelid narrower than interorbital space (2.4 vs. 3.5 mm); tympanum scarcely distinguishable externally, about 1.6 mm horizontal diameter. Relative lengths of fingers $3 > 4 > 2 > 1$, the first relatively long, when appressed extending past subarticular elevation of second; all fingers with grooved terminal discs slightly broader than penultimate phalanges, disc of third finger about 1.4× as broad as penultimate phalanx; subarticular and metacarpal tubercles low, rounded, indistinct. Toes unwebbed, relative lengths $4 > 3 > 5 > 2 > 1$, the first less than half length of appressed second; well-developed terminal discs on all toes, that of the fourth broadest and almost 1.5× as broad as that of third finger; subarticular elevations low, rounded, indistinct; inner metatarsal elevation (no outer) low, rounded, elongate. Dorsal and ventral skin surfaces smooth, a very weak postocular-supratympanic fold.

Fig. 6. Paratype of *Austrochaperina archboldi*, AMNH A66723, SVL 38.4 mm.

The dorsal surfaces of head, body, and limbs are pale brown with tiny, irregular, darker brown spots, less numerous on the limbs. The loreal region is slightly darker and unspotted, with the tip of the snout being a little paler than the top of the head. The anterior and posterior surfaces of the thighs are tan; the posterior has a few small, dark spots, and the anterior is slightly more heavily mottled. The throat is mottled dark and light brown, with the pattern changing on the chest to dark with lighter spots. On the sides of the body, where the light brown ground color of the dorsum pales into the abdominal ground color, the dorsal spotting overlaps and appears more distinct. Otherwise, the abdomen and undersides of the thighs are pale and unmarked; the undersurfaces of more distal limb segments are obscurely mottled, with soles and palms darker brown.

VARIATION IN TYPE SERIES: Means and ranges of selected proportions are in table 2, and regression statistics are in table 3. The largest specimen is a female 38.4 mm SVL with ova 2 mm in diameter; another adult female is 36.9 mm, and one possibly just maturing is 33.4 mm. Three adult males measure 34.7–35.1 mm, and the largest immature is 29.8 mm.

The larger specimens of the paratype series closely resemble the holotype in color and pattern. The chin and chest may appear either more spotted or more mottled, probably a metachromatic effect, and a mottled pattern may be present on the underside of the thigh. Three juveniles of 16–19 mm SVL lack the dorsal spotting characteristic of larger specimens. Three adult males have the snout tip slightly paler than the top of the snout, whereas in two juveniles the tip is undifferentiated.

ILLUSTRATIONS: Hand and foot, fig. 55C.

CALL: The call has not been described.

COMPARISONS WITH OTHER SPECIES: *Austrochaperina archboldi* is most similar to *A. guttata*; the two are compared in the account of the latter. Relatively large eyes, broad internarial spacing, and aspects of color pattern should differentiate most or all *archboldi* from *derongo* and *hooglandi*, the other species with which it is most likely to be confused.

HABITAT AND HABITS: Brass (1964: 201) characterized the forest at Arau as ‘‘a transition between mid-mountain fagaceous forest and a lower montane mixed rain forest . . . rich in herbaceous undergrowth.’’ Nothing specific is known of the habitat or habits. One of the paratypes had been eaten by a snake, *Tropidonophis statisticus*.

DISTRIBUTION: The species is known only from the type locality (fig. 19).

Austrochaperina basipalmata (van Kampen), new combination

Chaperina basipalmata van Kampen, 1906: 169 (type localities, ‘‘Tawarin’’ and ‘‘Timena-Fluss,’’ Irian Jaya; syntypes ZMA 5875, 5876, and RMNH 4628 from Timena River [see Type Material], collected April 6–7, 1903, by the Netherlands New Guinea Expedition).

Chaperina quatuorlobata Wandolleck, 1911: 9 (type locality, ‘‘Torricelligebirge,’’ West Sepik Province, Papua New Guinea; syntypes [2], MTKD D2215, destroyed in World War II [Obst, 1977: 173], collected in 1909 by Otto Schlaginhaufen).

Sphenophryne basipalmata: van Kampen, 1919: 54 (first use of combination, treats *punctata* as a synonym). Nieden, 1926: 46.

Sphenophryne macrorhyncha: van Kampen, 1923: 107 (part, *basipalmata* considered a synonym). Parker, 1934: 155 (part).

TYPE LOCALITIES: The Tawarin River is on the north coast of Irian Jaya, entering Walckenaer Bay at about 139°48′E (Wichmann, 1917, fig. 108). The Timena River is in the vicinity of Lake Sentani, southwest of Jayapura in the northwest coastal region of Irian Jaya. Schlaginhaufen’s collections in the Torricelli Mountains were made in the area southeast of Aitape (Schlaginhaufen, 1914, fig. 1); see also account of *Liophryne schlaginhaufeni*.

TYPE MATERIAL: Of the four syntypes of *basipalmata*, the juvenile from Tawarin is missing (Dann and Hillenius, 1966). Among the remaining three (from Timena River), the syntype for which van Kampen (1906) provided measurements and illustrated is ZMA 5875; ZMA 5876 was skeletonized, and RMNH 4628 is much smaller (SVL 23 vs. 31 mm). I designate ZMA 5875 lectotype of *Chaperina basipalmata*; ZMA 5876 and RMNH 4628 automatically become paralectotypes.

DIAGNOSIS: The possession of toe webbing distinguishes *A. basipalmata* from all *Austrochaperina* except *A. palmipes*, the only other congener with more than a trace of toe webbing. The greater amount of webbing (figs. 56C and 56D) distinguishes *palmipes* from *basipalmata*, as does the former’s possession of vomerine spikes. Smaller eyes also characterize *basipalmata* (EY/SVL 0.094–0.112 vs. 0.115–0.144).

MORPHOLOGY: Head slightly narrower than body; hind limbs moderately long (TL/SVL 0.429). Snout bluntly pointed seen from above, the same and projecting in profile; nostrils lateral, just visible from above,

TABLE 2
Body Proportions in *Austrochaperina*

	Mean ± σ_{m}	Range	N	Mean ± σ_{m}	Range	N
	TL/SVL			HW/SVL		
Large species						
archboldi	0.465 ± 0.004	0.445–0.485	10	0.375 ± 0.006	0.341–0.398	10
basipalmata	0.429 ± 0.004	0.400–0.455	17	0.366 ± 0.003	0.343–0.387	17
derongo[a]	0.428 ± 0.003	0.398–0.468	22	0.356 ± 0.002	0.336–0.375	22
derongo[b]	0.435 ± 0.003	0.396–0.468	33	0.351 ± 0.002	0.321–0.375	33
derongo[c]	0.435 ± 0.008	0.407–0.489	10	0.367 ± 0.006	0.339–0.396	10
derongo[d]	0.416 ± 0.005	0.388–0.451	14	0.364 ± 0.006	0.327–0.397	14
guttata	0.482 ± 0.005	0.441–0.505	14	0.364 ± 0.003	0.350–0.377	14
hooglandi	0.452 ± 0.011	0.412–0.485	6	0.353 ± 0.009	0.327–0.385	6
macrorhyncha	0.487 ± 0.007	0.459–0.516	10	0.364 ± 0.007	0.328–0.401	10
palmipes[a]	0.443 ± 0.003	0.423–0.469	23	0.384 ± 0.003	0.357–0.416	23
palmipes[e]	0.430 ± 0.002	0.407–0.466	29	0.365 ± 0.003	0.333–0.394	29
palmipes[f]	0.416 ± 0.003	0.395–0.423	11	0.381 ± 0.001	0.376–0.389	11
palmipes[g]	0.451 ± 0.004	0.416–0.508	35	0.378 ± 0.002	0.349–0.406	35
rivularis[h]	0.445 ± 0.004	0.404–0.475	17	0.379 ± 0.003	0.355–0.405	17
rivularis[b]	0.453 ± 0.003	0.413–0.476	20	0.366 ± 0.003	0.336–0.393	20
Small species						
adamantina	0.434	—	1	0.338	—	1
aquilonia	0.448	0.419–0.476	2	0.359	0.356–0.361	2
blumi	0.467 ± 0.005	0.430–0.496	13	0.355 ± 0.003	0.341–0.377	13
brevipes	0.408 ± 0.004	0.357–0.440	29	0.412 ± 0.003	0.379–0.443	29
gracilipes	0.464 ± 0.006	0.408–0.506	27	0.332 ± 0.003	0.292–0.369	38
kosarek	0.409	—	1	0.370	—	1
mehelyi	0.450 ± 0.006	0.422–0.482	10	0.368 ± 0.005	0.342–0.395	10
novaebritanniae	0.419 ± 0.004	0.387–0.452	29	0.352 ± 0.003	0.318–0.380	29
parkeri	0.444	—	1	0.350	—	1
yelaensis	0.454	—	1	0.385	—	1
	HD/SVL			FT/SVL		
Large species						
archboldi	0.226 ± 0.003	0.208–0.243	10	0.445 ± 0.009	0.390–0.491	10
basipalmata	0.248 ± 0.003	0.230–0.268	17	0.452 ± 0.004	0.425–0.492	17
derongo[a]	0.222 ± 0.002	0.207–0.236	22	0.433 ± 0.004	0.393–0.475	22
derongo[b]	0.238 ± 0.003	0.196–0.269	32	0.447 ± 0.004	0.406–0.508	32
derongo[c]	0.229 ± 0.005	0.204–0.257	10	0.445 ± 0.007	0.414–0.489	10
derongo[d]	0.220 ± 0.001	0.213–0.232	14	0.419 ± 0.003	0.400–0.439	14
guttata	0.254 ± 0.004	0.231–0.276	14	0.479 ± 0.005	0.438–0.505	14
hooglandi	0.228 ± 0.005	0.217–0.249	6	0.434 ± 0.007	0.416–0.456	6
macrorhyncha	0.261 ± 0.005	0.238–0.284	10	0.484 ± 0.006	0.455–0.512	10
palmipes[a]	0.262 ± 0.002	0.241–0.281	23	0.437 ± 0.003	0.407–0.465	23
palmipes[e]	0.272 ± 0.002	0.248–0.289	29	0.427 ± 0.003	0.390–0.456	29
palmipes[f]	0.270 ± 0.003	0.256–0.282	11	0.422 ± 0.005	0.389–0.440	11
palmipes[g]	0.273 ± 0.002	0.253–0.303	35	0.451 ± 0.004	0.401–0.511	35
rivularis[h]	0.237 ± 0.003	0.218–0.261	17	0.438 ± 0.004	0.413–0.464	17
rivularis[b]	0.251 ± 0.002	0.235–0.268	20	0.459 ± 0.005	0.420–0.496	20
Small species						
adamantina	0.224	—	1	0.445	—	1
aquilonia	0.215	0.210–0.219	2	0.441	0.439–0.442	2
blumi	0.247 ± 0.003	0.234–0.263	13	0.459 ± 0.005	0.430–0.494	13
brevipes	0.216 ± 0.002	0.195–0.233	29	0.442 ± 0.004	0.393–0.481	29

TABLE 2
Continued

	Mean ± σ_m	Range	N	Mean ± σ_m	Range	N
	HD/SVL			FT/SVL		
Small species						
gracilipes	0.221 ± 0.003	0.191–0.256	27	0.469 ± 0.005	0.421–0.506	27
kosarek	0.190	—	1	0.405	—	1
mehelyi	0.211 ± 0.003	0.200–0.224	9	0.469 ± 0.006	0.439–0.506	9
novaebritanniae	0.198 ± 0.002	0.185–0.216	29	0.412 ± 0.003	0.374–0.444	29
parkeri	0.209	—	1	0.425	—	1
yelaensis	0.205	—	1	0.454	—	1
	EY/SVL			EN/IN		
Large species						
archboldi	0.110 ± 0.001	0.105–0.117	10	0.687 ± 0.011	0.641–0.756	10
basipalmata	0.103 ± 0.001	0.094–0.112	17	0.753 ± 0.014	0.625–0.900	17
derongo[a]	0.089 ± 0.001	0.081–0.100	22	0.794 ± 0.008	0.727–0.897	24
derongo[b]	0.098 ± 0.001	0.085–0.111	32	0.769 ± 0.009	0.622–0.909	32
derongo[c]	0.101 ± 0.002	0.095–0.111	10	0.720 ± 0.017	0.643–0.800	10
derongo[d]	0.098 ± 0.002	0.086–0.115	14	0.806 ± 0.019	0.722–0.962	14
guttata	0.111 ± 0.002	0.095–0.122	14	0.700 ± 0.012	0.595–0.767	14
hooglandi	0.092 ± 0.003	0.083–0.103	6	0.705 ± 0.024	0.639–0.763	6
macrorhyncha	0.128 ± 0.002	0.116–0.137	10	0.736 ± 0.011	0.698–0.800	10
palmipes[a]	0.127 ± 0.001	0.119–0.143	23	0.832 ± 0.013	0.676–0.941	23
palmipes[e]	0.129 ± 0.001	0.115–0.144	29	0.830 ± 0.011	0.727–1.000	29
palmipes[f]	0.132 ± 0.001	0.127–0.139	11	0.890 ± 0.012	0.825–0.951	11
palmipes[g]	0.126 ± 0.001	0.115–0.135	35	0.802 ± 0.009	0.714–0.912	34
rivularis[h]	0.116 ± 0.001	0.107–0.124	17	0.736 ± 0.008	0.674–0.795	17
rivularis[b]	0.107 ± 0.002	0.096–0.123	20	0.754 ± 0.012	0.614–0.829	20
Small species						
adamantina	0.125	—	1	0.745	—	1
aquilonia	0.117	0.110–0.124	2	0.673	0.667–0.679	2
blumi	0.117 ± 0.002	0.109–0.133	13	0.756 ± 0.011	0.667–0.804	13
brevipes	0.123 ± 0.001	0.113–0.132	29	0.738 ± 0.006	0.667–0.787	29
gracilipes	0.103 ± 0.001	0.092–0.113	38	0.750 ± 0.008	0.651–0.848	38
kosarek	0.121	—	1	0.638	—	1
mehelyi	0.125 ± 0.006	0.119–0.134	10	0.605 ± 0.018	0.565–0.632	10
novaebritanniae	0.121 ± 0.001	0.107–0.135	29	0.699 ± 0.005	0.632–0.763	29
parkeri	0.105	—	1	0.672	—	1
yelaensis	0.123	—	1	0.696	—	1
	EN/SVL			IN/SVL		
Large species						
archboldi	0.076 ± 0.001	0.072–0.086	10	0.110 ± 0.001	0.104–0.114	10
basipalmata	0.074 ± 0.001	0.063–0.082	17	0.099 ± 0.001	0.086–0.105	17
derongo[a]	0.074 ± 0.001	0.064–0.081	22	0.094 ± 0.001	0.088–0.101	22
derongo[b]	0.074 ± 0.001	0.063–0.082	32	0.097 ± 0.001	0.088–0.102	32
derongo[c]	0.075 ± 0.002	0.066–0.085	10	0.105 ± 0.002	0.094–0.110	10
derongo[d]	0.078 ± 0.001	0.071–0.087	14	0.097 ± 0.002	0.089–0.105	14
guttata	0.076 ± 0.001	0.068–0.079	14	0.108 ± 0.001	0.100–0.117	14
hooglandi	0.074 ± 0.002	0.067–0.083	6	0.105 ± 0.001	0.102–0.108	6
macrorhyncha	0.077 ± 0.002	0.069–0.085	10	0.105 ± 0.001	0.098–0.111	10
palmipes[a]	0.079 ± 0.001	0.065–0.084	23	0.095 ± 0.001	0.089–0.102	23
palmipes[e]	0.077 ± 0.001	0.071–0.086	29	0.093 ± 0.001	0.080–0.102	29

TABLE 2
Continued

	Mean ± σ_m	Range	N	Mean ± σ_m	Range	N
	EN/SVL			IN/SVL		
Large species						
palmipes[f]	0.081 ± 0.001	0.075–0.086	11	0.091 ± 0.001	0.086–0.099	11
palmipes[g]	0.079 ± 0.001	0.071–0.088	35	0.099 ± 0.001	0.089–0.114	35
rivularis[h]	0.073 ± 0.001	0.068–0.080	17	0.099 ± 0.001	0.090–0.109	17
rivularis[b]	0.073 ± 0.001	0.066–0.079	20	0.097 ± 0.001	0.093–0.108	20
Small species						
adamantina	0.073	—	1	0.098	—	1
aquilonia	0.076	0.074–0.077	2	0.113	0.111–0.114	2
blum	0.077 ± 0.001	0.073–0.084	13	0.102 ± 0.001	0.097–0.111	13
brevipes	0.081 ± 0.001	0.071–0.087	29	0.110 ± 0.004	0.096–0.120	29
gracilipes	0.073 ± 0.001	0.061–0.082	36	0.097 ± 0.001	0.085–0.106	38
kosarek	0.071	—	1	0.112	—	1
mehelyi	0.072 ± 0.003	0.067–0.076	10	0.119 ± 0.004	0.112–0.124	10
novaebritanniae	0.070 ± 0.001	0.064–0.076	29	0.101 ± 0.001	0.091–0.108	29
parkeri	0.070	—	1	0.105	—	1
yelaensis	0.078	—	1	0.112	—	1
	FD/SVL			TD/SVL		
Large species						
archboldi	0.031 ± 0.0009	0.026–0.035	10	0.045 ± 0.0011	0.041–0.052	10
basipalmata	0.040 ± 0.0008	0.033–0.046	17	0.048 ± 0.0010	0.041–0.057	17
derongo[a]	0.031 ± 0.0005	0.025–0.035	22	0.042 ± 0.0006	0.038–0.047	22
derongo[b]	0.034 ± 0.0008	0.025–0.043	32	0.043 ± 0.0009	0.032–0.051	33
derongo[c]	0.031 ± 0.0015	0.025–0.039	10	0.040 ± 0.0015	0.032–0.050	10
derongo[d]	0.027 ± 0.0007	0.021–0.032	14	0.037 ± 0.0010	0.028–0.043	14
guttata	0.037 ± 0.0005	0.035–0.041	13	0.044 ± 0.0078	0.038–0.048	13
hooglandi	0.031 ± 0.0013	0.026–0.036	6	0.041 ± 0.0012	0.036–0.045	6
macrorhyncha	0.041 ± 0.0014	0.035–0.050	10	0.047 ± 0.0016	0.038–0.054	10
palmipes[a]	0.051 ± 0.0007	0.044–0.060	21	0.055 ± 0.0010	0.048–0.069	22
palmipes[e]	0.053 ± 0.0008	0.046–0.065	29	0.051 ± 0.0008	0.043–0.060	28
palmipes[f]	0.054 ± 0.0011	0.048–0.062	11	0.051 ± 0.0009	0.047–0.057	11
palmipes[g]	0.050 ± 0.0007	0.040–0.057	33	0.051 ± 0.0007	0.043–0.060	33
rivularis[h]	0.037 ± 0.0007	0.031–0.044	17	0.044 ± 0.0006	0.039–0.048	17
rivularis[b]	0.038 ± 0.0005	0.035–0.044	20	0.046 ± 0.0007	0.042–0.054	20
Small species						
adamantina	0.041	—	1	0.043	—	1
aquilonia	0.026	0.026–0.026	2	0.036	0.035–0.037	2
blumi	0.035 ± 0.0008	0.031–0.040	13	0.042 ± 0.0011	0.037–0.051	13
brevipes	0.022 ± 0.0004	0.016–0.025	27	0.031 ± 0.0006	0.023–0.037	27
gracilipes	0.025 ± 0.0003	0.022–0.028	18	0.036 ± 0.0006	0.031–0.040	18
kosarek	0.021	—	1	0.031	—	1
mehelyi	0.025 ± 0.0008	0.019–0.027	9	0.040 ± 0.0012	0.032–0.044	9
novaebritanniae	0.025 ± 0.0005	0.023–0.029	16	0.036 ± 0.0006	0.031–0.041	16
parkeri	0.031	—	1	0.042	—	1
yelaensis	0.029	—	1	0.039	—	1

[a] Simbu Prov., PNG.

[b] Western Prov., PNG.

[c] Idenburg River, Irian Jaya.

[d] Southern Highlands Prov., PNG.

[e] Mt. Dayman, Milne Bay Prov., PNG.

[f] Normanby Island, Milne Bay Prov., PNG.

[g] Huon Peninsula, Morobe Prov., PNG.

[h] Mt. Hunstein, West Sepik Prov., PNG.

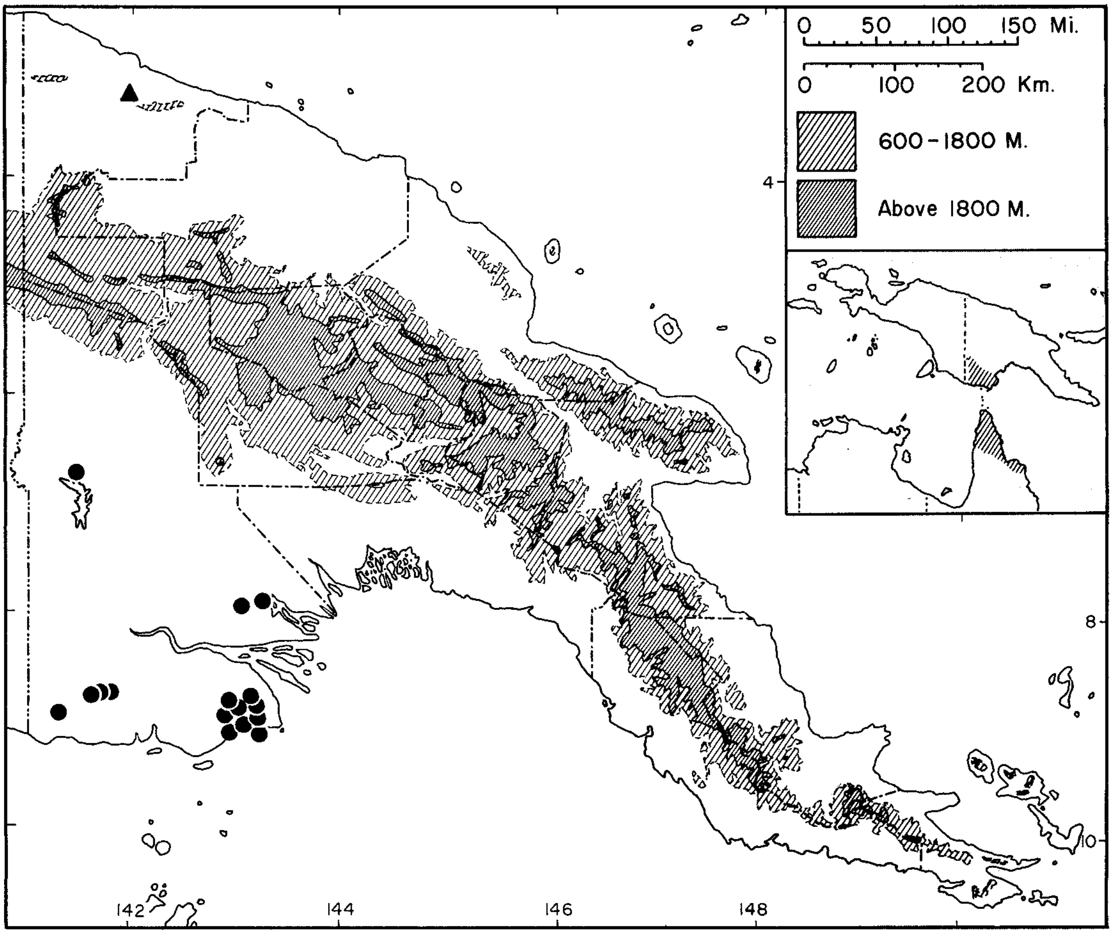

Fig. 7. Distribution of *Austrochaperina gracilipes* (circles, shading on inset indicates total distribution), *A. adamantina* (triangle), and *A. aquilonia* (triangle, one symbol covers three localities for these two species).

slightly closer to tip of snout than to eye; loreal region nearly vertical and flat, canthus rostralis distinct but rounded. Eyes moderately small (EY/SVL 0.103), eyelid half interorbital distance. Tympanum scarcely visible, less than half eye diameter. Relative lengths of fingers 3 > 4 > 2 > 1, first more than half length of second, all with expanded, rounded, terminally grooved discs, that of third finger about twice width of penultimate phalanx; subarticular and metacarpal elevations low, rounded, indistinct. Toes with basal webs, reaching almost half length on first toe and on inside of second; relative toe lengths 4 > 3 > 5 > 2 > 1, first less than half second, all with rounded, expanded, terminally grooved discs broader than those on fingers, that of fourth toe about twice width of penultimate phalanx; subarticular tubercles rounded, indistinct; inner metatarsal tubercle low, rounded, elongate, no outer tubercle. Body smooth to slightly rugose dorsally, smooth beneath; a weak, curved postorbital-supratympanic fold.

COLOR AND PATTERN: In preservative, these frogs are brown above, sometimes virtually patternless but more often with indistinct darker spotting or mottling. A small proportion have well-defined darker spots. The undersides are pale tan with variably distinct darker mottling on the chin, chest, and hind legs. The abdomen is unmarked except

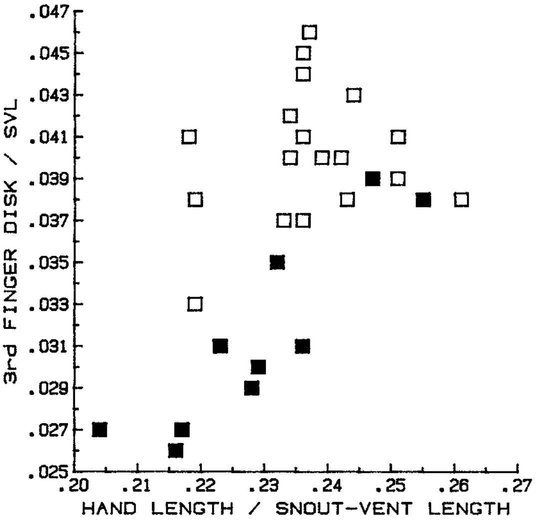

Fig. 8. Comparison of relative hand length and third finger disc width in *Austrochaperina basipalmata* (solid squares) and *A. derongo* (Idenburg River sample, open squares).

laterally. The posterior surfaces of the thighs are brown and the groin is much the same.

Variation in Size and Proportions: Adult males (those with vocal slits) range from 31.6 to 34.4 mm SVL, adult females from 33.3 to 39.0 mm. Males as large as 29.0 mm lack slits, and females appear to mature at about 30–32 mm. Variation in proportions is summarized in table 2; see table 3 for regression statistics.

Adult males have the tip of the snout somewhat pointed and conspicuously whitened. Adult females have a rounded snout and rarely show even a trace of white, and juveniles of both sexes have dark snouts.

Illustrations: 3rd finger terminal phalanx, fig. 71N; premaxilla, fig. 64E; sacral region, fig. 73B; vomer, fig. 65M; hand and foot, fig. 56C.

Call: Vocalizations are unknown.

Comparisons with Other Species: *Austrochaperina derongo* is the species most similar morphologically to *A. basipalmata*. They are of the same size and, apart from the toe webbing, there is little to distinguish them. The hands and digital discs of *basipalmata* tend to be slightly larger, and a simultaneous comparison of the HL/SVL and FD/SVL ratios of the two species provides a fairly good separation (fig. 8). See the account of *A. macrorhyncha* for a comparison of that species with *basipalmata*.

Habitat and Habits: Nothing has been published in this regard. However, Allen Allison (personal commun.) has informed me that *basipalmata* is closely associated with small mountain streams.

Distribution: Localities for this species span about 300 km in the north coast ranges, from the Tawarin River in Irian Jaya to the Torricelli Mountains southeast of Aitape, Papua New Guinea (fig. 24).

Locality Records and Specimens Examined: IRIAN JAYA: Tawarin River (van Kampen, 1906: 169); Timena River (RMNH 4628, syntype of *Chaperina basipalmata*; ZMA 5875, 5876, syntypes of *Chaperina basipalmata*); Mt. Nomo, 16 km SSW Mt. Bougainville (BMNH 1913.10.31.248). PAPUA NEW GUINEA: West Sepik Prov.: Mt. Somoro, Torricelli Mtns., 730–1420 m, 9 km N, 11 km E Lumi (AMNH A78176–78181); Mt. Nibo, Torricelli Mtns., 700–1550 m, 9 km N, 15 km E Lumi (AMNH A78158–78175 [78163 C&S], A129480–129513 [129495 C&S]).

Remarks: Van Kampen (1906) described this species and *macrorhyncha* in the same paper. He later (1919) considered *punctata* (van Kampen, 1913) a synonym of *basipalmata*, but in 1923 placed *basipalmata* and *punctata* in the synonymy of *macrorhyncha*, citing intermediate specimens as the basis. Nieden (1926) followed van Kampen's 1919 arrangement. Van Kampen (1919, 1923) included *quatuorlobata* in the synonymy of *basipalmata* (1919) and of *macrorhyncha* (1923), but with question. Parker (1934) examined a syntype of *quatuorlobata* and (presumably) compared it with a *macrorhyncha* from Mimika River and a syntype of *punctata* (which he thought erroneously to be a syntype of *basipalmata*), and referred all three specimens to *Sphenophryne macrorhyncha*.

Austrochaperina blumi, new species

Figure 9

Holotype: MZB 3562, also tagged UPNG 9538 (field no. Blum l979-59), collected in July 1979 by J. Paul Blum at Kosarek, elevation 1400 m, Jayawijaya District, Irian

Fig. 9. *Austrochaperina blumi*, holotype, MZB 3562, SVL 26.3 mm.

Jaya, Indonesia. This locality is on the north slope of the central dividing range of Irian Jaya, west of Nipsan and northeast of Anguruk.

PARATYPES: All collected by J. Paul Blum in Jayawijaya District, Irian Jaya. AMNH A157795, 157796, UPNG 9529–9531, 9534, 9537, same data as holotype; UPNG 9514, 9515, Bime, 1500 m, May 1975; UPNG 9546–9548, 9550 (C&S), Bime Valley, 1500 m, May 1975. See Referred Specimen, below.

ETYMOLOGY: I name this species for Dr. J. P. Blum in recognition of his important collections of frogs from Irian Jaya (e.g., Blum and Menzies, 1988).

DIAGNOSIS: The following characteristics, in combination, distinguish *A. blumi* from other *Austrochaperina*: size moderately small, maximum SVL about 26 mm; fingers with moderately large terminal discs (3rd finger disc/SVL 0.031–0.040), only that of the first finger not broader than the penultimate phalanx; hands moderately large (HD/SVL 0.23–0.26).

DESCRIPTION OF HOLOTYPE: Adult female (ova 2.2 mm in diameter) with the following measurements and proportions: SVL 26.3, HW 9.0, TL 11.3, EY 3.05, EN 2.15, IN 2.8, third finger disc 1.0 (penultimate phalanx 0.6), fourth toe disc 1.0 (appears slightly shrunken; penultimate phalanx 0.6), HD 6.3, FT 11.3; TL/SVL 0.430, HW/SVL 0.342, EY/SVL 0.116, EN/SVL 0.082, IN/SVL 0.106, EN/IN O.768, FD/SVL 0.038, TD/SVL 0.038, HD/SVL 0.240, FT/SVL 0.430.

Head relatively narrow; snout rounded, verging on truncate in dorsal aspect, high, rounded, and slightly projecting seen laterally; nostrils lateral, barely visible from above, widely separated but appearing close to tip of snout in lateral view; loreal region nearly vertical, shallowly concave, canthus rostralis rounded. Eyes moderately large, laterally placed and visible from beneath, EY greater than EN, interorbital span slightly greater than width of an eyelid. Tympanum small and indistinct, horizontal diameter of annulus less than one-half that of eye. Relative lengths of fingers 4 > 3 > 2 > 1, first well developed, all with rounded, grooved terminal discs, that on first finger scarcely broader than penultimate phalanx, others better developed, disc on third finger about 1.7× width of penultimate phalanx; subarticular and inner metacarpal elevations low, rounded, inconspicuous (fig. 56F). Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, all with rounded, grooved terminal discs, that on first toe scarcely broader than penultimate phalanx, others better developed, disc on fourth toe about 1.7× width of penultimate phalanx and equal to disc on third finger but apparently a bit dried and shrunken; subarticular elevations low and rounded, slightly more evident than those on fingers, a low, rounded, elongate inner metatarsal tubercle, no outer (fig. 56F). Dorsal surface of body nearly smooth, a slightly raised midvertebral line and a shallow fold from posterior corner of eye across upper edge of tympanum to forelimb insertion, no other conspicuous folds on dorsum; venter smooth.

The dorsal surfaces of head, body, and limbs are pale tan with numerous small, somewhat darker, irregular spots. The end of the snout and the upper loreal region are darker than the dorsal ground color, and there is a hint of this darker color on the postocular fold. The lips are pale with darker spotting. The groin and anterior and upper posterior surfaces of the thighs are dusky. The lower posterior surfaces of the thighs are colored

TABLE 3

Regression Statistics of Twenty Samples of *Austrochaperina*[a]

	TL/SVL				HW/SVL				HD/SVL				FT/SVL				EY/SVL			
	α	β	*r*	N	α	β	*r*	N	α	β	*r*	N	α	β	*r*	N	α	β	*r*	N
Large species																				
archboldi	0.586	0.936	0.992	14	0.460	0.951	0.989	14	0.130	1.155	0.986	14	0.552	0.940	0.973	14	0.334	0.688	0.983	14
basipalmata	0.690	0.866	0.976	28	0.686	0.823	0.948	27	0.310	0.923	0.967	28	0.665	0.883	0.973	28	0.516	0.544	0.919	28
derongo[b]	0.574	0.923	0.992	52	0.567	0.870	0.988	52	0.258	0.977	0.983	52	0.582	0.927	0.988	52	0.338	0.658	0.941	52
derongo[c]	0.604	0.903	0.988	38	0.713	0.808	0.989	38	0.275	0.939	0.983	38	0.490	0.963	0.978	38	0.472	0.540	0.915	38
derongo[d]	0.659	0.877	0.979	19	0.777	0.781	0.965	19	0.223	1.002	0.963	19	0.485	0.963	0.975	19	0.478	0.555	0.940	19
derongo[e]	1.295	0.666	0.926	14	0.800	0.768	0.842	14	0.202	1.026	0.978	14	0.657	0.868	0.971	14	0.864	0.361	0.765	14
guttata	0.520	0.978	0.984	15	0.611	0.862	0.987	15	0.245	1.008	0.980	15	0.498	0.989	0.985	15	0.333	0.706	0.950	15
hooglandi	1.298	0.710	0.951	6	2.491	0.469	0.960	6	0.539	0.762	0.989	6	0.838	0.819	0.986	6	1.318	0.278	0.865	6
macrorhyncha	0.421	1.043	0.991	15	0.473	0.924	0.913	15	0.188	1.098	0.983	15	0.387	1.065	0.993	15	0.240	0.815	0.976	15
palmipes[c]	0.762	0.849	0.966	32	0.523	0.913	0.932	32	0.324	0.940	0.929	32	0.694	0.871	0.942	32	0.186	0.896	0.930	32
palmipes[f]	0.625	0.896	0.975	40	0.350	1.011	0.976	40	0.356	0.925	0.957	40	0.654	0.882	0.969	40	0.163	0.935	0.934	40
palmipes[g]	0.502	0.952	0.996	37	0.487	0.935	0.998	37	0.203	1.082	0.994	37	0.503	0.957	0.993	37	0.225	0.863	0.992	37
palmipes[h]	0.646	0.898	0.969	54	0.554	0.892	0.981	54	0.154	1.165	0.975	54	0.348	1.077	0.911	54	0.214	0.850	0.964	54
rivularis[i]	0.405	1.027	0.995	55	0.522	0.921	0.992	55	0.249	1.000	0.993	55	0.432	1.013	0.993	55	0.355	0.709	0.987	55
rivularis[b]	0.574	0.935	0.981	24	0.681	0.831	0.971	24	0.271	0.978	0.971	24	0.460	0.998	0.959	24	0.424	0.624	0.847	24
Small species																				
blumi[j]	2.158	0.515	0.669	13	1.010	0.669	0.816	13	0.531	1.089	0.810	13	1.220	0.691	0.715	13	0.116	1.001	0.685	13
brevipes	0.828	0.770	0.865	37	0.770	0.800	0.952	37	0.280	0.915	0.912	37	0.873	0.779	0.889	37	0.309	0.704	0.886	37
gracilipes	0.822	0.804	0.931	61	0.528	0.843	0.966	73	0.440	0.764	0.886	61	0.775	0.828	0.931	61	0.358	0.577	0.897	39
mehelyi	0.781	0.809	0.969	12	0.513	0.891	0.934	12	0.292	0.887	0.962	12	0.961	0.864	0.969	11	0.345	0.650	0.955	12
novaebritanniae	0.672	0.838	0.965	43	0.692	0.768	0.958	43	0.215	0.972	0.977	43	0.574	0.887	0.973	43	0.347	0.638	0.944	43

TABLE 3
Continued

	EN/SVL				IN/SVL				FD/SVL				TD/SVL			
	α	β	*r*	N	α	β	*r*	N	α	β	*r*	N	α	β	*r*	N
Large species																
archboldi	0.131	0.849	0.967	15	0.189	0.847	0.990	15	0.012	1.271	0.975	13	0.057	0.931	0.967	13
basipalmata	0.153	0.799	0.904	28	0.154	0.876	0.942	28	0.024	1.147	0.908	28	0.053	0.974	0.864	28
derongo[b]	0.133	0.843	0.983	52	0.134	0.909	0.982	52	0.032	1.015	0.947	50	0.049	0.959	0.951	52
derongo[c]	0.176	0.762	0.971	38	0.205	0.783	0.978	38	0.034	0.972	0.945	38	0.053	0.939	0.962	38
derongo[d]	0.253	0.652	0.956	19	0.185	0.832	0.964	19	0.022	1.094	0.876	19	0.036	1.024	0.896	19
derongo[e]	0.087	0.968	0.901	14	0.418	0.572	0.884	14	0.003	1.659	0.920	14	0.053	0.885	0.695	14
guttata	0.160	0.802	0.978	15	0.196	0.841	0.973	15	0.025	1.098	0.990	14	0.037	1.047	0.975	14
hooglandi	0.383	0.559	0.830	6	0.165	0.876	0.992	6	0.067	0.781	0.879	6	0.031	1.066	0.939	6
macrorhyncha	0.104	0.916	0.891	15	0.119	0.961	0.974	15	0.048	0.961	0.918	15	0.052	0.073	0.917	15
palmipes[c]	0.064	1.057	0.838	32	0.157	0.862	0.929	32	0.015	1.334	0.870	30	0.026	1.204	0.869	31
palmipes[f]	0.126	0.864	0.913	40	0.187	0.806	0.922	40	0.041	1.071	0.882	40	0.103	0.806	0.814	39
palmipes[g]	0.109	0.923	0.992	37	0.180	0.822	0.993	37	0.039	1.090	0.983	37	0.048	1.017	0.981	37
palmipes[h]	0.093	0.956	0.981	54	0.189	0.816	0.975	54	0.047	1.014	0.925	52	0.065	0.934	0.938	52
rivularis[i]	0.124	0.861	0.991	55	0.142	0.905	0.975	55	0.037	1.001	0.979	55	0.069	0.879	0.974	55
rivularis[b]	0.083	0.966	0.951	24	0.123	0.937	0.975	24	0.028	1.080	0.959	24	0.067	0.901	0.913	24
Small species																
blumi[j]	0.096	0.930	0.738	13	0.077	1.089	0.810	13	0.039	0.970	0.522	13	0.125	0.654	0.359	13
brevipes	0.251	0.636	0.891	37	0.249	0.736	0.902	37	0.044	0.783	0.705	34	0.054	0.821	0.729	34
gracilipes	0.232	0.606	0.925	39	0.260	0.665	0.939	39	0.035	0.882	0.869	21	0.080	0.727	0.749	21
mehelyi	0.107	0.863	0.961	12	0.195	0.829	0.977	12	0.062	0.675	0.680	11	0.052	0.908	0.811	11
novaebritanniae	0.109	0.851	0.961	43	0.196	0.772	0.972	43	0.009	1.356	0.966	18	0.035	1.006	0.934	17

[a] Power curves of the form $Y = \alpha X^{\beta}$.
[b] PNG: Western Prov.
[c] PNG: Simbu Prov.
[d] Irian Jaya: Idenburg River.
[e] PNG: Southern Highlands Prov.
[f] PNG: Milne Bay Prov.; Mt. Dayman.
[g] PNG: Milne Bay Prov.; Normanby Island.
[h] PNG: Morobe Prov.; Huon Peninsula.
[i] PNG: West Sepik Prov.; Mt. Hunstein.
[j] Because of the small size range (SVL 22.0–26.3 mm), the regression data for this sample are inadequate.

and patterned like the dorsum, but with a paler ground color and more conspicuous spotting. There is no dark seat patch. The ventral ground color is pale tan, almost white, with numerous small, slightly darker spots on the throat and chest and a sparser scattering of these on the abdomen. The soles are dark and unspotted.

VARIATION IN TYPE SERIES: Averages and ranges of selected proportions are in table 2, and regression statistics are in table 3. The largest of 13 specimens is the holotype, a gravid female 26.3 mm SVL. Females at 22.1 and 22.9 mm are possibly immature, but one of 22.7 mm is gravid and other larger individuals are mature. Four males 22.6 to 24.4 mm SVL have vocal sac openings and thus are presumably mature.

Except for minor differences, the description of the holotype could stand for the other specimens as well. The dorsal surfaces are not always as smooth as in the holotype, but may bear a scattering of inconspicuous, tiny warts. In 11 of 13 specimens the disc on the fourth toe is slightly but distinctly broader than on the third finger, and in one of the exceptional cases the toe disc appears to be shrunken. There is no significant variation in color or pattern.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71L; premaxilla, fig. 64C; sacral region, fig. 73E; vomer, fig. 65K; hands and feet, fig. 56F.

CALL: This has not been described.

COMPARISONS WITH OTHER SPECIES: The description and illustration of *Chaperina punctata* van Kampen (here considered a synonym of *Austrochaperina macrorhyncha*) resemble *Austrochaperina blumi* in several respects, and the type series of *punctata* comes from the upper reaches of the Lorentz River, not greatly distant (though across the central divide) from the localities for *blumi*. The most striking difference between *blumi* and *macrorhyncha* is their size. The largest of 14 *blumi* is only 26.3 mm SVL, and both males and females of less than 23 mm are mature. In contrast, *macrorhyncha* matures at about 30 mm and reaches 36.8 mm.

Three species that resemble *blumi* in most proportions are *A. gracilipes, A. novaebritanniae,* and *A. yelaensis*. These are smaller species reaching maximum size at 22–23 mm SVL, whereas this is approximately the minimum size at maturity of *blumi*. In addition, *blumi* has relatively larger finger discs (table 3). The species are widely separated geographically, with *novaebritanniae* and *yelaensis* being insular and *gracilis* being an Australian species found also in the southern lowlands of Papua New Guinea.

REFERRED SPECIMEN: A single specimen from western Papua New Guinea agrees with the type series in most respects, although it has slightly larger EN and HW measurements and a greater IN than do others of similar size. I tentatively refer this specimen to this species, but exclude it from paratype status because of its geographic remoteness (some 250 km east of the localities in Irian Jaya) and because I had no opportunity to compare it directly with the specimens from Irian Jaya.

HABITAT AND HABITS: Dr. Harold Cogger (personal commun.) found the referred specimen, a male, on an egg mass in a fissure in a clay bank in a regrowth area.

DISTRIBUTION: The type-series localities for *Austrochaperina blumi* lie at 1400–1500 m on the north slope of the central dividing range of Irian Jaya (fig. 10).

LOCALITY RECORDS AND SPECIMENS EXAMINED: Localities of the holotype and paratype specimens are cited above. The referred specimen, AMS R127758, has the following data: Papua New Guinea: West Sepik Prov.; ca 2 km W Atemkinkin Village, itself ca 7 km W Telefomin, 141°34′E, 05°06′S, collected April 13, 1987.

REMARKS: Dr. Blum noted the native names for this frog as ‘‘tanaofoge’’ at Kosarek and ‘‘calap’’ at Bime Valley.

Austrochaperina brevipes (Boulenger), new combination

Figures 11, 31B

Liophryne brevipes Boulenger, 1897: 11 (type locality, ‘‘Mount Victoria, Owen Stanley Range, New Guinea’’; holotype, BMNH 1947.2.12.50, formerly 1896.10.31.31, collected by A. S. Anthony; see account of *Liophryne rhododactyla* for information on locality and date of collection).

Sphenophryne brevipes: Parker, 1934: 158 (first use of combination).

TYPE MATERIAL: The holotype is in mod-

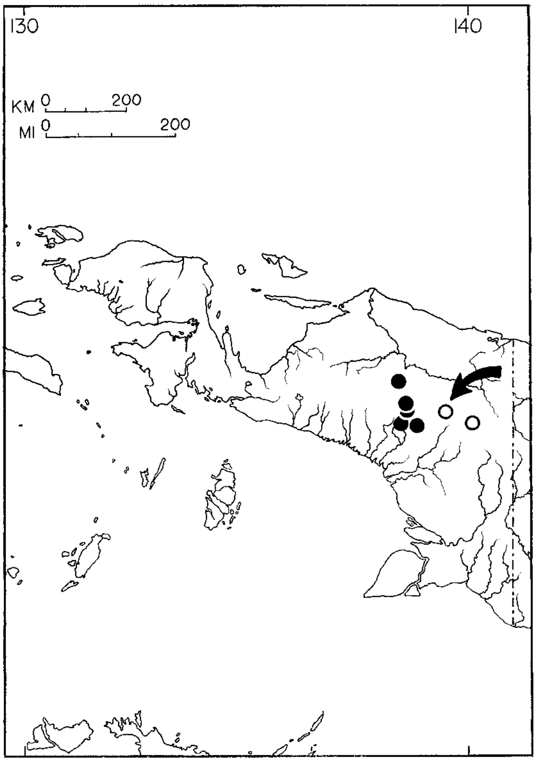

Fig. 10. Distribution of three *Oxydactyla* and *Austrochaperina* species in the highlands of Irian Jaya. Closed circles, *O. brevicrus*; open circles, *A. blumi*; arrow, *A. kosarek* (sympatry).

erately good condition though somewhat faded. It has not been sexed. Parker (1934) referred to it as juvenile, although from its size (20.5 mm SVL by my measurement, 22 mm by Parker's earlier measurement) it could be an adult male or subadult female (see below). There are no paratypes. Measurements and proportions of the holotype are: SVL 20.5, TL 7.4, HW 8.4, HD 4.3, FT 8.2, EY 2.65, EN 1.69, IN 1.93; TL/SVL 0.361, HW/SVL 0.410, HD/SVL 0.210, FT/SVL 0.400, EY/SVL 0.129, EN/SVL 0.082, IN/SVL 0.094, EN/IN 0.876. The finger and toe tips are too dried to be measured with accuracy.

DIAGNOSIS: Distinguished from most of its congeners by its relatively small digital discs: those of the fingers not (or scarcely) broader than the penultimate phalanges; those of the toes broader than on the fingers but still only slightly expanded. *Austrochaperina kosarek* has even less development of finger discs, with indistinct terminal grooves and only the disc of the third finger slightly expanded. Two species, *A. aquilonia* and *A. mehelyi*, have finger discs similar to those of *brevipes* but differ in body size and other proportions (see Comparisons).

Fig. 11. *Austrochaperina brevipes*, AMNH A130535, SVL 23.9 mm male and associated eggs.

MORPHOLOGY: A small (SVL up to 28 mm), stocky, relatively broad-headed frog (HW/SVL mean 0.412) with hind legs of moderate length (TL/SVL mean 0.408) and relatively large eyes (EY/SVL mean 0.123). Snout bluntly pointed to almost rounded seen from above, high and almost vertical but slightly rounded in profile; nostrils lateral, almost terminal in profile, scarcely visible from above; loreal region a moderately steep slope, canthus rostralis abrupt but not sharp. Eyes prominent, visible from beneath, upper lid about 60% of interorbital distance. Tympanum indistinct, horizontal diameter half that of the eye or less. Relative lengths of fingers 3 > 4 > 2 > 1, first well developed, more than half the length of second; finger tips flattened and disclike with (except possibly the first) terminal grooves, equal in width to penultimate phalanges or scarcely broader (fig. 54B); subarticular and metacarpal elevations low, rounded, not at all obvious. Relative lengths of toes 4 > 3 > 5 > 2 > 1, all unwebbed and with flattened, grooved, slightly broadened terminal discs distinctly larger than those of fingers (fig. 54B); subarticular and inner metacarpal elevations low, rounded; no outer metacarpal elevation. A straight fold of skin diagonally downward from posterior corner of eye, touching upper edge of tympanum and be-

TABLE 4
Call Statistics for *Austrochaperina brevipes*[a]

Museum no.	Tape no.	Temp., °C	Call duration, sec		Notes/call		Notes/sec		Dominant, Hz	No. of calls
			Mean	Range	Mean	Range	Mean	Range		
UPNG 7419	253	16.7	1.60	1.38–1.69	23.2	20–25	14.3	14.2–14.4	3200	4
AMNH A130540	252	12.8	2.63	2.54–2.73	28.0	27–29	10.4	10.4–10.5	3150	3
No voucher	252	12.8	2.71	2.62–2.76	28.7	27–30	10.4	10.1–10.6	3200	3
No voucher	253	12.5	3.24	3.07–3.38	35.6	34–37	10.8	10.8–10.9	2900	5
No voucher	253	12.8	2.01	1.95–2.08	23.5	23–24	11.4	11.3–11.5	3050	2
No voucher	253	12.9	2.79	2.68–2.87	30.3	29–31	10.7	10.6–10.8	3250	3

[a] All recordings made at Myola Guest House, Northern Prov., Papua New Guinea.

coming obscure on flank. Dorsal surfaces of hind legs somewhat warty; a few scattered, small protuberances on back; ventral surfaces smooth.

COLOR AND PATTERN: Dorsal surfaces of preserved specimens range from pale yellowish tan to dark grayish brown, more often tending to the darker shades. Usually there is little dorsal pattern except for a thin, pale, midvertebral line that is always at least partly evident. There may be a few dark spots, often associated with small warts. Lumbar eye spots are present in a few specimens but are indistinct. The facial region, including upper and lower lips, is dusky but rarely dark enough to produce a face-mask effect. A narrow area below the canthus rostralis is darkened, and a similarly situated dark band follows the postocular fold. Many individuals have a more or less distinct light line along the canthus rostralis. The ventral surfaces are mottled with brown on pale gray, more densely so on the chin and coarser under the hind limbs. A dark, triangular area has its apex just below the vent.

The colors in life are not greatly different from those of the preserved specimens. A frog from Myola (field notes) was reddish brown on all dorsal surfaces with a yellow vertebral line. The loreal area was dark brown, almost black, and the chin, chest, and undersurfaces of hind limbs gray had lighter gray flecks, palms gray, and soles dark gray. The abdominal region is similar to the other ventral surfaces except for being somewhat translucent. Other individuals as seen in color photographs had a brown to yellowish brown dorsal ground color rather than reddish brown. The iris is golden above the horizontal pupil and dark gray elsewhere except for a gold spot beneath the pupil.

VARIATION IN SIZE AND PROPORTIONS: The largest specimen among 37 measured is a female 28.0 mm SVL. Females of 20.0 and 21.9 mm appear to be maturing, and others 21.9 mm or longer (n = 12) are adult. The largest of 18 males measures 23.9 mm. Specimens 18.3 mm and smaller lack vocal slits and thus presumably are immature, whereas those 19.7 mm and larger have slits. (See table 2 for statistics on proportions, and table 3 for regression data.)

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71E; premaxilla, fig. 63D; hyoid, fig. 69B; sacral region, fig. 72D; vomer, fig. 65D; skull, fig. 67C; ear, fig. 60; hand and foot, fig. 57E.

CALL: The call is a series of short, harsh chirps uttered at intervals of one to several minutes (fig. 77E). Based on 20 tape-recorded calls of six frogs (table 4), calls range from about 1.4 to 3.4 sec and include 20–37 notes, with each note being 0.03–0.05 sec long. Notes are pulsed, with 11–13 pulses in a note and the first two or three pulses more widely spaced than the remaining ones. The dominant frequency lies at 2900–3200 Hz. Note repetition rate ranges from 10.1 to 14.4 notes per sec. The expected positive correlation with temperature is evident: Calls of one frog recorded at 16.7°C had a mean of 14.3 notes per sec, whereas those of four others recorded at 12.5–12.9° averaged 10.4–11.4 notes per sec. The correlation (negative) of duration with temperature is less close, and that of notes per call (positive) is even poorer.

COMPARISONS WITH OTHER SPECIES: *Austro-*

chaperina aquilonia and *A. mehelyi* resemble *A. brevipes* in disc proportions, although they have larger toe discs. *Austrochaperina* is distinguished by relatively shorter legs and longer eye-naris distance that, in combination, afford clear separation (fig. 2).

Austrochaperina brevipes is microsympatric with *Liophryne similis* and probably also with its sibling *L. rhododactyla*, larger species that otherwise look much like *brevipes*. Juvenile *similis* can easily be confused with *brevipes*, alive or preserved. The undersurfaces of *similis* tend to be more heavily pigmented, with the throat and chest appearing dark with light flecks in contrast to the paler, mottled pigmentation of *brevipes*. A narrow, pale vertical stripe on the snout of *similis* bifurcates at the level of the nares, whereas in *brevipes* the pale color of the top of the snout typically converges to a point below the level of the nares. These features, and the tendency for *similis* to have much darker loreal and postocular regions, should permit correct identification of questionable specimens. Confirming the sexual maturity of specimens in the problematic size range is also a helpful approach.

HABITAT AND HABITS: *Austrochaperina brevipes* lives on the floor of mossy montane rain forest. While collecting in August 1987 (Zweifel and Parker, 1989), we took most of our specimens from beneath logs during the daytime and found the balance at night as we searched through the leaf litter for calling individuals. We saw none active on the surface of the leaf litter, although such small frogs might easily be overlooked.

A male, SVL 23.9 mm SVL, was found associated with a clutch of 14 eggs (fig. 11) on the verge of hatching (most of the capsules ruptured when preserved). The dimensions of an intact egg (external capsule) are 5.8 × 5.2 mm. A female of 22.9 mm contained 10 well-yolked eggs about 2 mm in diameter.

DISTRIBUTION: *Austrochaperina brevipes* is known from only two localities 38 km apart: Mount Victoria and Myola Guest House in the Owen Stanley Mountains (fig. 42). It likely has a wider range in these mountains than is known at present, but it has not been taken in seemingly appropriate habitat in Morobe Province to the northwest, and it may be replaced by *Oxydactyla crassa* in mountains to the southeast.

LOCALITY RECORDS AND SPECIMENS EXAMINED: PAPUA NEW GUINEA: Central Prov.(?): Mt. Victoria (BMNH 1947.2.12.50, holotype). Northern Prov.: Myola Guest House, 2080 m, 7 km S, 6 km W Mt. Bellamy (AMNH A130512–130523, A130525–130541; UPNG 7084–7091, 8276).[4]

REMARKS: This species, described in 1896, was known only from the type specimen until rediscovered by James Menzies at Myola Guest House in 1986.

Inasmuch as *A. brevipes* and *L. rhododactyla* are similar morphologically at the size of the holotype of *brevipes*, and the two species share a common type locality, I have considered the possibility that the holotype of *brevipes* may be a juvenile *rhododactyla*. In some measurements, in fact, the holotype does hew more closely to the *rhododactyla* regression lines. As the holotype has faded somewhat, the characters of pigmentation are not available. There is, however, no firm basis for identifying *brevipes* with *rhododactyla*. That Boulenger, with fresh specimens at hand, recognized a close affinity of the two but regarded them as distinct is sufficient reason for not complicating the nomenclature.

Austrochaperina derongo, new species

Figures 12, 32H

Sphenophryne macrorhyncha: Zweifel, 1956 (part, specimens from vicinity of Idenburg River, Irian Jaya).

HOLOTYPE: AMNH A82289, collected on April 7, 1968 by Fred Parker at Derongo, 400 m, Western Province, Papua New Guinea.

PARATYPES: Papua New Guinea (collected by Fred Parker unless otherwise noted). Western Prov.: AMNH A82287, A82288, A82290, A92794–92798 (C&S), A145507 (C&S), A157805–157819, MCZ A92510, A132847–133016, type locality, Apr. 5–7, 1969; MCZ A80992, 81222, 81223, Wang-

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[4] 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.

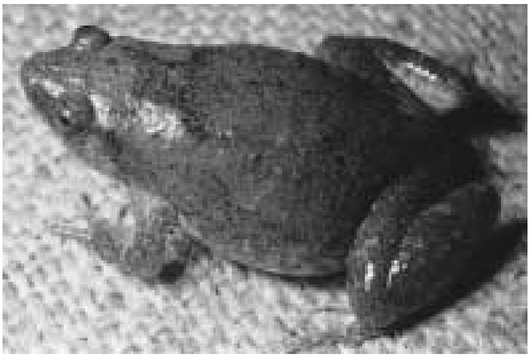

Fig. 12. *Austrochaperina derongo*, MCZ A132824, SVL 41.9 mm, photo by Fred Parker.

bin, 1460 m, Dec. 22, 1969; QM J67253, 67254, collected by M. Cunningham, S. Richards, and A. Dennis, 5 km W Tabubil (5°18′S, 141°11′30″E), 580 m, Nov. 18, 1994; QM J67252, collected by Cunningham, Richards, and Dennis, 9 km S Tabubil, Nov. 4, 1994; AMNH A90400, 90401, MCZ A87511, A133034, Gigabip, 1520 m, Aug. 23–24, 1972; MCZ A133035, Kavorabip, 1520 m, Aug. 25, 1972. Simbu Prov.: AMNH A79974, MCZ A133032, 133033, Soliabedo, 550 m, Sept. 24, 1967; MCZ A132824, Ining River at Soliabedo, 370 m, Sept. 24, 1967; AMS R133070, collected by S. Donnellan at Haia village, 720 m, 145°00′E 6°42′S, June 12, 1984; AMS R133062–133069, R133071–133079, collected by S. Donnellan at Haia Bush Camp, 880 m, 145°01′S 6°40′E, June 17–18, 1984. Gulf Prov.: AMNH A79975, A157843–157845, MCZ A132834–132840, Weiana, 8 km S, 1 km E Soliabedo, 460 m, Sept. 28, 1967; MCZ A133023, 133024, A132828, Camp II, Pio River, 6.5 km S, 1 km E Soliabedo, 300 m, Sept. 27–29, 1967; MCZ A132829, A133026–133029, Camp III, Nimi River, 13.5 km S, 1 km E Soliabedo, 430 m, Sept. 29, 1967; MCZ A133017–133022, between Camp II, 6.5 km S, 1 km E Soliabedo, and Weiana, 8 km S, 1 km E Soliabedo, 430–730 m, Sept. 29, 1967; MCZ A132826, 132827, Bol and Nimi headwaters, 370–610 m, Sept. 30, 1967; MCZ A132841, Uraru, 90 m, Oct. 2, 1967; MCZ A132831–132833, Koni, Purari River, 80 m, Oct. 4, 1967; UPNG 2503, collector not noted, Purari River, Powaia No. 1, Oct. 12, 1970. Southern Highlands Prov.: UPNG 6979, collected by Roy Mackay, Nov. 1984 on Mt. Bosavi, 1200 m; ZSM 109/1999, collected by T. G. Schultze-Westrum, in Sept. 1966 at Didessa, north slope of Mt. Bosavi; AMS R122166–122169, R122232, R122235–122239, collected by S. Donnellan at Namosado, 615′S, 14247′E; AMS R122294, R122295, R122785, collected by S. Donnellan at Magidobo. Indonesia: Irian Jaya: AMNH A49531–49533, A49537, A49538, A49540–49541, A49572, A49617–49619, A49621–49626, A49656, A49661, collected by W. B. Richardson on the Indisch-Amerikanische Expeditie (Third Archbold Expedition to New Guinea), 5 km SW of Bernhard Camp, Idenburg River, 850 m,[5] in Apr. 1939 (approximately 139°14′E, 3°26′S; note that the Idenburg River has been renamed Taritatu River); QM J67250, MZB 3563, collected by S. Richards and D. Iskandar on Apr. 9 and 13, 1998, respectively, at Wapoga Alpha Camp, 1100 m, 3°08.687′S, 136°34.423′E.

Type Locality: Derongo is a village located approximately 29 km N, 4 km W of Ningerum and 12 km from the border with Irian Jaya.

Etymology: The name of the village that was the provenance of many specimens is used as a noun in apposition.

Diagnosis: A moderate-size species of *Austrochaperina* with maximum SVL of females and males being 42 and 37 mm, respectively, but some populations are evidently smaller—females to 36 and males to 33 mm. The dorsal ground color is brown in preservative, olive to reddish brown in life, sometimes with dark speckles. Diagnostic proportions include finger discs relatively small, mean FD/SVL ≤ 0.031, EY/SVL ≤ 0.101, and IN/SVL ≤ 0.104.

Description of Holotype: Adult female with the following measurements and proportions: SVL 35.6, HW 12.8, TL 15.2, EY 3.2, EN 2.7, IN 3.5, HD 7.9, FT 15.4, disc of third finger 0.9 (penultimate phalanx 0.6), disc of fourth toe 1.25 (0.55); HW/SVL 0.360, TL/SVL 0.427, EY/SVL 0.090, EN/

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[5] Earlier (Zweifel, 1956: 13), I gave this locality as 4 km, overlooking a footnote in Archbold et al. (1942: 239) that corrected several Expedition localities referred to Bernhard Camp.

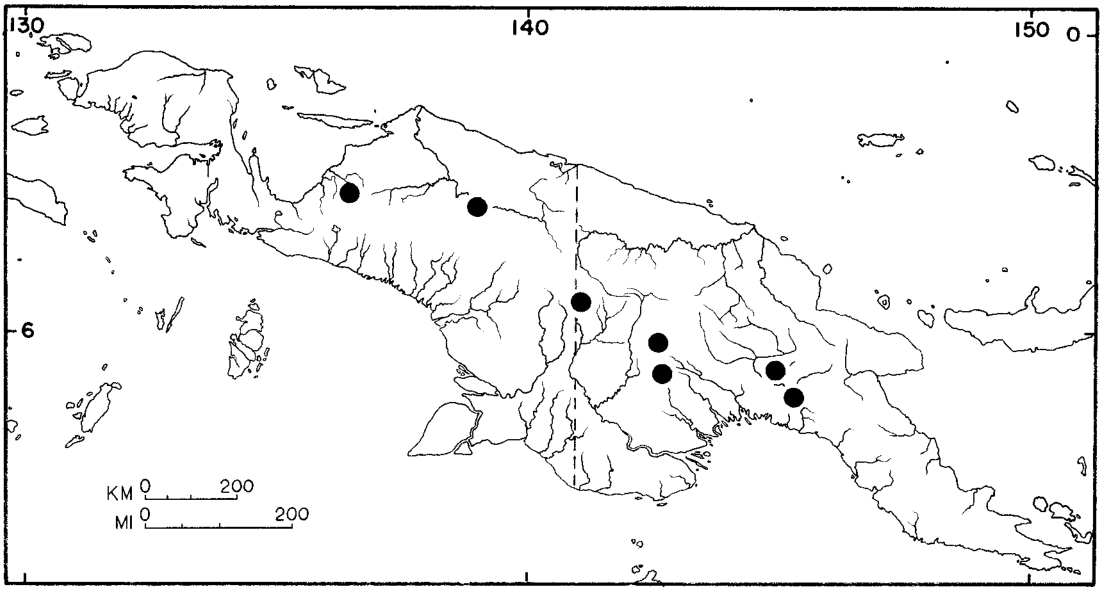

Fig. 13. Distribution of *Austrochaperina derongo.*

SVL 0.076, IN/SVL 0.098, EN/IN 0.771, HD/SV 0.222, FT/SV 0.433, FD/SVL 0.025, TD/SVL 0.035.

Head narrower than body; snout subacute in dorsal view, more so when viewed laterally, strongly projecting; nostrils much closer to tip of snout than to eye, lateral, barely visible from above; canthus rostralis rounded, loreal region nearly vertical, shallowly concave. Eyes small, lateral, interorbital space more than twice width of upper eyelid. Tympanum obscure, about 2 mm diameter, about its own diameter from posterior corner of eye. Relative finger lengths 3 > 4 > 2 > 1, first reaching to anterior edge of subarticular elevation of second; all with terminal discs, that of third finger twice width of penultimate phalanx, of first finger only slightly broader than penultimate phalanx; subarticular elevations low, rounded, and inconspicuous, inner and outer metacarpal elevations scarcely evident. Relative toe lengths 4 > 3 > 5 > 2 > 1, first toe short, reaching to base of subarticular elevation of second; all toes with terminal discs, that of fourth toe about twice width of penultimate phalanx and wider than disc of third finger; subarticular elevations low, rounded, and inconspicuous, inner metatarsal elevation low, no outer elevation. Body essentially smooth, with only a weak postocular fold passing diagonally from the eye over the upper edge of the tympanum toward the arm.

The dorsal ground color in preservative is gray-brown with inconspicuous darker speckles and a pale band extending a short distance behind the eye on the dorsal surface of the head. The paler ground color of the loreal region extends to the ear and is overlain with darker speckles on the loreal region and upper lip. The sides of the body, the groin, and anterior surfaces of the thighs also show a pale ground color with darker speckles, verging on mottling on the thighs. The upper surfaces of the limbs are colored and patterned like the dorsum of the body, but with the markings more clustered. The posterior surfaces of the thighs resemble the dorsum—brown with darker speckling in no particular pattern. The ventral surfaces are pale and unmarked except for faint melanic clusters on the shanks. The soles are brown with pale irregular markings.

VARIATION IN TYPE SERIES: Among specimens from Western, Simbu, and Gulf Provinces, the largest of ten adult males measures 36.9 mm SVL, the largest of 33 adult females 49.7 mm. Males in this series mature at about 32–33 mm SVL, for individuals both with and without vocal slits lie in this

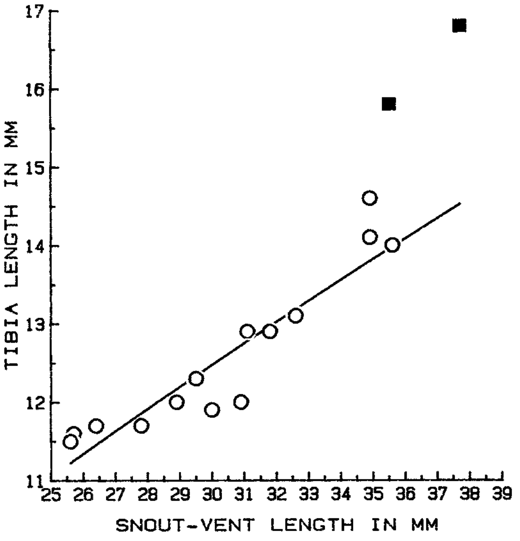

Fig. 14. Comparison of tibia lengths in *Austrochaperina derongo* (circles) and *A. rivularis* (squares) from Southern Highlands Province, Papua New Guinea. For regression data, see table 3.

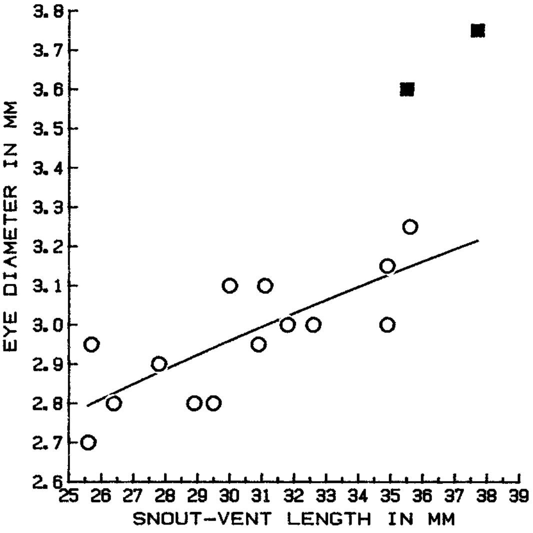

Fig. 15. Comparison of eye diameters in *Austrochaperina derongo* (circles) and *A. rivularis* (squares) from Southern Highlands Province, Papua New Guinea. For regression data, see table 3.

size range. Mature females may be as small as 31 mm SVL, but others as large as 35 mm have ova only slightly enlarged. In the series of 19 specimens from Irian Jaya there are five gravid females in the range of 33.0–35.4 mm SVL, whereas a 28- mm specimen is immature. Five males 29.0 to 34.8 mm have vocal slits, and a 26.7-mm specimen does not. The specimens from Southern Highlands Province include six adult females 29.5 to 35.6 mm SV and one apparently maturing at 27.8 mm. Five males 25.6 to 32.6 mm have vocal slits. The four largest females (SVL 44.7–49.7 mm) are all from one locality, Gigabip in Western Province. Thus, there appears to be geographic variation in size at maturity and in maximum size.

Differences in proportions as well as in size are evident among the widely scattered samples of *derongo* (table 2). Regression data are in table 3.

Variations from the color pattern described for the holotype include: dorsum largely without dark speckles; no postocular pale band; chin and chest darker than abdomen; tip of snout pale, almost white, in both sexes. In life, the individual illustrated from Soliabedo (fig. 12) was light olive-drab dorsally and somewhat yellower bordering the abdomen. The iris was similar to the dorsal ground color (as seen in a color transparency). A specimen from Derongo (color transparency) was reddish brown dorsally with darker markings, the border of the abdomen creamy white, and the iris brownish gold. Color transparencies of two specimens from Irian Jaya show a light gray ground color in one, a darker gray in the other. Each has a darker scapular mark, and the darker individual has the eyelids and anterior of the head darker gray (fig. 31H).

Most males (and some females) have the tip of the snout much paler than the rest of the head.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71Q; 3rd finger disc, fig. 50; premaxilla, fig. 64H; sacral region, fig. 73D; vomer, fig. 65L; hand and foot, fig. 55B.

CALL: Stephen Richards recorded the call of this species at Wapoga Alpha Camp in Irian Jaya on April 9, 1998. The call is a series of brief, harsh, pulsed notes (table 5). Mr. Richards estimates that his recording lacks the first three notes of the call, so by extrapolation the complete call would have lasted about 13 sec and comprised of about 24 notes. Five notes average 0.075 sec in length (0.070–0.077) with an average of 13 pulses (12–15).

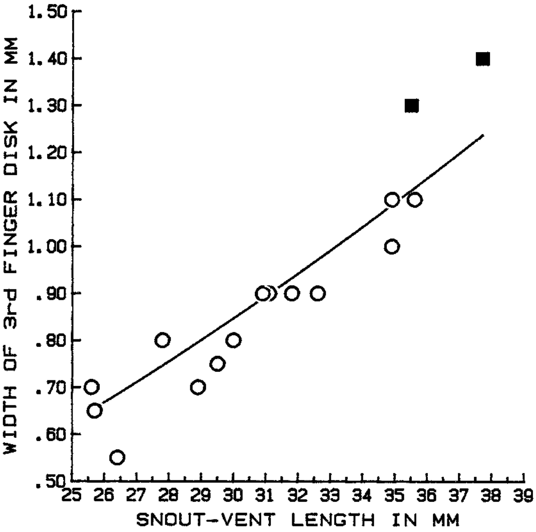

Fig. 16. Comparison of third finger disc widths in *Austrochaperina derongo* (circles) and *A. rivularis* (squares) from Southern Highlands Province, Papua New Guinea. For regression data, see table 3.

A typical note (fig. 80A) begins with three brief pulses followed by several longer, louder ones gradually diminishing in duration and intensity. The note repetition rate is about 1.9/sec, the dominant frequency being 2650 Hz (see also Vocalizations).

The frog called from beneath a leaf in a creekbed adjacent to a small stream beside a trickle of water (S. Richards, personal commun.). The voucher specimen is QM J67250; a copy of the recording is on AMNH Herpetology tape no. 284. A call by another specimen (MZB 3564) recorded at the same locality sounds the same but is masked by the noise of running water.

COMPARISONS WITH OTHER SPECIES: *Austrochaperina derongo* is much like *archboldi, hooglandi*, and *guttata*; only the last, with its large size, large finger discs, and long legs (table 2) stands out much from *derongo*. Color pattern adequately distinguishes *hooglandi*, and most *archboldi* can be separated by their greater internarial span and larger eyes.

HABITAT AND HABITS: The association of a calling individual with water (see above) and the capture of other specimens in the same habitat (S. Richards, personal commun.) represent the only information on the habits and habitat of this species. Most of the localities in Papua New Guinea fall in areas mapped by Paijmans (1975) as "Medium Crowned Lowland Hill Forest." The two highest sites (Wangbin, 1460 m; Mt. Bosavi, 1200 m) are within Lower Montane Forest zones. Archbold et al. (1942) described the region where the Irian Jaya specimens were taken as heavily mossed rainforest.

DISTRIBUTION: Most locality records for *A. derongo* are at moderate to low elevations along the southern flank of the central dividing range from just east of the Irian Jaya–Papua New Guinea border to the Purari River drainage in Gulf and Simbu provinces; the Irian Jaya localities are north of the central ranges and nearly 200 km from the closest station in Papua New Guinea (fig. 13). The elevation range is 80–1460 m.

REMARKS: If I am correct in associating "*Sphenophryne* sp. B" of Mahony et al. (1992) with *derongo* (see Karyology), then this species is unique among the few *Austrochaperina* for which there are data in having the chromosome number 2N of 24 rather than 26.

There is one known instance of sympatry between *A. derongo* and *A. rivularis* based on specimens collected by S. Donnellan at Namosado, Southern Highlands Province, Papua New Guinea. Two adult male *A. rivularis* (AMS R122164, R122165) taken along with ten *A. derongo* (AMS R122166–122169, R122232, R122235–122239) stand out for their relatively large size: one (SVL 37.7 mm) is larger than any of the 10 *derongo* (maximum is a 35.6 mm female) and the other, at 35.5 mm, is at the upper range of that series. In all proportions in which *derongo* and *rivularis* differ, the two large males resemble *rivularis* rather than *derongo*. Figures 14–16 illustrate the greater tibia length, eye size, and disc width of *rivularis* at the site of sympatry.

Variations in size and proportions among the geographically scattered samples of this species lead me to suspect that *derongo* may be a composite of two or more species. However, I am unable to subdivide the species to my satisfaction. More recordings of calls might resolve the question; the only recording at present is from the most remote part of the range.

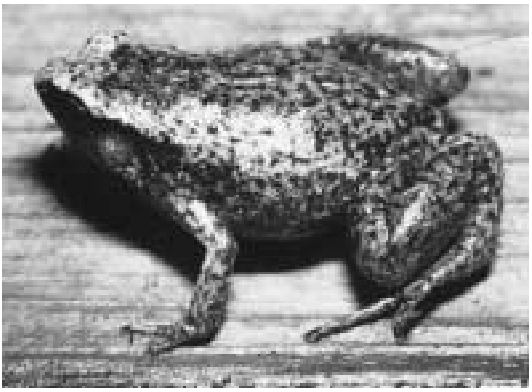

Fig. 17. *Austrochaperina gracilipes*, AMNH A83072, SVL 18.0 mm.

Austrochaperina gracilipes Fry

Figure 17

Austrochaperina gracilipes Fry, 1912: 93 (type locality, ‘‘Somerset, Cape York, North Queensland,’’ Australia; holotype, AMS R4536, collected by C. Hedley and A. R. McCulloch in October 1907).

S[phenophryne]. gracilipes: Nieden, 1926: 48 (first use of this combination).

Sphenophryne gracilipes: Parker, 1934: 155. Zweifel, 1962: 31; 1985b: 289.

Sphenophryne robusta: Zweifel, 1965: 2 (part, *gracilipes* considered a synonym).

DIAGNOSIS: A small *Austrochaperina*—females to almost 23 mm SVL, males to 20 mm—with well-developed digital discs, small eyes (EY/SVL < 0.115), long legs (TL/SVL mean of 0.464), and a call consisting of a train of high-pitched peeps. No other known New Guinean *Austrochaperina* has this combination of characteristics.

MORPHOLOGY: Size small, less than 23 mm SVL. Head narrow, tapering to bluntly rounded snout, more pointed in profile, and overhanging the somewhat undershot lower jaw. Loreal region flat, nearly vertical; nostrils lateral, scarcely visible from above, about halfway between eye and snout tip but appearing closer to latter in profile. Eyes lateral, easily visible from below; eyelid slightly narrower than interorbital space. Tympanum inconspicuous, annulus one-half eye diameter or less. Relative lengths of fingers $3 > 4 > 2 > 1$, first less than half length of second; fingers 2–4 with grooved terminal discs slightly broader than penultimate phalanges, disc of first finger not broadened; subarticular and inner metacarpal elevations moderately prominent (fig. 57C). Toes unwebbed, relative lengths $4 > 3 > 5 > 2 > 1$, first less than half length of second; grooved terminal discs of toes 2–5 broader than penultimate phalanges and larger than finger discs, disc on first toe small, not broader than penultimate phalanx; subarticular and inner metatarsal elevations moderately prominent (fig. 57C). Body smooth above and below; a weak, curved postocular-supratympanic fold.

COLOR AND PATTERN: The dorsal ground color in preservative is brown. A dark loreal streak often continues as an ill-defined dorsolateral streak separating the paler side of the body from the darker middorsal region. Small dark spots often are present on the dorsal and lateral ground color, and most individuals have a pale vertebral hairline. The upper surfaces of the limbs are tan with darker spots and speckles. The groin is paler, immaculate, or with indistinct darker flecks. Anterior and posterior surfaces of the thighs have a similarly pale ground color but are more heavily marked, comparable to the dorsal surfaces. The chin and chest are spotted to mottled with gray-brown on a tan ground, with the intensity of spotting being quite variable. The tip of the snout is gray. The abdomen is typically less heavily marked, whereas the undersides of the thighs are more like the chin and chest.

Living frogs from Wipim, Western Province (fig. 17), had the dorsum grayish to golden brown anteriorly, changing to reddish brown posteriorly and on the hind legs; a fairly distinct dark stripe on the canthus rostralis and through the ear, and a diffuse darker band dorsolaterally on the back; central area of the back somewhat darker than the sides; a fine vertebral hairline; remainder of the dorsal pattern mostly in the form of dark brown to black maculations on the ground color; undersides mottled with dark and light gray, mottling more intense on the chin and farther back on the ventral surfaces; and iris golden in the upper half, much darker reddish gold in the lower half. Australian frogs of this species have bright orange in the axilla and groin as well as on the hidden surfaces of the thighs and upper arm; no such color was present in the Papuan frogs. Australian specimens are illustrated in color in Cogger (1992) and Cameron and Cogger (1992).

VARIATION IN SIZE AND PROPORTIONS: The largest of about 100 specimens from Papua New Guinea is a female 22.8 mm SVL, and all eight frogs measuring more than 20 mm are females. Males reach 19.6 mm and are mature (calling) by at least 17.5 mm. Females are mature by at least 19.1 mm, probably smaller. Statistics for proportions are in table 2, and those for regressions in table 3. Minor average differences in some proportions between Australian and New Guinean samples do not appear to be significant (Zweifel, 1985b).

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71J; premaxilla, fig. 64A; sacral region, fig. 72I; vomer, fig. 65I; hand and foot, fig. 57C.

CALL: ‘‘The call is a train of relatively high-pitched peeps (about 3700–4300 Hz) uttered over a period of about 10–29 seconds, each peep about 0.14–0.17 seconds in length . . . . the number of notes per minute ranges from 77 to 100 and the number of notes per call from 15 to 33 . . . . a minute or more may elapse between calls’’ (Zweifel, 1985b: 291). The quoted description includes Papuan (fig. 77D) and Australian samples with a temperature range of 23.4–24.8°C. No geographic differentiation is evident.

COMPARISONS WITH OTHER SPECIES: This is a rather generalized species of *Austrochaperina* with no particularly distinguishing morphological features except its small size, but it differs from other New Guinean species in its call and lowland, seasonal habitat. No other known New Guinean *Austrochaperina* has a repetitive, peeping call (although several *Cophixalus* and *Oreophryne* do), and no other *Austrochaperina* is known from grassy or savanna habitats at low elevations.

Austrochaperina adelphe of Northern Territory, Australia, is identical in morphology to *A. gracilipes* but differs in the advertisement call. Curiously, whereas Australian and New Guinean *gracilipes* differ in that the former have bright orange pigmentation in the axilla and groin, *adelphe* and New Guinea *gracilipes* are alike in lacking this feature.

HABITAT AND HABITS: Where I collected *A. gracilipes* at Wipim, the frogs had climbed up blades of grass at night to call where the vegetation was grassy woodland with denser gallery forest along small streams. Other Papuan localities appear to be in similar vegetation. In Australia the species lives at similar sites but also evidently invades pockets of rainforest (Cameron and Cogger, 1992; Zweifel, 1985b).

Parker (1982) recorded *gracilipes* (as *Sphenophryne robusta*) as the prey of a snake, *Tropidonophis mairi* (as *Amphiesma mairi*).

DISTRIBUTION: *Austrochaperina gracilipes* is the only species of microhylid frog known to inhabit both Australia and New Guinea (fig. 7). In the former area it occurs on the Cape York Peninsula of Queensland. The known range in Papua New Guinea encompasses the non-rainforested lowlands of Western Province. It is likely that *gracilipes* occurs also in adjacent parts of Irian Jaya, although the species is not yet reported from there.

LOCALITY RECORDS AND SPECIMENS EXAMINED: See Zweifel (1985b: 292–293) for this information.

REMARKS: *Austrochaperina gracilipes* may be a junior synonym of *Microbatrachus pusillus*; see the account of that questionable taxon.

Austrochaperina guttata, new species

Figures 18, 31C

HOLOTYPE: MCZ A92812 (field no. Y22785), collected by W. Hutton at 30 km N, 14 km W Kikori, Gulf Province, Papua New Guinea, on September 11, 1975.

PARATYPES: All from Papua New Guinea. MCZ A132842–132846, AMNH A157842, collected by Fred Parker at Uraru, 90 m, Simbu Province, Oct. 2, 1967; MCZ 132825, collected by Fred Parker at Ining River, Soliabedo, 360 m, Simbu Province, Sept. 24, 1967; BPBM 13107, 13137, QM J67256, collected at Ivimka Field Station, 5.5 km S, 5.6 km W of Tekadu Airstrip, 7°44.10′S, 146°29.77′E, 120 m, Gulf Province, by A. Allison, Oct. 15, 1996 and S. Richards on Nov. 19, 1996. I also designate BPBM 13157 as paratype, which was taken from the last locality. A tape recording of its call and a

Fig. 18. Holotype of *Austrochaperina guttata*, MCZ A92812, SVL 42.8 mm.

color transparency examined are sufficient, in my view, to include this specimen in the type series although I did not examine it physically.

ETYMOLOGY: The Latin adjective *guttata*, meaning "spotted," refers to the dorsal color pattern.

DIAGNOSIS: A relatively large *Austrochaperina*—males to 43 mm, females to 44 mm SVL—with large digital discs (FD/SVL $\geq$ 0.035), long legs (TL/SVL mean of 0.479), and a dorsal pattern of irregular dark brown spots on a gray-brown background. The call is distinctive and diagnostic (see Call below).

DESCRIPTION OF HOLOTYPE: Adult female with the following measurements and proportions: SVL 42.8, HW 16.1, TL 21.6, EY 4.5, EN 3.4, IN 4.5, HD 11.8, FT 21.4, disc of third finger 1.6 (penultimate phalanx 0.85), disc of fourth toe 1.9 (1.0), TY 2.3; HW/SVL 0.376, TL/SVL 0.505, EY/SVL 0.105, EN/SVL 0.079, IN/SVL 0.105, EN/IN 0.756, HD/SVL 0.276, FT/SVL 0.500, third finger disc/SVL 0.037, fourth toe disc/SVL 0.044.

Head narrower than body. Snout subacute viewed from above, projecting in lateral aspect; nostrils lateral, just visible from above; loreal region a steep slope, slightly concave; canthus rostralis rounded. Eye outline just visible from beneath; eyelid 3.0, interorbital 4.5 mm (space/lid = 1.5). Tympanum small, inconspicuous. Relative lengths of fingers $3 > 2 > 4 > 1$; first finger greater than one-half length of appressed second, reaching past subarticular elevation, all-with well developed terminal discs, that of third almost twice width of penultimate phalanx; subarticular elevations low, rounded, inconspicuous; inner metacarpal elevation elongate, rounded, slightly more conspicuous than the subarticular elevations, outer metacarpal elevation barely evident. Toes unwebbed, relative lengths $4 > 3 > 5 > 2 > 1$, first reaching almost to distal end of subarticular elevation of second, all with well-developed terminal discs, that of fourth toe wider than that of third finger; subarticular elevations low, rounded, inconspicuous; inner metatarsal elevation low, elongate, more conspicuous than subarticular elevations. A moderately conspicuous postocular-supratympanic fold curves downward to the arm insertion; otherwise, body surfaces are smooth.

In preservative, the dorsum is gray-brown with small but distinct, irregular dark brown spots from snout to tip of body; the snout tip is not noticeably paler than the top of the head. The color pattern on the dorsal surfaces of limbs, hands, and feet is similar to that of the body. The loreal region is darker than the dorsal ground color but is not sharply defined. The lips are spotted and barred, and an ill-defined dark mark lies along the postocular fold. The sides of the body and anterior surface of the thighs are spotted, verging on mottling, whereas the posterior surface of thighs has diffuse dark and light spotting. The chin is pale with moderate darker spotting around the rim and diffuse dark spotting elsewhere. The chest, abdomen, and undersides of thighs are pale and unspotted, but the undersides of the shanks are heavily spotted and the soles are darkened.

VARIATION IN TYPE SERIES: Body proportions of the 11 frogs comprising the type series, all adults, are summarized in table 2, and regression data are in table 3. Six adult males range from 37.2 to 43.3 mm SVL, five adult females from 40.9 to 43.8 mm.

There is little variation in color pattern in the paratypes. One has dorsal spotting encroaching on the undersides of the thighs. In another, the smallest male, the dorsal pattern of spots is much denser, almost reticulate, and the anterior and posterior surfaces of the thighs are similarly marked. The snout tip is slightly paler than the rest of the head in some but not all males, but not in two calling males.

As seen in color transparencies, one individual has a gray ground color with dark gray to black spotting, the other has a tan ground color and dark brown to black spotting.

ILLUSTRATIONS: Hand and foot, fig. 55B.

CALL: Through the courtesy of Stephen Richards and Allen Allison, I have tape recordings of the calls of two individuals of this species, QM J67256 and BPBM 13157. The call is a prolonged series of brief, harsh notes given at a rate of about 7 per sec at 24.2° and 26.4°C (fig. 79C, table 5). The mean note duration is 0.048 sec in two calls (range 0.040–0.052, dominant frequency 2050–2200 Hz). Each note typically has six or seven pulses about equal in length or with the last longer, although one or two weak additional pulses may sometimes be detected (figs. 79C, 80B, see Vocalizations). Two peculiarities of this species' call are its duration and infrequency of utterance. A nearly complete sequence—S. Richards estimated (personal commun.) that it lacks the initial 3–8 seconds—lasts 1 min 22 sec. Even more striking is the second call, the recording of which lasts 2 min 37 sec and lacks an estimated 10–15 sec (Allen Allison, personal commun.) S. Richards reported that his recorded individual called only three or four times in an hour.

COMPARISONS WITH OTHER SPECIES: The features noted in the Diagnosis render *guttata* a rather distinctive species. *A. archboldi*, probably a smaller species, resembles *guttata* in relative eye size and leg length but has a wider internarial span, smaller hands and finger discs, and a dorsal pattern of finer dark markings. The other most similar species—*derongo* and *hooglandi*—differ in critical ratios (table 2), and the latter has a distinctive color pattern. *A. guttata* and *A. derongo* occur in sympatry at Uraru, Gulf Prov., Papua New Guinea.

HABITAT AND HABITS: Two of the localities for the species are in areas mapped by Paijmans (1975) as Medium Crowned Lowland Hill Forest, whereas the type locality appears to be in ''small crowned forest on plains and fans.'' Stephen Richards reports (personal commun.) that a specimen he tape-recorded and collected was ''calling from under litter at the base of a small shrub. . . . The forest here is lowland alluvial rainforest.'' Allen Allison (personal commun.) described the calling site of another individual: ''. . . on the ground in a small, apparently natural 'shelter' approx. 10 cm wide, 10 cm deep and 15 cm high formed by a few leaves that had fallen around a clump of grass.''

DISTRIBUTION: The species is known from localities around the head of the Gulf of Papua (fig. 19), two in Gulf Province and two in Simbu Province; see Holotype and Paratypes for specifics. Three known elevations of capture are 90, 120, and 360 m, and the fourth is likely within or below this range.

Austrochaperina hooglandi (Zweifel), new combination

Figure 20

Sphenophryne hooglandi Zweifel, 1967a: 2 (type locality, ''Mt. Hunstein, Sepik District, Territory of New Guinea [West Sepik Province, Papua New Guinea], at an elevation of 4000 feet'' [1220 m]; holotype, AMNH A77597, collected by R. D. Hoogland on August 13, 1966).

DIAGNOSIS: A relatively large *Austrochaperina*, with males and females reaching 43–44 mm SVL, a size otherwise attained in the *hooglandi* species group only by *guttata*. Among other *Austrochaperina*, this size is attained or exceeded only in some populations of *palmipes* and *rivularis*. The color pattern of *hooglandi* is distinctive, with the dark middorsal region abruptly differentiated from paler lateral areas and with reddish shades prominent, especially laterally and on the groin and thighs.

MORPHOLOGY: The holotype, a male, is described in detail in Zweifel (1967a). Its measurements and proportions are: SVL 40.1, HW 14.5, TL 17.6, EY 3.8, EN 3.1, IN 4.1,

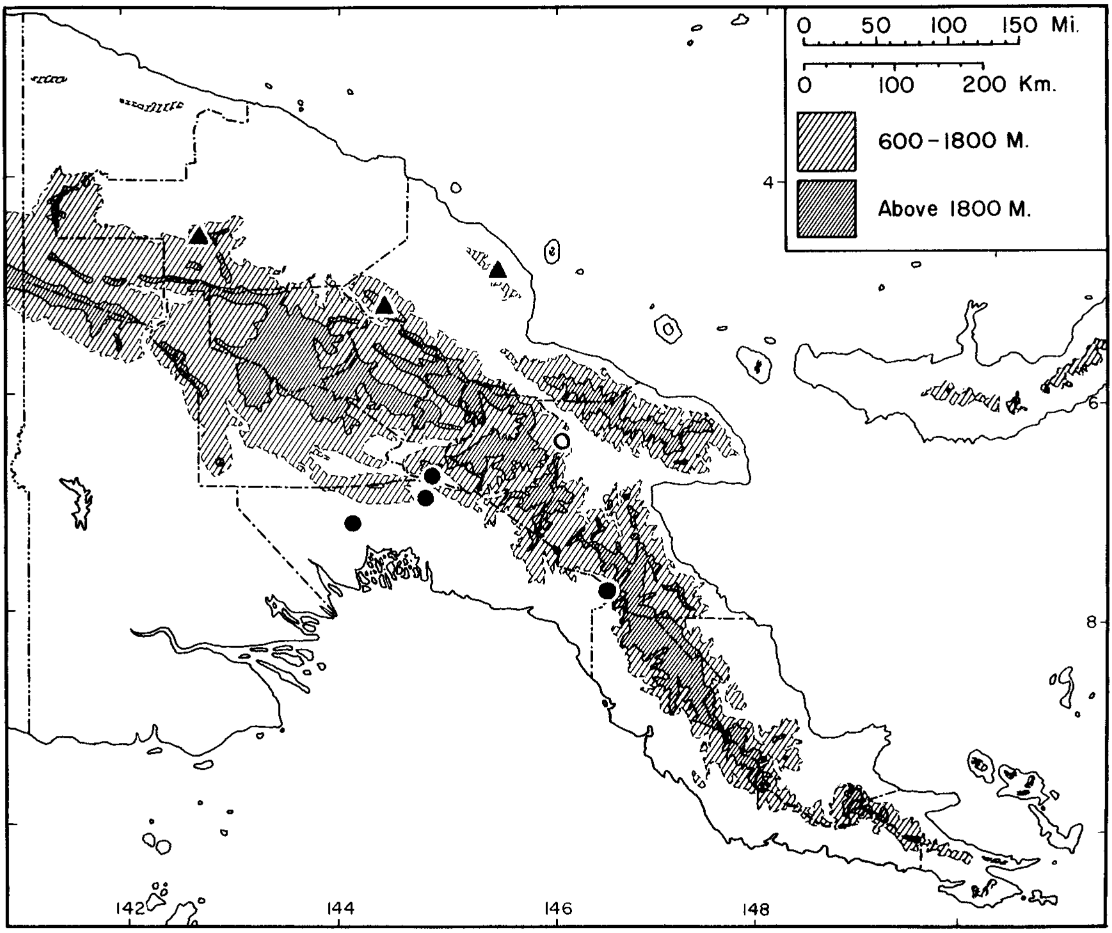

Fig. 19. Distribution of three species of *Austrochaperina*: *A. archboldi* (open circle), *A. guttata* (closed circles), and *A. hooglandi* (triangles).

HD 9.3, FT 17.6, disc of third finger 1.05 (penultimate phalanx 0.7), disc of fourth toe 1.45 (0.85); TL/SVL 0.439, HW/SVL 0.361, EY/SVL 0.095, EN/SVL 0.077, IN/SVL 0.102, EN/IN 0.756, HD/SVL 0.232, FT/SVL 0.439, disc of third finger/SVL 0.026, disc of fourth toe/SVL 0.036.

A relatively large *Austrochaperina*, adults about 40 mm SVL or longer, with narrow head (HW/SVL 0.353) and moderately long hind legs (TL/SVL 0.444). Snout acute but blunt, projecting beyond anterior margin of lip (fig. 21); loreal region nearly vertical, shallowly concave, canthus rostralis rounded but not obscure; nostrils directed laterally, IN greater than EN (EN/IN O.731; IN/SVL 0.105); eyes unusually small (EY/SVL 0.091), interorbital span almost twice eyelid width; tympanum small, obscure. Hands of average size (HD/SVL 0.227); all fingers and toes with distinct discs bearing marginal grooves, those of third finger about 1.6× width of penultimate phalanges, of fourth toe 2.0× (FD/SVL 0.030, TD/SVL 0.041); relative lengths of fingers 3 > 4 > 2 > 1, of toes 4 > 3 > 5 > 2 > 1; no trace of webbing on hands or feet; no distinct subarticular, palmar or solar tubercles, only low rounded elevations. Dorsal and ventral surfaces smooth except for slight roughening of the eyelids and top of head; a weak postocular-supratympanic fold. Male has a single subgular vocal sac.

COLOR AND PATTERN: The dorsum was

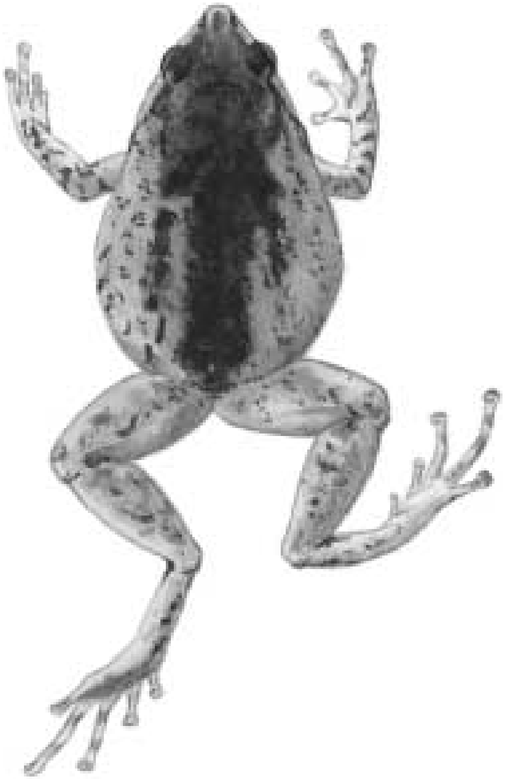

Fig. 20. *Austrochaperina hooglandi*, holotype, AMNH A77597, SVL 40.1 mm.

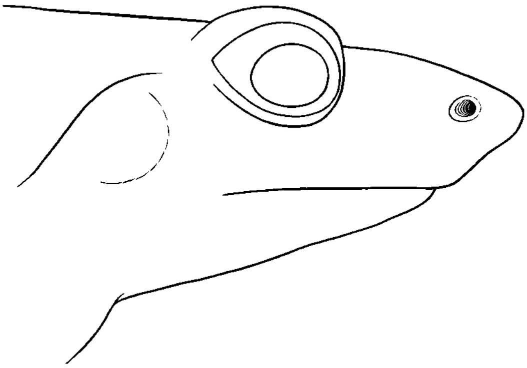

Fig. 21. Head of *Austrochaperina hooglandi*, AMNH A77597 (holotype) in profile; note projecting snout.

pale pinkish brown after several months in preservative, and the darker markings, flecks, and mottling were dark brown. The groin, anterior and posterior sides of the thighs, and inside of the shank were light peach in color, probably being brighter and redder in life. The ventral surfaces are pale tan, almost white. The chin and hind limbs are lightly spotted and mottled with brown, the chest and abdomen immaculate. James Menzies (personal commun.) described a specimen from the Adelbert Mtns.: ''dorsal mid and light brown, speckled, becoming reddish posteriorly; groins and back of thighs dull red; arms and legs as back; tympanum buffy; iris brown; throat speckled, rest of belly plain white but mottled below arms and legs.''

VARIATION IN SIZE AND PROPORTIONS: The largest specimen is an adult female 44.2 mm SVL; the largest male is 43.4 mm SVL. A 35.1-mm female is subadult, whereas one of 37.3 mm is adult. Two males are mature at 40.1 mm, but one of 28.6 mm is not. See table 2 for statistics on proportions and table 3 for regression data.

As is true of some other *Austrochaperina*, males and females of *hooglandi* differ in that the snout of mature males is pale, almost white, and projects more than the darker, shorter snout of females and immature individuals.

ILLUSTRATIONS: Hand and foot, fig. 55D.

CALL: This has not been described.

COMPARISONS WITH OTHER SPECIES: The chief distinction of *A. hooglandi* is in the color pattern—no other species has the dark middorsal region and pink to reddish shade of the groin and thighs. There is broad overlap of the standard morphological ratios with *derongo*, a circumstance confused by geographic variation of some proportions in that species. Greater eye size of *archboldi* (no overlap in ratios) as well as color pattern distinguish that species from *hooglandi*. *A. guttata* differs not only in color pattern, but in several proportions.

HABITAT AND HABITS: Nothing specific is on record. The type locality falls in a region mapped by Paijmans (1975) as Medium Crowned Lowland Hill Forest.

DISTRIBUTION: This species is known from the Hunstein, Schrader, and Adelbert Mountains, West Sepik and Madang Provinces, Papua New Guinea (fig. 19).

LOCALITY RECORDS AND SPECIMENS EXAMINED: PAPUA NEW GUINEA: West Sepik Prov.: Mt. Hunstein, 1200 m (AMNH A77592–77597); Madang Prov.: Malanga

River near Yilu, southwest slope of the Schrader Mountains, 600 m, approximate coordinates 144°9′E, 5°7′S (UPNG 8396); Kervat, Adelbert Mtns., 800 m (UPNG 8135).

REMARKS: The specimen from the Adelbert Mtns., collected by James Menzies on Nov. 14, 1988, resembles topotypic *hooglandi* closely in color and pattern. Its IN/SVL ratio is smaller than in other *hooglandi*, but other ratios are within ranges. The identity in color and pattern with other *hooglandi* leads me to associate it with that species.

Austrochaperina kosarek, new species

HOLOTYPE: MZB 3561, also tagged UPNG 9532 (field no. Blum 1979-38), collected in July 1979 by J. Paul Blum at Kosarek, elevation 1400 m, Jayawijaya District, Irian Jaya, Indonesia.

PARATYPES: The holotype is the only known specimen.

ETYMOLOGY: The name of the type locality serves as a noun in apposition.

DIAGNOSIS: A small *Austrochaperina* (only specimen 21 mm SVL) with short legs (TL/SVL 0.409) and with finger tips (except that of the first) flattened and disclike but with weak terminal grooves and only the disc of the third finger broader than the penultimate phalanx. *A. brevipes* of the far distant Owen Stanley Mountains resembles *kosarek* in size and most proportions but has better developed (though not broader) finger discs and a narrower head (*kosarek* HW/SVL, 0.370; minimum in *brevipes* 0.379).

DESCRIPTION OF HOLOTYPE: Adult female (ova 1.7 mm in diameter) with the following measurements and proportions: SVL 21.0, HW 7.8, TL 8.6, EY 2.55, EN 1.5, IN 2.35, HD 4.0, FT 8.5, disc of third finger 0.45 (penultimate phalanx 0.4), disc of fourth toe 0.65 (0.35); HW/SVL 0.370, TL/SVL 0.409, EY/SVL 0.121, EN/SVL 0.071, IN/SVL 0.112, EN/IN 0.638, HD/SVL 0.190, FT/SVL 0.405, disc of third finger/SVL 0.021, disc of fourth toe/SVL 0.031.

Head almost as wide as body; snout tapering to a sharply rounded tip, rounded and slightly projecting in profile; nostrils visible from above, rather widely spaced, equidistant from snout tip and eye; canthus rostralis rounded, loreal region sloping, slightly concave. Eyes large, corneal margin visible from beneath, eyelid about 75% of interorbital space. Tympanic annulus obscure. Relative lengths of fingers 3 > 4 > 2 > 1, first about half length of second; tips (except for first finger) flattened, somewhat disclike with faint suggestions of terminal grooves, but only that of third finger slightly expanded; subarticular and metacarpal elevations low, rounded (fig. 53F). Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, first much less than half length of second, all but first with grooved discs broader than penultimate phalanges; subarticular elevations rounded, inconspicuous, inner metatarsal elevation rounded, elongate (fig. 53F). A weak postorbital-supratympanic skin fold, skin otherwise smooth above and below.

The top of the snout is gray, the tip almost white. The loreal region and area below and behind the eye are dark brown, with pale spots on the upper lip. The dorsal surface of the body is light brown with obscure, small, darker markings and a dark mark above the cloacal opening. The dark brown postorbital color continues along the flank to the groin and on the anterior side of the thigh, but is much interrupted by irregular light spotting on the flank and thigh. The front legs are heavily spotted above with brown. The hind legs are pale brown above with fine melanic stippling and heavily mottled beneath, and the thighs are mottled on their posterior surfaces. The chin and chest are dark brown with small light spots, and the abdomen abruptly paler with irregular brown spotting.

VARIATION IN TYPE SERIES: There is only the holotype specimen, so nothing can be said of variation.

ILLUSTRATIONS: Hand and foot, fig. 53F.

CALL: This has not been described.

COMPARISONS WITH OTHER SPECIES: *Austrochaperina blumi* is sympatric with *kosarek* and of similar size but may immediately be distinguished from *kosarek* by its well-developed finger and toe discs.

HABITAT AND HABITS: Nothing is on record.

DISTRIBUTION: The only known locality, Kosarek, is at 1400 m elevation on the north slope of the central dividing range of Irian Jaya, west of Nipsan and northeast of Anguruk, about 110 km west of the border with Papua New Guinea (fig. 10).

Austrochaperina macrorhyncha (van Kampen), new combination

Figures 22, 31D

Chaperina macrorhyncha van Kampen, 1906: 168 (type locality, ''Manikion-Gebiet,'' Irian Jaya, Indonesia; holotype, RMNH 4630, collected February 14–21, 1903, by the Netherlands New Guinea Expedition).

Chaperina punctata van Kampen, 1913: 463 (type localities, ''Went-Gebirge, 800–1050 m.'' and ''Hellwig-Gebirge, ±2500 m.,'' Irian Jaya, Indonesia; 12 syntypes [see below], collected by H. A. Lorentz in October and November 1909).

Chaperina basipalmata: Boulenger, 1914: 251 (specimen from Mimika River).

Sphenophryne macrorhyncha: van Kampen, 1919: 54 (first use of combination). Van Kampen, 1923: 107 (part, *basipalmata* considered a synonym). Parker, 1934: 155 (part). Loveridge, 1948: 421 (paratype of *punctata*).

TYPE LOCALITIES: The ''Manikion region'' is not shown on maps available to me, but during the period specified the Expedition operated at the southeastern corner of the Vogelkop Peninsula (Wichmann, 1917: 103–116, map 2). The Went and Hellwig mountains are south of Mt. Wilhelmena (Peak Tricora) in the southern drainage of the central mountain chain of Irian Jaya. Labels associated with several of the Went Mountains specimens specify ''Henvelbivak,'' which Nouhuys (1913: pl. 5) placed on the Lorentz River, 3.5 km W, 9 km N Alkmaar.

TYPE MATERIAL: Eight of the 12 syntypes of *punctata* remain in Amsterdam (Daan and Hillenius, 1966): ZMA 5747–5750 (Went Mtns., 800 m, Oct. 11, 1909 and 1050 m, Oct. 12, 1909); ZMA 5751–5753 (Henvelbivak, 800 m, Nov. 9, 1909); ZMA 5754, Hellwig Mtns., 2500 m, Oct. 1909). The remaining specimens are distributed as follows: AMS R30834 (formerly Macleay Museum 56; Went Mtns., 1050 m); BMNH 1947.2.14.91 (Went Mtns., 800 m, Oct. 11, 1909)[6]; FMNH 100117 (formerly in E. H. Taylor collection; Henvelbivak, 800 m, Nov. 6, 1909); MCZ A10773 (Went Mtns., Oct. 11–12, 1909).

Fig. 22. *Austrochaperina macrorhyncha*, BPBM 13860, SVL 31.6 mm.

DIAGNOSIS: Moderate size, females mature at about 32 mm SVL, males slightly smaller, dorsal pattern obscure or of dark flecks or vermiform markings on a slightly paler background; finger disc moderately large (FD/SVL $\geq$ 0.035), legs long and eyes large (TL/SVL $\geq$ 0.46, EY/SVL $\geq$ 0.116).

MORPHOLOGY: Van Kampen's (1906) description of the holotype (there are no paratypes) is quite thorough, omitting only the sex. I did not dissect the specimen when I examined it (in 1964), so the sex remains undetermined. The specimen was rather dried and the skin of the head had been split down the middle and loosened; hence, some of my measurements may be less exact than

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[6] Parker (1934) mistakenly listed this specimen, then bearing the number BMNH 1928.2.10.3, as a cotype of *Chaperina basipalmata*.

TABLE 5
Characteristics of Calls of Four *Austrochaperina* Species[a]

Species	Duration, min:sec	Notes/sec	Note duration, sec	Pulses/note	Dominant, Hz	Temp., °C
derongo	0:13	1.9	0.075	13	2600	22.6
guttata	<1:22	7.5	0.048	7	2100	26.3
	<2:37	7.6	0.045	7	2100	24.2
macrorhyncha	0:57	2.6	0.120	9	2800	21.6
rivularis	1:25	3.0	0.070	7	2700	—

[a] Figures are averages except for call duration, where N = 2 for *guttata* and N = 1 for the other species.

could be desired: SVL 21.3, TL 10.1, HW 8.2, EY 2.9, IN 2.5, EN 1.7, TY 1.2, FD 0.67, TD 1.0.

This description is based on FMNH 100117, an adult male (vocal slits present) syntype of *punctata*. SVL 29.7, HW 9.75, TL 14.1, EY 3.9, EN 2.2, IN 3.15, HD 7.3, FT 13.6, third finger disc 1.25 (penultimate phalanx 0.6), fourth toe disc 1.35 (0.7); HW/SVL 0.328, TL/SVL 0.475, EY/SVL 0.131, EN/SVL 0.074, IN/SVL 0.106, EN/IN 0.698, HD/SVL 0.246, FT/SVL 0.458, FD/SVL 0.042, TD/SVL 0.045.

Head narrower than body; snout bluntly pointed, slightly projecting, loreal region steep, slightly concave; canthus rostralis obvious but rounded; nostrils lateral, barely visible from above, closer to tip of snout than to eye. Eyes large, eyelid about 86% of interorbital distance; tympanum small and indistinct. Relative lengths of fingers 3 > 4 > 2 > 1, first about half length of second, all with broadened, rounded discs, that on third finger slightly more than 2× penultimate phalanx width; subarticular and metatarsal elevations low, rounded, scarcely evident. Toes with a trace of webbing, relative lengths 4 > 3 > 5 > 2 > 1, all with well-developed, rounded discs, that on fourth toe broader than disc of third finger; subarticular elevations low and indistinct, inner metatarsal elevation low and elongate, scarcely visible. Skin smooth above and below, some slight wartiness on side of body and upper surface of shank. Other specimens do not vary significantly from this description.

COLOR AND PATTERN: The syntypes of *punctata* are faded with little or no pattern discernable. Van Kampen (1913: 464) described them as brownish or gray, the back with dark rounded flecks or marbling, loreal region and upper half of temporal region mostly dark, extremities with indistinct dark crossbands or flecked, lower surfaces light, with gray or brown marbling on the throat and limbs. One of the four specimens from Timeka has a gray dorsal ground color with sharply defined, dark vermiform markings on head and body; on the upper surfaces of the legs these coalesce to form a reticulum. The loreal region is dark, the upper lip light spotted, and there is a dark postocular, supratympanic streak. The groinand anterior and posterior of thigh are pale with darker spots more evident on the posterior surface. Chin through chest is maculated dark and light gray, and the abdomen is pale and immaculate. Soles and palms are dark gray. The other three specimens have the markings much less evident, almost indistinguishable in one.

A color transparency shows a reddish brown dorsal ground color with dark brown markings (fig. 31D).

Neither of the adult male specimens has a pale snout tip.

VARIATION IN SIZE AND PROPORTIONS: In the type series of *punctata*, two male specimens (SVL 24.6 and 28.1 mm) lack vocal slits, whereas one (SVL 29.7 mm) has them, suggesting size at maturity of about 30 mm. Three females in the range 23.7–28.2 mm SVL are immature, one of 31.6 mm has 1.3 mm ova, and five at 32.4–36.5 mm are gravid, suggesting size at maturity of about 32 mm. Among the other six specimens, the largest are two males of 36.8 and 36.9 mm. A male of 28.1 mm lacks vocal slits, a female of 31.6 mm has 1.3 mm ova, and two larger females (32.4 and 36.6 mm) are more conspicuously gravid. Table 2 summarizes variation in proportions; table 3 provides regression data.

ILLUSTRATIONS: Hand and foot, fig. 56B. Van Kampen (1906: fig. 3) illustrated the holotype of *macrorhyncha* and (1913: pl. 9, fig. 7) one of the syntypes of *punctata*, probably ZMA 5751.

CALL: This is known from a single call recorded by Stephen Richards at Wapoga Alpha Camp, Irian Jaya, on April 13, 1998 (table 5). There are approximately 130 brief, harsh notes uttered over a duration of 57 sec at a rate of 2.6 per sec. Ten notes average 0.120 sec in length (0.112–0.130) and have an average of 8.9 (7–10) pulses. Typically, each note begins with a brief pulse separated from a series of longer, less discrete pulses (fig. 80B). The voucher specimen is MZB 3564; a copy of the tape recording is in the AMNH Herpetology Department tape collection on reel no. 284.

COMPARISONS WITH OTHER SPECIES: *Austrochaperina basipalmata* and *A. macrorhyncha* are of similar size but differ in the distinctive character of toe webbing in *basipalmata*. Additionally, *basipalmata* has shorter legs and smaller eyes than *macrorhyncha*; neither TL/SVL nor EY/SVL ratios overlap (table 2). *Austrochaperina rivularis* evidently is much larger than *macrorhyncha*. Males in the Western Province sample of *rivularis* (geographically closest to *macrorhyncha*) mature at about 35 mm SVL compared to 30 mm for *macrorhyncha*, females at 35 vs. 32 mm. The largest specimens of *macrorhyncha* are males 36.8 and 36.9 mm, the largest *rivularis* is a 49-mm female. A more distant population of *rivularis* (Mt. Hunstein, E. Sepik Prov.) has even larger individuals. The two samples differ also in relative eye size and tibia length (table 2). There is overlap in both proportions, but graphing the two together provides good separation (fig. 3).

The sample of *A. derongo* from Irian Jaya is superficially similar to *macrorhyncha* and requires comparison. The two differ notably in several respects: *macrorhyncha* has longer legs, larger eyes, larger hands, and larger digital discs. Among individuals of similar sizes, there is little overlap in regression plots for TL, HD, and third finger disc, and none at all in eye size. Comparisons of ratios are meaningful as the average size of specimens in the two samples is nearly identical (SVL 32.1 mm in *macrorhyncha*, 32.6 mm in *derongo*). The maximum TL/SVL of *derongo* equals about the mean for *macrorhyncha*; there is no overlap in EY/SVL; HD/SVL and FD/SVL only slightly overlap. Figure 23 shows that a complete separation between the two species is achieved by plotting EY/SVL against TL/SVL. The distinctions are maintained in sympatry at the Wapoga Alpha Camp in Irian Jaya.

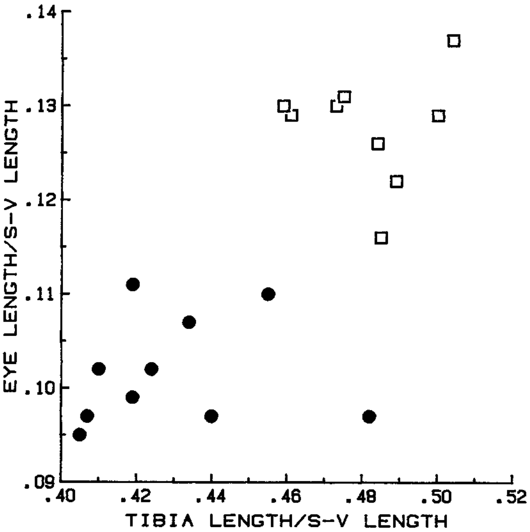

Fig. 23. Comparison of eye size and tibia length in *Austrochaperina derongo* from the Idenburg River (circles) and of *A. macrorhyncha* (squares). Adult individuals only plotted.

HABITAT AND HABITS: The frog tape-recorded by S. Richards (see above) was calling during rain under thick vegetation on a large, mossy boulder next to a waterfall of a small torrential stream. Another individual was on a trail next to a small torrential stream at night (S. Richards, personal commun.). Allen Allison (personal commun.) described the site near Timika as mossy midmontane forest.

DISTRIBUTION: Irian Jaya, from the southeastern corner of the Vogelkop Peninsula along the south flank of the central ranges to the Lorentz River, at elevations from 800 to 2500 m, and at least a short distance eastward on the north flank (fig. 24).

LOCALITY RECORDS AND SPECIMENS EXAMINED: IRIAN JAYA: Manikion region (RMNH 4630, holotype); Went Mtns., 800 and 1050 m (AMS R30834 [formerly Ma-

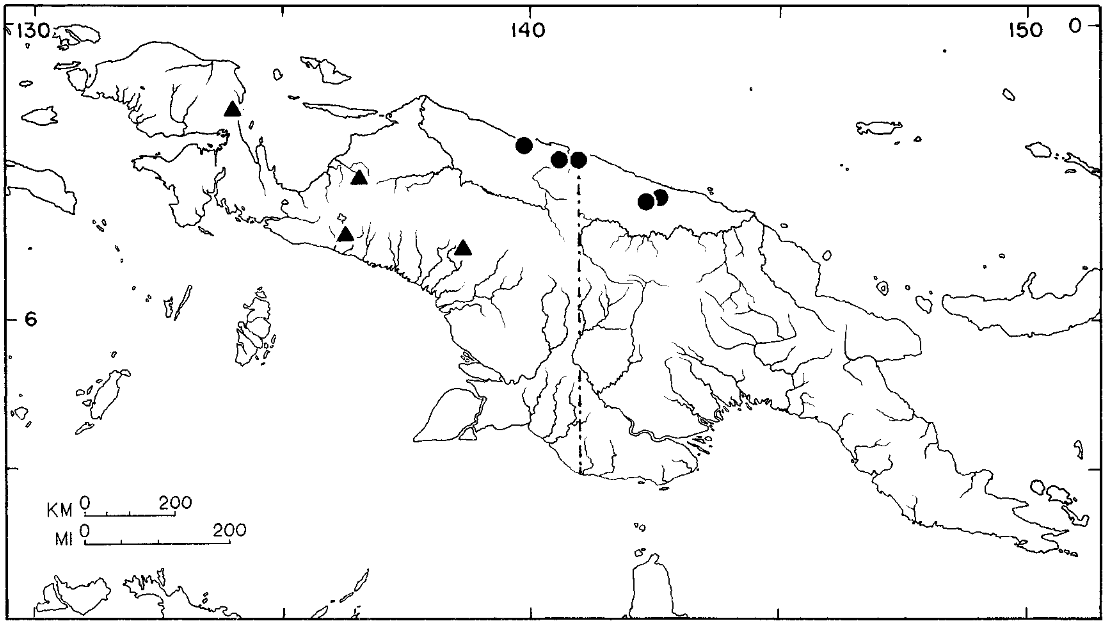

Fig. 24. Distribution of two *Austrochaperina* species in New Guinea. Solid circles, *A. basipalmata*; triangles, *A. macrorhyncha*.

cleay Museum 56], MCZ A10773, ZMA 5747–5750); Hellwig Mtns., 2500 m (ZMA 5754); Henvelbivak, Lorentz River, 800 m (FMNH 100117 [formerly in E. H. Taylor collection], ZMA 5751–5753); Mimika River (BMNH 1913.10.31.248); about 35 km (airline) NNE Timika airport, 1500 m (BPBM 13860–13862); Wapoga Alpha Camp, 1100 m, 3°08.67′S, 136°34.423′E (QM J67251, MZB 3564).

REMARKS: The holotype of *A. macrorhyncha* is a juvenile (on the basis of size), is in less than good condition, and was taken at a place remote from localities of samples of presumably related species. These circumstances create a problem in defining which, if any, of the known species populations should be associated with the name *macrorhyncha*.

If *basipalmata* of the north-coast ranges can be excluded on the basis of its possession of toe webbing, there are two population samples to be considered: (1) frogs from the Idenburg River region of Irian Jaya, north of the central dividing range (assigned to *macrorhyncha* by Zweifel, 1956; here referred to *derongo*) and some 600 km from the type locality; (2) the syntype series of *Chaperina punctata* (placed by Parker, 1934, in the synonymy of *macrorhyncha*) from the Lorentz River region south of the central range in Irian Jaya, also 600 km from the type locality. These samples are augmented by specimens from Wapoga Alpha Camp and near Timika, about 300 km closer to the type locality.[7]

The two samples in question are of modest size (14–15 specimens) and moderately well distributed by body size. Therefore, the method of choice is comparison of the measurements of the holotype with those predicted for a frog of its size by the regressions of the two competing samples. The resemblance of the holotype to the augmented *punctata* sample is striking. In HW, TL, EY, EN, and IN, the difference between the holotype and the predicted measurement (rounded to 0.1 mm) ranges from −0.1 to +0.2 mm, and is 0.0 in two instances (EY and EN). The finger disc measurement is smaller than predicted (0.7 vs. 0.9 mm), but the toe disc measurements are identical (1.0 mm). The Idenburg River sample predictions

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[7] The specimen from Mimika River (see Specimens Examined) is in execrable condition and useless for comparative purposes.

are also close to those of the holotype, but deviate more, from −0.5 to +0.3 mm; only the finger disc is closer to the holotype's dimension.

The principal diagnostic differences between the Idenburg and augmented *punctata* samples are the larger eyes and longer legs of the latter. In both these characters the holotype is closer to the measurements predicted for the *punctata* sample—eye size identical, tibia length 0.1 mm shorter; comparable figures for the Idenburg prediction are −0.3 and −0.5 mm. Given the difficulty of obtaining accurate digital disc measurements from specimens in poor condition, I am inclined to dismiss the seemingly contradictory indication of finger disc size. Accordingly, I agree with continuing *punctata* as a synonym of *macrorhyncha*, and regard the Idenburg sample as representing a population of *A. derongo*.

Austrochaperina mehelyi
(Parker), new combination

Chaperina fusca: Méhelÿ, 1901: 207, 257.

Sphenophryne fusca: van Kampen, 1923: 109 (part, New Guinea specimens only).

Sphenophryne mehelyi Parker, 1934: 156 (type locality, ''Sattelberg, New Guinea'' [Morobe Province, Papua New Guinea]; holotype, MNH 2414/11, collected by Ludwig Biró [no date given, but see below], destroyed in 1956). Zweifel, 1980: 411 (part).

TYPE MATERIAL: Parker based the description on two specimens cataloged under MNH 2414/11, designating the female as holotype and the male as paratype. Both were destroyed in the Hungarian uprising of 1956. Neither Méhelÿ (1901) nor Parker (1934) indicated a date of collection, but from the account of Biró's travels in Wichmann (1912), it appears the types were taken either during July–December 1898 or March–August 1899.

DIAGNOSIS: A small species (maximum known SVL about 21 mm) with finger discs equal to or scarcely broader than penultimate phalanges, relatively long legs (TL/SVL mean 0.45) and moderate eye–naris distance (EN/SVL mean 0.072). These features in combination will distinguish *mehelyi* from its congeners. (However, see account of *A. polysticta*.)

MORPHOLOGY: Size small, largest male 20.6 SVL, largest female 20.0, though a slightly greater maximum is probable. Head slightly narrower than the relatively slender body. Snout rounded, slightly projecting; nostrils lateral, scarcely or not visible from above; canthus rostralis rounded, loreal region a steep slope. Eyes relatively large, slightly less to slightly more than snout length, corneal outline notably projecting as viewed from beneath; eyelid width about three-fourths interorbital distance. Tympanic annulus scarcely distinguished externally, slightly less to slightly more than half eye diameter; ear emphasized by paler color. Relative lengths of fingers 3 > 4 > 2 > 1, fourth little longer than second, first greater than half of second; fingertips disclike with terminal grooves but not or scarcely broader than penultimate phalanges; subarticular and palmar elevations hardly evident. Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, first less than half length of second, all with rounded, grooved discs, only that on first toe not clearly broader than penultimate phalanx; subarticular elevations indistinct, inner metatarsal elevation small, low, rounded, no outer elevation. Skin smooth above and below except for a postocular-supratympanic fold indistinct in some specimens.

COLOR AND PATTERN: The snout, loreal region, and upper lip of preserved specimens are purplish brown with a few light spots on the lip and sometimes a trace of a light canthal line. The top of the head and middorsal region are brown with numerous small, irregular, darker brown spots. In some specimens the brown ground color continues onto the flanks whereas in others an ill- defined dorsolateral band of paler, grayer ground interrupts, below which the lateral region is darker brown spotted and blotched with white. An irregular dark brown streak above and behind the tympanum merges with the lateral brown of the body. The tympanum itself is yellowish brown. The chin and chest are dark brown with light spots that are discrete or coalesce into blotches. This pattern gives way abruptly to a pale venter marked with a coarse network of brown (Méhelÿ: 1901, pl. XII, fig. 3). The front legs are brown above with a few light spots, and beneath they are brown with white markings.

Above, the hind legs are colored like the middorsal region and below like the venter, but with the brown more conspicuous. The posterior surfaces of the thighs are a variable mixture of brown and white markings.

James Menzies (personal commun.) noted that in life, frogs from the Adelbert Mountains were dark purple-brown dorsally with numerous fine white spots on the flanks and fewer dorsally, sometimes coalescing into lateral bands. The venter was dark with large white blotches.

VARIATION IN SIZE AND PROPORTIONS: The seven specimens I examined range from 16.0 to 20.6 mm SVL. Four males are 17.4–20.6 mm (the smallest with vocal slits) and a gravid female is 20.0 mm SVL. Published information on the sizes of the type specimens is confusing. Méhelÿ (1901) stated that the largest was 24.5 mm long. In his key, Parker (1934) stated "*circa* 28 mm.," but in his species account gave 20 mm. Regression and proportion statistics are in tables 2 and 3.

ILLUSTRATIONS: Hand and foot, fig. 57D. Méhelÿ (1901) illustrated the skull (pl. VI, figs. 4, 5) and terminal phalanx of the 4th toe (pl. X, fig. 7) of *A. mehelyi* (as *Chaperina fusca*).

CALL: The call is unknown.

COMPARISONS WITH OTHER SPECIES: *Austrochaperina mehelyi* resembles the insular species *A. novaebritanniae*, which led Tyler (1967) to assign the New Britain frogs to *mehelyi*. The two are close in size and in most proportions and have similar color patterns, although the abdomen of *novaebritanniae* with uniform pale spots differs from the reticulated venter of *mehelyi*. The internarial distance of *novaebritanniae* is narrower than that of *mehelyi*–IN/SVL maximum 0.108 in *novaebritanniae* vs. minimum 0.112 in *mehelyi*, and the legs average shorter. A plot of TL/SVL and IN/SVL of the two species emphasizes their distinctness (fig. 25). The finger discs of the two are similar in width, but they appear more acute than rounded in *novaebritanniae* and are better developed.

HABITAT AND HABITS: The habitus of this species—large eyes, small digital discs, moderately long legs—is that of an active leaf-litter form rather than a burrower or a climber. James Menzies (personal commun.) collected specimens in "good secondary forest" in the Adelbert Mountains. I visited one of the localities for the species, Tumnang, which is atop a ridge in steep, mountainous terrain with rainforest where such has not been degraded to grassland or gardens.

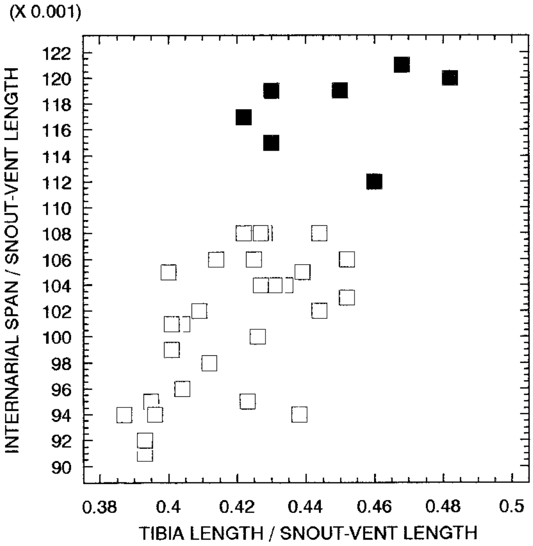

Fig. 25. Comparison of relative tibia length and internarial span in *Austrochaperina mehelyi* (solid squares) and *A. novaebritanniae* (open squares).

DISTRIBUTION: This species has so far been found only at moderate elevations (1200–1600 m) in the Adelbert Mountains and in the mountains of the Huon Peninsula (fig. 28).

LOCALITY RECORDS AND SPECIMENS EXAMINED: PAPUA NEW GUINEA. Madang Prov.: Mambimap, 1500 m, Adelbert Mtns. (UPNG 7239–7241); near Kowat, 900 m, Adelbert Mtns. (UPNG 8115–8119). Morobe Prov. (all localities on the Huon Peninsula): Tumnang, 1340 m (MCZ A28399, 28400); Joangeng, 1220 m (MCZ A28406); Mindik, 1200–1600 m (BPBM 5288); Sattleberg (Méhelÿ, 1901).

REMARKS: I am not entirely satisfied that the frogs I treat here are the same species that Méhelÿ (1901) referred to *Chaperina fusca* and that Parker (1934) later named *Sphenophryne mehelyi*. The destruction of the type specimens renders direct comparisons impossible, and the descriptions of the same specimens by Méhelÿ and Parker, although reasonably thorough, lack critical measurements.

In most respects the specimens I examined agree with the descriptions of *mehelyi*: size (though Parker was inconsistent, see above); eye and snout proportions; tympanum size; sizes of digital discs; ventral coloration (virtually identical with the illustration in Méhelÿ; pl. 12, fig. 3). Relative leg length cannot be assessed accurately, but both authors describe the tibia-tarsal joint as reaching the eye, which suggests a relatively long-legged frog, as are those examined. Differences include: interorbital space twice eyelid width (about 1.3× in my specimens); uniform brown above (all examined have many small, dark brown spots). The differences notwithstanding, I think it best to refer these specimens to *mehelyi*. The alternative of treating *mehelyi* as a synonym of *A. polysticta* seems less desirable (see that species account for comments).

With new material available, I conclude that a specimen from near Lae that I referred to *mehelyi* (Zweifel, 1980) was incorrectly attributed. I describe it herein as *Austrochaperina parkeri*.

***Austrochaperina novaebritanniae*, new species**

Figure 26

Sphenophryne mehelyi: Tyler, 1967: 188 (initial published reference to *A. novaebritanniae*).

HOLOTYPE: AMNH A83058, collected on August 28, 1969, by Harold Cogger (Alpha Helix Expedition) about 12 miles (19 km) from Rabaul, East New Britain Province, Papua New Guinea, on the road to Keravat.

PARATYPES: All localities in East New Britain Province. AMNH A83053–83057, A88569 (C&S), AMS R29243, 29246, 29251, 29253–29255, 29259, 29266, 29268, 29272, 29279, 29282, 29285, 29286, 29296, 29305, 29313, 29314, 29317, 29318, 29324, 29328, 29329, 29331, 29333, 29334, 29343–29346, 29349, 29351, 29352, 29355, 29361–29363, 29366, 29368, 29370–29372, all with same data as holotype; AMNH A79870–79872, MCZ A73085, 73086, BMNH 1968.525, collected by D. Morgan at Keravat in March and July 1966; ZMUC R9151–9164, collected on the Noona Dan Expedition (Wolff, 1966), May 10–22, 1962, at Yalom, 1000 m (4°25′S, 151°47.5′E).

Fig. 26. *Austrochaperina novaebritanniae*, AMS specimen, not individually identified. Harold Cogger photo.

ETYMOLOGY: The species name is a Latin substantive in the genitive, formed from the adjective *novus* and the noun *Britannia*, meaning ‘‘of New Britain,’’ and refers to the species’ provenance.

DIAGNOSIS: A small species, males to 19 and females to 21 mm SVL, with finger discs slightly broadened and a dorsal color pattern of tiny white spots on a dark background, the venter similar but with slightly larger spots.

DESCRIPTION OF HOLOTYPE: Adult female, gravid, with the following measurements and proportions: SVL 18.2, HW 6.5, TL 8.5, EY 2.1, EN 1.35, IN 1.9, HD 3.7, FT 7.8, third finger disc 0.45, fourth toe disc 0.70, TY 0.8; TL/SVL 0.467, HW/SVL 0.357, EY/SVL 0.115, EN/SVL 0.074, IN/SVL 0.104, EN/IN 0.710, HD/SVL 0.203, FT/SVL 0.429, TY/EY 0.405, third finger disc/SVL 0.025, fourth toe disc/SVL 0.036.

Snout bluntly rounded seen from above, rounded and slightly projecting in profile; nostrils lateral, slightly visible from above, widely spaced and closer to tip of snout than to eye, appearing almost terminal in lateral view; loreal region flat with a moderate slope, canthus rostralis rounded, not at all angular; eyes lateral, relatively large, upper lid about 75% of interorbital space; tympanum small, less than one-half eye diameter, outline of annulus scarcely visible. Relative lengths of fingers 3 > 2 = 4 > 1, first about one-half length of second, all with somewhat pointed, grooved terminal discs slightly broader than the terminal phalanges, subarticular and metacarpal elevations barely indicated (fig. 57B). Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, discs larger than those on fingers, slightly pointed and grooved, subarticular elevations barely evident, a small inner but no outer metatarsal elevation (fig. 57B). A brief, weak postocular fold; other dorsal and ventral body surfaces smooth.

A color transparency furnished by Harold Cogger shows a frog with a dark, almost black ground color, an abundance of small white spots, and between these are numerous smaller, brick-red spots.

The dorsal ground color in preservative is tan with no regional differentiation except that the loreal region is slightly duskier. A pattern of tiny pale spots on all the dorsal surfaces, including the legs, is uniform except for greater density on the eyelids. The ventral surfaces are slightly paler with a uniform pattern of pale spots larger and sparser than those of the dorsum.

VARIATION IN TYPE SERIES: Variation in proportions is set forth in table 2, and regression data are in table 3. The largest of 61 specimens I measured is a female, SVL 21.9 mm. Females as small as 18.2 mm are gravid, whereas one at 17.1 mm appears just to be maturing. The largest male measured 19.0 mm. Tyler (1967) reported adult males 15.5–17.2 mm SVL and adult females 17.0–20.1 mm SVL.

There is little variation in color pattern. The dorsal ground color of preserved specimens may range from light to dark brown with the top of the snout and loreal region even darker, and the light spots may be less abundant medially on the back, snout and eyelids.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71K; premaxilla, fig. 64B; vomer, fig. 65J; hand and foot, fig. 57B.

CALL: The call has not been described.

COMPARISONS WITH OTHER SPECIES: Tyler (1967: 188) characterized the coloration of specimens from Keravat as agreeing ''in all respects with that of the holotype'' of *Sphenophryne mehelyi*, which Parker (1934: 156) described as ''uniformly brown above, the flanks with scattered lighter dots; lower surfaces dirty white, the throat and chest washed with pale brown and irregularly spotted with white.'' Méhelÿ's (1901: pl. 12, fig. 3) illustration of the ventral surface of *mehelyi* (as *Chaperina fusca*) agrees with Parker's description rather than with the light brown, white spotted chin, chest, and abdomen of *novaebritanniae*. For additional comparison with *mehelyi*, see the account of that species. *A. novaebritanniae* and the similar *yelaensis* are compared the account of the latter.

HABITAT AND HABITS: Tyler (1967) described the Keravat locality as one that three months prior to the collection of the frogs had been cleared of virgin rainforest. Large numbers of frogs were aggregated beneath piles of decomposing vegetation—rotting grass and reeds laid upon ground covered with leaf mould. Numerous frogs were in small depressions, sitting on clumps of five or six eggs. The frogs in attendance were said to be females, although it is not clear whether the collector segregated the associated individual specimens with their egg clutches or if sex was merely assumed.

DISTRIBUTION: The only known localities for this species (see Holotype and Paratypes, above) are at the northern end of New Britain (fig. 30).

Austrochaperina palmipes (Zweifel), new combination

Figure 31F

Sphenophryne palmipes Zweifel, 1956: 15 (type locality, ''north slope of Mt. Dayman, Maneau Range, Territory of Papua [Milne Bay Province, Papua New Guinea], at an elevation of 700 meters''; holotype AMNH A57331, collected by G. M. Tate on the Fourth Archbold Expedition to New Guinea, July 16, 1953.

DIAGNOSIS: This species differs from other *Austrochaperina* in its extensively webbed toes and usually in having a prominent, downward-directed, spikelike projection on each vomer.

MORPHOLOGY: The holotype, an adult male 36.1 mm SVL, is described in detail in Zweifel (1956: 15–17). Size moderately large among *Austrochaperina*, maximum about 40 to 49 mm SVL, evidently varying among populations (see Variation, below), with many body proportions falling in the midrange for the genus as a whole. Head average in width (HW/SVL, 0.38), narrower than body. Snout obtusely pointed in dorsal view, similar and projecting in profile; loreal region sloping, very shallowly concave, canthus rostralis verging on angular, but not sharply defined; nostrils lateral, barely visible from above, appearing close to end of snout in profile. Eyes large, visible from beneath, EY/SVL about 0.13, rarely equaled and not exceeded in any other *Austrochaperina*; eyelid slightly narrower than interorbital space. Tympanum present but no external sign of it or its annulus. Relative lengths of fingers 3 > 4 > 2 > 1, first well developed, each with a prominent disc bearing a terminal groove; disc on third finger about 2.5× width of penultimate phalanx, typically slightly narrower than disc on fourth toe but occasionally equal or a little broader. Relative lengths of toes 4 > 3 > 5 > 2 > 1, all with well-developed discs, largest of any *Austrochaperina*, disc on fourth toe about twice width of penultimate phalanges; toes webbed to base of disc of fifth toe and about to proximal subarticular elevation on both sides of fourth toe. Fingers and toes with low, rounded subarticular elevations; a low, elongate inner metacarpal elevation flanked by a broader, round middle-outer elevation; a low, elongate inner metatarsal elevation but no outer. A narrow, straight, postorbital fold passing diagonally from eye to forearm insertion. Dorsal body surface generally smooth, without conspicuous folds, but with a tendency to develop an elevated network of low ridges; ventral surfaces smooth. Males lack vocal sac openings.

There are no maxillary or premaxillary teeth. Near its medial end each vomer typically possesses a bony spike (fig. 65O) projecting from the roof of the mouth. This structure is not always so spikelike as illustrated. It may be more broadly buttressed, or less often is represented by a mere nubbin scarcely evident in the preserved specimen.

COLOR AND PATTERN: Color in preservative is dull gray-brown dorsally with vague darker markings rarely well enough defined to be called a pattern. A narrow dark line follows the lower edge of the postorbital fold and below that a broader pale streak. The dorsolateral area of the body may be somewhat darker than the middle of the back, and the lateral area is slightly mottled. In some specimens there is a pattern associated with the dorsal fold network mentioned above. The ventral ground color is pale tan, with conspicuous darker mottling on the throat, a variable scattering of melanophores on the chest and abdomen, and a dusky shade to the undersides of the hind limbs. Occasional individuals are dark beneath on all ventral body surfaces, with coarse light mottling. There is no conspicuous patterning to the groin or thighs.

The dorsal color in life is brown or a mixture of brown and green. Menzies (1976, pl. 11c) published a color photo. My field notes mention ‘‘brown without any distinct pattern . . . faint light interocular bar. . . . Greenish brown with obscure darker markings . . . W-shaped scapular mark. . . . Dark brown with light green flecks. . . . greenish brown with . . . darker brown mottling.’’ The undersurfaces are gray or greenish gray with darker gray or brown spotting and mottling on the chin, with this pattern being fainter on or entirely absent from the chest and abdomen. There are no flash colors in the groin or on the thighs. The iris is dark, much the same as the dorsal ground color, with the horizontally elliptical pupil narrowly margined with gold.

VARIATION IN SIZE AND PROPORTIONS: Adult *A. palmipes* have sexual dimorphism in the shape and color of the snout. In males the snout is slightly more projecting and is pale, almost white, in larger individuals, whereas females retain a less projecting snout, with the darker ground color common to juveniles of both sexes. Male *palmipes* lack a vocal sac, so my usual criterion of male maturity, presence of vocal slits, is inapplicable. Hence, I have used the presence of a distinctly pale snout as indication of sexual maturity in males.

There is geographic variation in maximum size and size at sexual maturity, with frogs on Normanby Island attaining a larger size than those elsewhere. Seven adult females measure 43 to 49 mm SVL (six of them 45 mm or greater), whereas the largest in any other sample is only 44 mm. Males are smaller than females in all samples, but again those from Normanby are the largest: three from Normanby are 36 to 38 mm, contrasted to a maximum of 37 mm in all other samples. The smallest frogs are those of the Huon Peninsula, where adult females (N = 21) measure from 32 to 40 mm and adult males from 28 to 33 mm (N = 7). Samples intermediate between these extremes, but not necessarily identical among themselves, include those from Goodenough Island, Mt. Dayman, the Wau-Garaina area, and Simbu Province.

Visual comparison of regression lines for several proportions in four samples of *palmipes* shows little geographic variation. Only in the case of slightly larger eyes in the Normanby Island sample does one line stand out much from the rest. Regression and proportion statistics are in tables 2 and 3.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71P; premaxilla, fig. 64G; sacral region, fig. 73C; vomer, fig. 65O; finger disc, fig. 51; hand and foot, fig. 56D. Kuramoto and Allison (1989) illustrated the karyotype.

CALL: Menzies (1976: 55) mentioned ''a quiet clicking noise which I believed was made by a *palmipes* by the side of a forest stream.'' Verification that *palmipes* calls (though lacking vocal slits) is needed.

COMPARISONS WITH OTHER SPECIES: Within its geographic range there is no *Austrochaperina* species with which *palmipes* could readily be confused, as the combination of extensive toe webbing and relatively large digital discs is unique. The closely related species *rivularis*, *macrorhyncha*, and *basipalmata* are allopatric to *palmipes*, so far as is known, and either lack or have only slight toe webbing.

HABITAT AND HABITS: This is a riparian species of foothill and lower montane rainforest, ranging in elevation from less than 100 m to at least 1700 m. I have found these frogs by day under streamside rocks and at night on mossy rocks in small streams. Menzies (1976: 55) reported that frogs ''were clinging to wet rocks, especially near waterfalls . . . . When disturbed, they dived into the water and reappeared a little distance away.'' For descriptive accounts of areas where this species occurs, see Brass, 1956 (Mt. Dayman and Goodenough Island) and 1959 (Normanby Island).

Although it probably is the most aquatic of the New Guinean microhylids, *A. palmipes* still must resort to land for breeding. Dr. Allen Allison (personal commun.) reports an individual attending eggs ''in a depression under leaf litter along the bank of a small stream.'' A female about 35 mm SVL contained 19 ova each of which was 3 mm in diameter.

DISTRIBUTION: This species occupies the Huon Peninsula, the northeast slopes of the mountains from the Huon Gulf to the eastern tip of New Guinea, and the D'Entrecasteaux Islands (not yet recorded from Fergusson Island). In addition, there is an apparently isolated population on the west side of the central ranges in the Purari River drainage of Gulf and Simbu Provinces (fig. 29). This isolated area is more than 200 km from the nearest locality for the species to the east in Morobe Province. Additional collecting may be expected to narrow the gap, but there are few passes as low as the maximum elevation that *palmipes* is known to attain. It is likely that the populations truly are disjunct. A similar apparent range disjunction occurs in another microhylid frog, *Cophixalus cheesmanae* (Zweifel: 1979, fig. 8). Records range in elevation from 60 to 1750 m.

LOCALITY RECORDS AND SPECIMENS EXAMINED: PAPUA NEW GUINEA: Gulf Prov.: Camp III, Nimi River, 13.5 km S, 1 km E Soliabedo, 425 m (AMNH A79973; MCZ A111901–111914). Simbu Prov.: Camp I, 13.5 km S, 2 km E Karimui, 1070 m (MCZ A111918); Soliabedo, 550 m (MCZ A111916, 111917); Camp II, Pio River, 6.5 km S, 1 km E Soliabedo, 300 m (MCZ A111919–111922); between Camp II, 6.5 km S, 1 km E Soliabedo, and Weiana, 8 km S, 1 km E Soliabedo, 430–730 m (MCZ A133017); Haia Village, 720 m, 145°00′, 6°42′(AM 32257); Haia Bush Camp, 880 m, 145°01′, 6°40′ (AMS R32443, R32450, R32451, R32471–32476). Morobe Prov.: Ulap, 800–1100 m (BPBM 5322); Boana, 880 m (MCZ A111874–111895); Areganang (AMNH A81200–81209); Gang Ck., 1340 m (AMNH A75048–75053 [75050 and 75053 dry skeletons], A76038–76047); near Zangaren, 1370 m (AMNH A76031, A76032); Masba Ck. (AMNH A76033); Numbut, 1220 m (AMNH A76034–76037); Tewep, 1350 m, 11 km E, 8 km N Boana (BPBM 1048);

Finschhafen (SAM 5684 [8 specimens]); Rari Village, Mt. Shungol, 1250 m (BPBM 5157, 5167); Mt. Missim, about 10 km NE Wau, 1600 m (BPBM 6409–6416, 6494, 6495; 9352); Black Cat Gap, Mt. Missim, 1700–1750 m (BPBM 4142, 4153); Coldwater Ck., 1055 m, Mt. Missim (BPBM 9645); Wau, 1700 m (BPBM 3054); Kunai Ck., 1350 m, 2 km W Wau (AMNH A81219, A81220, A130550); 3 km E, 5 km S Wau, 1400 m (AMNH A81218, A83067, A83068; YPM 5316); Garaina, 700 m (AMNH A83059, A83060, 83064–83066; YPM 5315); Gapaia Ck., 1360 m, 1 km N Saureli (AMNH A81213). Northern Prov.: Kokoda, 370 m (AMNH A75047). Milne Bay Prov.: North slope Mt. Dayman, 700 m (AMNH A56602–56604, A57062, A57066, A57074–57076, A57079, A57104, A57105, A57115, A57122–57124, A57131–57134, A57146–57148, A57162–57164, A57168–57170, A57213–57215, A57232–57236, A57331 holotype, A57335, A57339, A57340); Goodenough Island, 900 m (AMNH A56885, A56893, A57343–57346); Goodenough Island, 1600 m (AMNH A56586–56594, A56895–56901, A56948–56955, A56959, A56961–56963, A56968–56970, A56974, A56975, A56977–56983, A56985, A56987–56996, A57055, A57056); Normanby Island, Mt. Pabinama, 820 m (AMNH A60172–60181, A92805–92807 (C&S), A135370–135396); Alotau, 60–150 m (Tyler and Menzies, 1971: 81).

Austrochaperina parkeri, new species

Figure 27

Sphenophryne mehelyi: Zweifel, 1980: 411 (part).

HOLOTYPE: MCZ A89220 (Field No. F14424), collected by Fred Parker on March 7, 1974, in Morobe Province, Papua New Guinea, at 4 km north of Lae.

PARATYPES: The holotype is the only specimen of the species.

ETYMOLOGY: The patronym honors Fred Parker who, through his collecting activities, is the peerless contributor to knowledge of the Papuan herpetofauna.

DIAGNOSIS: A species of moderate size (SVL 30.6 mm, one specimen) with relatively small eyes (EY/SVL 0.105), small hands (HD/SVL 0.209), and well- developed digital discs of moderate size (3rd finger disc/SVL 0.031).

Fig. 27. Holotype of *Austrochaperina parkeri*, MCZ A89220, SVL 30.6 mm.

DESCRIPTION OF HOLOTYPE: Adult female (ova 3 mm in diameter) with the following measurements and proportions: SVL 30.6, HW 10.7, TL 13.6, EY 3.2, EN 2.15, IN 3.2, HD 6.4, FT 13.0, width of disc of third finger 0.95 (penultimate phalanx 0.55), width of disc of fourth toe 1.3 (0.65); HW/SVL 0.350, TL/SVL 0.444, EY/SVL 0.105, EN/SVL 0.070, IN/SVL 0.105, EN/IN 0.672, HD/SVL 0.209, FT/SVL 0.425, third finger disc/SVL 0.031, fourth toe disc/SVL 0.042.

Head conspicuously narrower than body, snout rounded, slightly more bluntly so and projecting a little in lateral view; nostrils lateral, slightly visible from above; loreal region a flat, steep slope passing into the gently rounded canthal region. Eyes moderate, size equal to distance from anterior corner of orbit to tip of snout, visible from beneath, upper eyelid about two-thirds as wide as interorbit. Tympanum scarcely distinct, annulus slightly greater than half eye diameter. Relative lengths of fingers 3 > 4 > 2 > 1, first about half as long as second, all with distinct but not greatly expanded discs, that of third finger about 1.7× as broad as penultimate phalanx; subarticular and metacarpal elevations scarcely evident. Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, all with moderately expanded discs, that of fourth toe larger than that on third finger and about 2.7× the penultimate phalanx; subarticular elevations low, rounded; inner metatarsal elevation low, rounded, elongate; no outer elevation. Skin smooth above and below, postocular fold lacking.

This is a light brown frog with nothing in the way of distinguishing markings except for small light dorsal spots more numerous laterally. Such spotting is present on the front legs but scarcely indicated on the hind legs. The facial area is darker than its surroundings. The chin and chest bear somewhat larger and denser pale spots than the back, whereas the abdomen is finely mottled with darker on lighter brown. The front legs are brown beneath with light spots, like the chest. The hind legs are patterned beneath like the abdomen, only more coarsely so. The posterior surfaces of the thighs are lightly mottled brown.

VARIATION IN TYPE SERIES: The type is unique.

ILLUSTRATIONS: Hand and foot, fig. 56E.

CALL: The call is unknown.

COMPARISONS WITH OTHER SPECIES: Earlier, I referred the unique specimen of *A. parkeri* to *Sphenophryne mehelyi* (Zweifel, 1980: 411). With several specimens of *mehelyi* now available (compared to only one before), significant differences between the species are evident. Most conspicuously, *mehelyi* is a much smaller species, with males being mature as small as 17 mm SVL and the largest specimen, a gravid female, measuring 21 mm SVL compared to the 30 mm length of *parkeri*.

HABITAT AND HABITS: There is no specific information on the habitat of this species, although its habitus is that of a terrestrial, probably litter-dwelling form. The rainforested area around Lae is one of the wetter parts of Papua New Guinea, with an annual average rainfall of 4581 mm (35 years of data as of 1975; Papua New Guinea National Meteorological Service, 1976).

DISTRIBUTION: Known only from the type locality (fig. 28).

Austrochaperina polysticta (Méhelÿ), new combination

Chaperina polysticta Méhelÿ, 1901: 258 (type locality, ‘‘Sattleberg’’ [Morobe Province, Papua New Guinea]; holotype MNH 2414/12, collected by Ludwig Biró [date not given, but see account of *A. mehelyi*], destroyed in 1956).

Sphenophryne polysticta: van Kampen, 1923: 108. Parker, 1934: 157 (part, holotype only).

DIAGNOSIS: Possibly the smallest species of *Austrochaperina*, the sole specimen said to be adult at 16.5 mm SVL; discs of fingers scarcely broader than penultimate phalanges; abdomen unmarked.

MORPHOLOGY: The unique type specimen has been destroyed and I know of no other specimen referable to the species. Hence, I cannot prepare a description in the format followed in other species accounts. What follows is adapted from the descriptions in Méhelÿ (1901) and Parker (1934). Parker discussed *polysticta* without having examined specimens of the Australian species *A. robusta* Fry and *A. brevipes* Fry[8] that he referred to the synonymy of *polysticta*. If Parker incorporated in his discussion features of the Australian species (taken from Fry’s descriptions), that could account for discrepancies.

Snout short, somewhat shorter than diameter of eye, bluntly rounded; canthus rostralis rounded, loreal region steeply inclined; nasal opening about as far from tip of snout as from eye (Méhelÿ) or closer to tip of snout than to eye (Parker). Interorbital space almost twice width of eyelid. Tympanum distinct, nearly half length of eye opening. Relative lengths of fingers 3 > 4 > 2 > 1; discs distinct, scarcely broader than penultimate phalanges, disc of first finger narrower. Relative lengths of toes 4 > 3 > 5 > 2 > 1, third considerably longer than fourth; discs

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[8] The latter is now *A. fryi* (Zweifel), not *A. brevipes* (Boulenger).

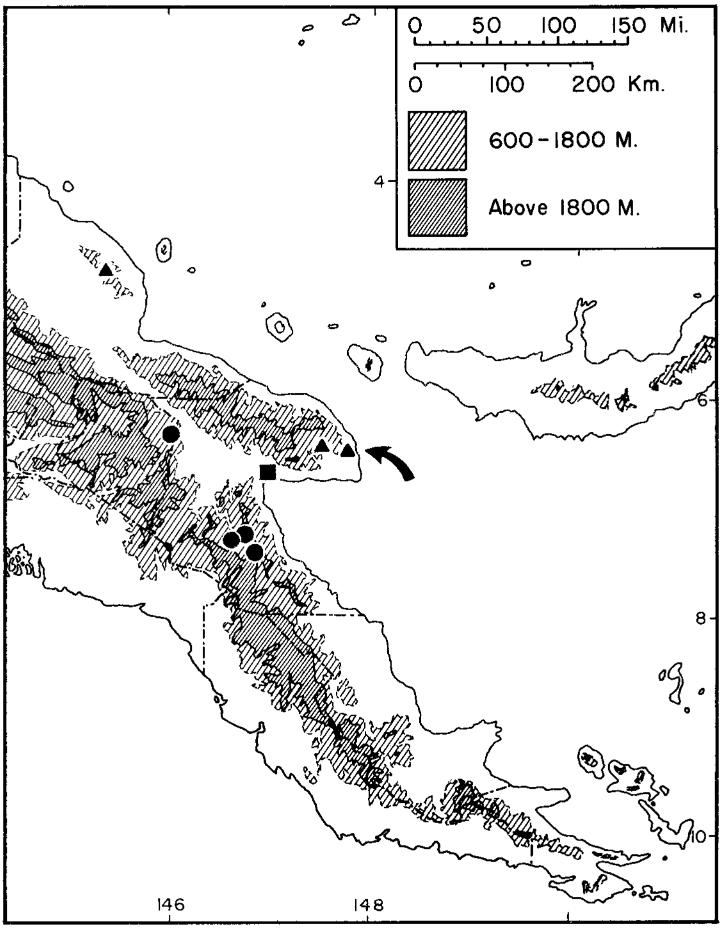

Fig. 28. Distribution of *Liophryne allisoni* (circles), *Austrochaperina mehelyi* (triangles), *A. polysticta* (triangle with arrow), and *A. parkeri* (square) in Papua New Guinea.

broader than those of fingers, but disc of fourth toe no broader than half tympanic diameter; subarticular elevations scarcely evident, inner metatarsal elevation small, elongate. Tarso-metatarsal joint (Méhelÿ) or tibiotarsal joint (Parker) reaches tympanum (TL/SVL probably about 0.39; see below). Skin smooth above and beneath.

The pectoral girdle is typical of *Austrochaperina* (and the other genyophrynine genera with the primitive girdle), with the clavicle reaching from the scapula almost to the midline (Méhelÿ 1901: 259).

Méhelÿ (1901: 259) described the color and pattern: "The formalin preserved specimen is bright yellowish red above and below, only the dorsal region somewhat brownish; the upper eyelids, upper and lateral sides of the snout blackish. A light streak on the upper lip passes to and beneath the eye. A dark red-brown stripe with undulating upper and lower edges begins at the posterior corner of the eye, touches the tympanum on its upper edge and rear half, and proceeds about to the middle of the body. The whole dorsum, the sides of the body, as well as the upper and lower sides of the fore- and hind limbs are set with moderately large, irregular red-brown flecks, more or less coalesced on the edges. Throat and anterior chest marmorated red-brown; abdomen and underside of forelimbs unmarked, some small red-brown speckles are on the undersides of the hind limbs."

VARIATION IN SIZE AND PROPORTIONS: Both Méhelÿ (1901) and Parker (1934) gave the size (presumably SVL or close to that measurement) as 16.5 mm. Parker noted ‘‘ad.’’ but did not specify the sex.

ILLUSTRATIONS: Whole body, dorsal aspect (Méhelÿ, 1901: pl. XII, fig. 4); pectoral girdle (Méhelÿ, 1901: pl. X, fig. 3).

CALL: This has not been described.

COMPARISONS WITH OTHER SPECIES: This species must be compared with the sympatric *A. mehelyi*, but critical data are lacking. With only one specimen known, the possibly smaller size of *polysticta* cannot be confirmed. Méhelÿ's description and illustration suggest that *polysticta* has a shorter, blunter snout than *mehelyi*, and the mottled venter of that species contrasts with the unmarked abdomen of *polysticta*. If the illustration of *polysticta* is correctly proportioned, the legs are relatively shorter than those of *mehelyi* (TL/SVL 0.39 vs. minimum of 0.42 in *mehelyi*).

HABITAT AND HABITS: Nothing is on record.

DISTRIBUTION: Sattleberg, the type and only locality, is the site of a mission station near the tip of the Huon Peninsula, Morobe Province, Papua New Guinea (fig. 28).

REMARKS: I have considered but rejected the possibility that *Austrochaperina polysticta* and *A. mehelyi*, small species of similar configuration with the same type locality, are synonyms. Both Méhelÿ and Parker, with specimens in hand, considered them as different taxa, and the geographically pertinent specimens I examined are closer to *mehelyi* in most respects. I prefer to maintain the status quo pending the acquisition of new material that favors reconsideration.

Austrochaperina rivularis, new species

Figure 31E

Sphenophryne macrorhyncha: Zweifel, 1967: 6. Hyndman and Menzies, 1990: 272.

HOLOTYPE: AMNH A130551 (Field No. RZ 12802), collected by Fred Parker and Papuan assistants at Finalbin, 840 m, 5 km N, 2 km W Tabubil, Western Province, Papua New Guinea, on July 27, 1987.

PARATYPES (all from Papua New Guinea): Western Prov.: AMNH A130552–130559, UPNG 8273, same data as holotype; AMNH A84541, A84542; MCZ A81000, 81224–81230, 81451, 81452, Imigabip, 1280 m, collected by Fred Parker, Dec. 1969; AMNH A84543; MCZ A81002, 81003, Bolangon, 1280 m, collected by Fred Parker, Dec. 1969; MCZ A81001, Migalsimbip, 790 m, collected by Fred Parker, Dec. 1969. West Sepik Prov.: QM J67247, 67255, Mt. Stolle, 1600 m, collected by Stephen Richards and G. R. Johnston, July 4, 1993. East Sepik Prov.: AMNH A77550–77588, A84445 (C&S), A129514–129558, Mt. Hunstein, 1220 m, collected by Ru Hoogland Aug. 14–15, 1966. Southern Highlands Prov.: AMS R122164, R122165, Namosado, collected by S. Donnellan.

ETYMOLOGY: The specific name is a Latin adjective pertaining to small brooks or streams, in reference to the habitat of this species.

DIAGNOSIS: A moderate- to large-sized *Austrochaperina*, maturing at 35 mm SVL or larger (geographically variable), with relatively large finger discs (FD/SVL $\geq$ 0.035), moderate leg length and eye size (TL/SVL $\leq$ 0.46, EY/SVL $\leq$ 0.116), and a dorsal pattern of small, dark markings on a slightly paler ground.

DESCRIPTION OF HOLOTYPE: Adult female with the following measurements and proportions: SVL 49.0, HW 17.1, TL 21.8, EY 4.8, EN 3.4, IN 4.8, HD 12.6, FT 23.8, third finger disc 1.95, fourth toe disc 2.3; HW/SVL 0.349, TL/SVL 0.445, EY/SVL 0.098, EN/SVL 0.069, IN/SVL 0.098, EN/IN 0.708, HD/SVL 0.257, FT/SVL 0.486, FD/SVL 0.040, TD/SVL 0.047.

Head narrower than body. Snout rounded to almost subacute seen from above, rounded and slightly projecting in profile; loreal region moderately steep, slightly concave, canthus rostralis rounded but distinct; nostrils lateral, just visible from above, slightly closer to tip of snout than to eye. Eyes relatively large, outline visible from beneath, lid almost as wide as interorbital span. Tympanic outline scarcely visible, diameter less than half that of eye. Relative lengths of fingers 3 > 4 > 2 > 1, first more than half length of second, all with expanded, rounded, grooved discs, that of third finger twice width of penultimate phalanx or a little less; subarticular and metacarpal elevations indistinct. Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, all with discs larger than those of fingers, that of fourth toe about twice width of penultimate phalanx; subarticular elevations low, rounded, scarcely evident; inner metatarsal elevation small, elongate, rounded. Skin smooth above and below except for very weak, diagonal postorbital fold.

Purplish brown above in preservative with a few darker flecks, weak, convergent dark lines in the scapular region, and an ill-defined dark stripe above the postocular fold. The fingers and toes are marked with dark and light in no particular pattern. The ventral ground color is pale tan with gray-brown mottling from chin to posterior tip of abdomen as well as beneath the limbs. The intensity of the mottling is slightly less on the abdomen than elsewhere.

VARIATION IN TYPE SERIES: Populations referred to *A. rivularis* have different maximum body sizes. The sample from Western Province includes apparently immature males (no vocal slits) of 30.2 and 31.5 mm, mature males of 35.7 and 36.5 mm, females just maturing at 35.9 and 36.9 mm, and adult females of 39.1 to 49 mm. Several males from Mt. Hunstein, East Sepik Province, in the range of 39–45 mm lack vocal slits whereas others 42–45 mm have them. Whether this indicates variability in the vocal apparatus of adult males or variability in size at maturity is not evident, but the greater size of males in this sample is clear. The series of females from Mt. Hunstein includes a juvenile as large as 44.0 mm, one maturing at 44.8 mm and adults 47.6–51.5 mm. Proportions of specimens in the two major samples are quite similar (table 2). Regression data are in table 3.

In life, frogs from Western Province were scarcely more distinctively colored than in preservative, being olive-brown above with darker brown markings, a faint lumbar ocellus, and the tympanic area pale yellowish tan. Undersides were gray-brown with faint darker mottling most evident on the chin. The iris is dark golden brown above and below the horizontal pupil, little differentiated from the dorsal color.

REFERRED SPECIMENS: SAMA 6385–6403, 6409–6414, 6416–6418, collected by Barry Craig at Busilmin, West Sepik Province, on May 7, 1965. I lack a complete suite of measurements on these specimens and thus could not make critical comparisons. Although I exclude them from paratype designation, it is likely that they represent this species.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71O; premaxilla, fig. 63F; sacral region, fig. 73A; vomer, fig. 65N; skull, fig. 68A; hand and foot, fig. 56A.

CALL: Through the courtesy of Stephen Richards, I have tape recordings of the calls of two individuals of this species and have examined one of the voucher specimens. The call (fig. 79B, table 5) is a series of harsh notes each about 0.06–0.08 sec long, composed of six to eight pulses, and repeated at a rate of about three notes per second. Individual notes characteristically begin with a long pulse, followed by others half its length (fig. 80C), although occasional notes have all the pulses approximately the same length (see Vocalizations). The dominant frequency is approximately 2600 Hz in one instance and 2700 in the other. One complete call (i.e., initiated after recording began and terminated voluntarily) lasted 1 min 25 sec; the other (presumably incomplete) call was at least 38 sec long. Both frogs called from beside small creeks. The air temperature recorded for one call was 21.3°C.

Stephen Richards recorded one of the frogs at 1600 m on Mt. Stolle, West Sepik (Sanduan) Prov., the other about 5 km west of Tabubil (elevation about 600 m by my estimate and close to the type locality), Western Prov. The localities are about 75 km apart.

COMPARISONS WITH OTHER SPECIES: *Austrochaperina rivularis* is compared with two similar species—*macrorhyncha* and *palmipes*—in the accounts of those species. The two species *basipalmata* and *derongo* are smaller, with maximum male and female sizes approximating the sizes at which *rivularis* matures. Presence of toe webbing distinguishes *basipalmata*, and average tibia length, eye, hand, and disc sizes are smaller in *derongo*.

HABITAT AND HABITS: The frogs found at Finalbin, when uncovered from beneath leaves lying beside small streams in mossy, hilly forest, jumped into the water and swam well in attempting escape. Except for the note above on a recorded individual, nothing else is known about the habits of this species.

DISTRIBUTION: The known localities are in or on the fringe of the central mountainous region of western Papua New Guinea in Western, West Sepik, East Sepik, and Southern Highlands Provinces (fig. 29). The species undoubtedly occurs in eastern Irian Jaya, as the type locality is only 22 km from the border. The known range in elevation is about 600 to 1600 m. For locality records and specimens examined, see above under Holotype, Paratypes, and Referred Specimens.

REMARKS: The question of whether *A. rivularis* is a species distinct from *A. derongo* is answered by their distinction in sympatry in Southern Highlands Province of Papua New Guinea as well as by differences in advertisement calls. See the account of *A. derongo* for details of the sympatric locality.

Another question is whether *rivularis* includes more than one species. The larger body size seen in the Mt. Hunstein sample is suggestive, but there are no other morphological characters sufficiently trenchant to mark species lines. Also, geographic variation in body size is seen in the related species *derongo* and *palmipes*. Information on advertisement calls might be helpful in resolving the question if more populations can be sampled.

Austrochaperina yelaensis, new species

HOLOTYPE: AMNH A135406, collected by R. F. Peterson on the Fifth Archbold Expedition between October 12 and 20, 1956, at an elevation of 700 m on the south slopes of Mt. Rossel, Yela (= Rossel) Island, Milne Bay Province, Papua New Guinea.

PARATYPES: There are no paratypes.

ETYMOLOGY: The Latin adjectival suffix -*ensis* (origin) reflects the provenance of the holotype, the name of which has been changed from Rossel Island to Yela Island.

DIAGNOSIS: A small *Austrochaperina*—SVL 20.5 mm in the single specimen, a female at or close to adulthood—with moderately well-developed digital discs, an obscurely mottled dorsal color pattern, small pale spots prominent on the face and side of body, and mottled abdomen.

DESCRIPTION OF HOLOTYPE: A female, at or close to maturity (ova 1.5 mm in diameter), with the following measurements and proportions: SVL 20.5, HW 7.9, TL 9.3, EY 2.8, EN 1.6, IN 2.3, HD 4.2, FT 9.3, disc of third finger 0.6 (penultimate phalanx 0.4), disc of fourth toe 0.8 (0.4); HW/SVL 0.385, TL/SVL 0.454, EY/SVL 0.127, EN/SVL 0.078, IN/SVL 0.112, EN/IN 0.696, HD/SVL 0.205, FT/SVL 0.454, FD/SVL 0.029, TD/SVL 0.039.

Head scarcely narrower than body, snout obtusely rounded, barely projecting in profile; loreal region sloping and flat, canthus rostralis rounded; nostrils barely visible from above, nostril closer to tip of snout than to eye. Eyes relatively large, visible from beneath, interorbital distance about 80% of an eyelid width; tympanum hidden. Relative lengths of fingers $3 > 4 > 2 > 1$, first finger well developed, about half length of second, all fingers with small, grooved terminal discs; subarticular and inner metacarpal elevations low and rounded (fig. 57A). Toes unwebbed, relative lengths $4 > 3 > 5 > 2 > 1$, all with grooved terminal discs, those of third and fourth toes about twice width of penultimate phalanges; subarticular and inner metatarsal elevations low but discrete, no outer metatarsal elevation (fig. 57A). Skin smooth above and below, a faint trace of a postocular-supratympanic fold.

The dorsum is brown and faintly mottled. Small white spots are prominent atop the snout, on the upper lips and sides of the face through the tympanic region, and along the side of the body. The upper surfaces of the hands, arms, and front legs and hind legs are similarly spotted. The throat and chest are brown with white spots, the abdomen and undersides of hind legs mottled. The groin and anterior surface of the thigh are brown with irregular, small light marks; the posterior surface is similar but with slightly larger markings.

VARIATION IN TYPE SERIES: There is only the single specimen, so the extent and nature of variation are unknown. That the specimen is mature at less than 21 mm SVL indicates that this is one of the smallest species of *Austrochaperina*.

ILLUSTRATIONS: Hand and foot, fig. 57A.

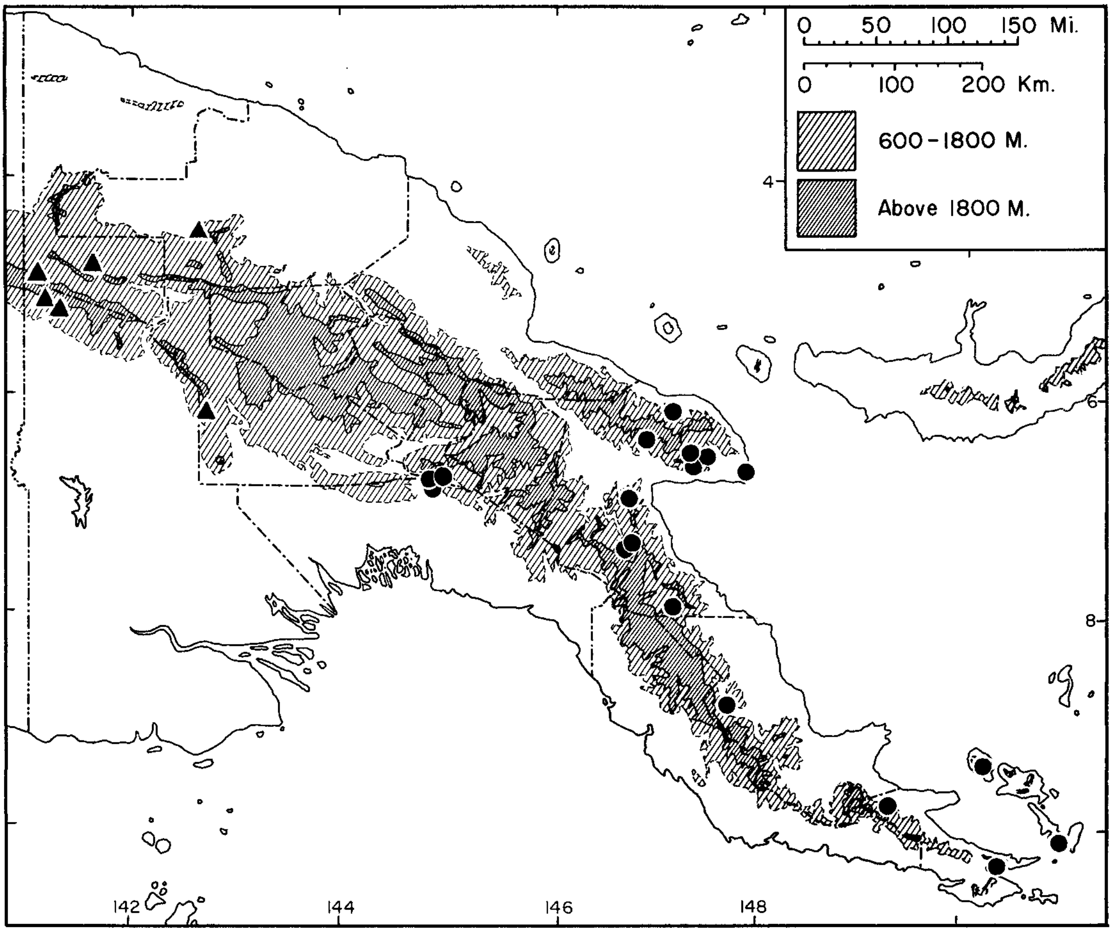

Fig. 29. Distribution of *Austrochaperina palmipes* (circles) and *A. rivularis* (triangles) in Papua New Guinea.

CALL: The vocalizations, if any, are unknown.

COMPARISONS WITH OTHER SPECIES: *Austrochaperina yelaensis* is most similar to another insular species, *A. novaebritanniae*, found 700 km distant on a geologically unrelated island, New Britain. The single specimen of *yelaensis* has the middorsal region unspotted (spotted in *novaebritanniae*), the abdomen mottled rather than spotted, and slightly longer hind legs than in any of the series of 29 adult *novaebritanniae* (TL/SVL 0.454 vs. 0.452). No other species of *Austrochaperina* is known from Yela Island. There is also similarity in size, proportions, and color pattern between *yelaensis* and *mehelyi*, a species slightly more remote geographically from *yelaensis* but on the New Guinea mainland. Slightly larger finger discs, longer EN and smaller IN spans may also characterize *yelaensis*, although confirmation will require more specimens of that species.

HABITAT AND HABITS: No information particular to the specimen is available. The surroundings of the camp included a mountain ridge with "mossy, wind-clipped forest" and "an abundance of woody undergrowth" (Brass, 1959: 57).

DISTRIBUTION: Known only from the type locality (fig. 30).

Genus *Liophryne* Boulenger

Liophryne Boulenger, 1897: 11. Type species not specified between the two new species Boulen-

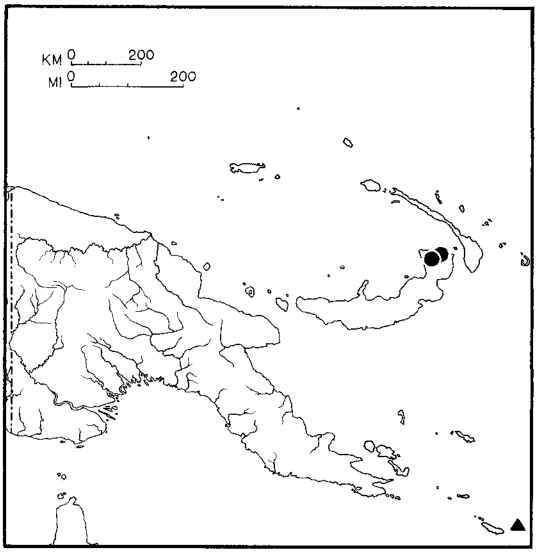

Fig. 30. Distribution of *Austrochaperina novaebritanniae* on New Britain (circles) and *A. yelaensis* (triangle) on Yela (Rossel) Island.

ger assigned to the new genus, *L. rhododactyla* and *L. brevipes*. Parker (1934: 152) stated "Type species *Liophryne rhododactyla*," which constitutes a valid subsequent designation (International Commission on Zoological Nomenclature, 1985: Art. 69(a)(iv)).
Sphenophryne: Parker, 1934: 152.

CONTENT: Six species: *Liophryne allisoni*, new species; *Liophryne dentata* (Tyler and Menzies); *Liophryne similis*, new species; *Liophryne rhododactyla* Boulenger; *Liophryne rubra*, new species; *Liophryne schlaginhaufeni* (Wandolleck).

DIAGNOSIS: A genus of genyophrynine microhylid frogs (sensu Zweifel, 1971 and Burton, 1986) with the following combination of morphological characters: clavicles long and slender, reaching from scapula almost to midline of pectoral girdle; fingers and especially toes with relatively prominent (rather than low), rounded subarticular elevations; tips of fingers and toes expanded into small discs with terminal grooves, those of fingers narrower than of toes; span of T-shaped tip of terminal phalanx of third finger not or scarcely wider than base of phalanx; legs long, minimum mean TL/SVL (0.488) and minimum mean FT/SVL (0.488) greater than means of any other genyophrynine species with the primitive pectoral girdle.

MORPHOLOGY: The species of *Liophryne* present a spectrum of sizes, from adult males of *allisoni* as small as 20 mm SVL to a female record size of 60 mm in *rhododactyla*, the largest size attained by any genyophrynine microhylid. Species of *Liophryne* are rather broad-headed frogs, including the two highest and six of the nine highest mean HW/SVL ratios of all genyophrynines considered herein. The vast majority of genyophrynine frogs show scarcely any development of subarticular elevations, being usually low, rounded ones at best. The species I assign to *Liophryne* agree in having discrete subarticular structures and also share, on the average, the relatively longest legs (as measured by the TL/SVL and FT/SVL ratios) of any of the species with the primitive pectoral girdle. The finger and toe discs are small, neither reduced or absent as in *Oxydactyla* nor enlarged as in *Sphenophryne* and many *Austrochaperina*. In three species, *rhododactyla* (and probably also *similis*), *dentata*, and *schlaginhaufeni*, the medial plate of the vomer is large and the lateral arm relatively thick (fig. 65F–H), possibly an indication of close relationship, though the vomer of *allisoni* is somewhat more delicately formed (fig. 65E). Five species, excepting *allisoni*, have a relatively large and distinct ear. For body proportions, see table 6; regression statistics are in table 7.

DISTRIBUTION: Found throughout much of New Guinea, from near sea level to 2700 m and from Timeka in western Irian Jaya to Milne Bay at the eastern tip of Papua New Guinea, but not known from any satellite islands.

REMARKS: Advertisement calls are diverse—single and unpulsed in *rhododactyla*, trains of unpulsed notes in *allisoni* and *similis*, a train of pulsed notes in *schlaginhaufeni*, and a long variable train of pulsed notes in *dentata*. The call of one species, *rubra*, is unknown.

KEY TO *LIOPHRYNE*

1. Adults $\leq$ 30 mm SVL, ear obscure . . *allisoni*
   Adults $>$ 30 mm SVL, ear distinct 2
2. Adults $<$ 45 mm SVL 3
   Adults $>$ 45 mm SVL 5

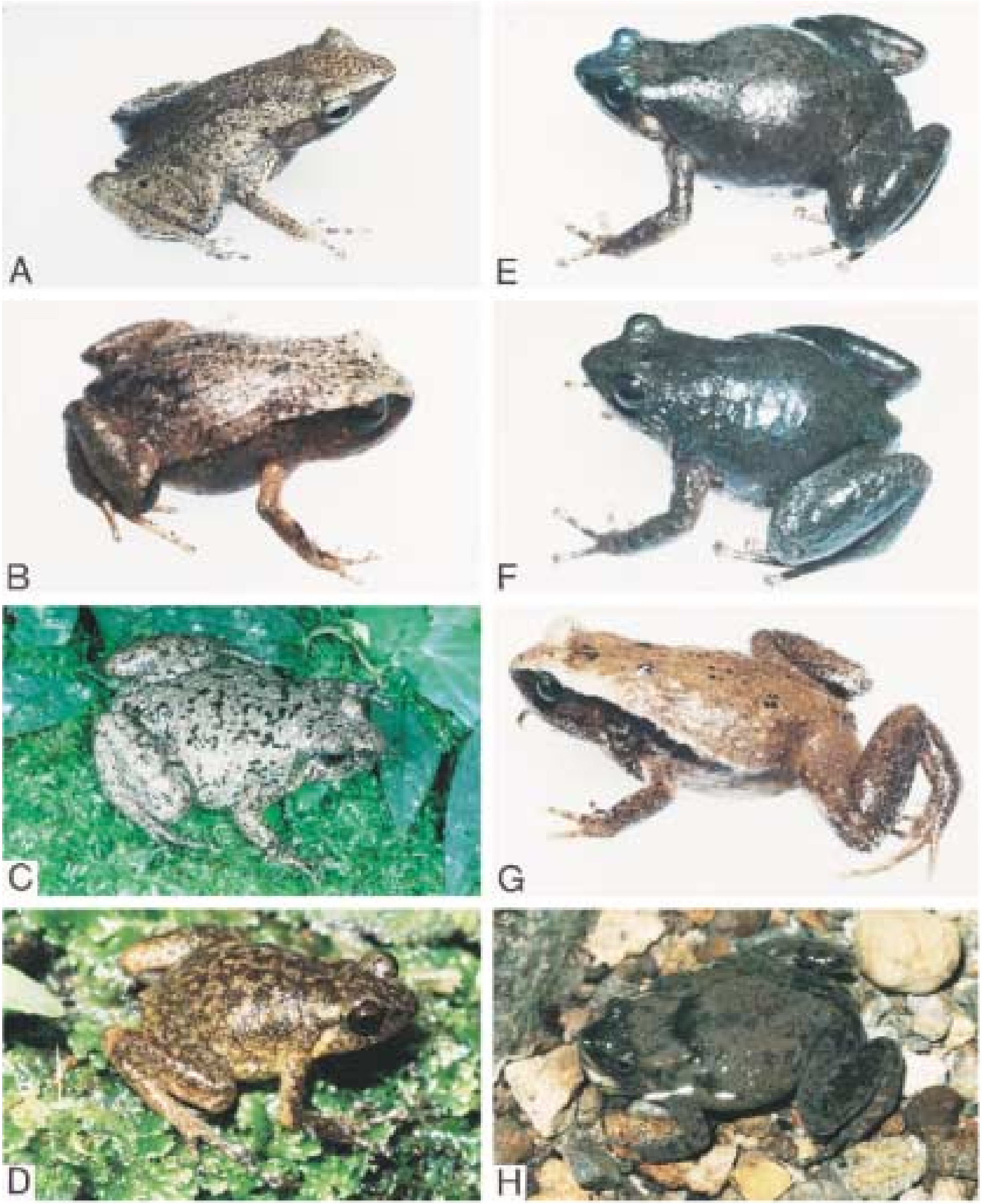

Fig. 31. Examples of *Austrochaperina*, *Liophryne*, and *Sphenophryne*. **A.** *S. cornuta*, AMNH A130544, adult. **B.** *A. brevipes*, AMNH A130534, SVL 21.9 mm. **C.** *A. guttata*, QM J67256, SVL 43.2 mm. **D.** *A. macrorhyncha*, MZB 3564, SVL 36.8 mm. **E.** *A. rivularis*, holotype, AMNH A130551, SVL 49.0 mm. **F.** *A. palmipes*, AMNH A130550, adult. **G.** *L. similis*, AMNH A130564, SVL 40.0 mm. **H.** *A. derongo*, MZB 3563, SVL 36.7 mm. Photos C, D, and H by S. Richards.

3. EN/SVL < 0.082 . . . . *rubra*
   EN/SVL ≥ 0.082 4
4. Canthus rostralis sharp, loreal region nearly vertical, postocular fold straight . . . . *schlaginhaufeni*
   Canthus rostralis rounded, loreal region sloping, postocular fold curves down abruptly behind ear . . . . *dentata*
5. Advertisement call a single note repeated every several seconds, males possess vocal slits . . . . *rhododactyla*
   Advertisement call a series of rapidly repeated notes, males lack vocal slits . . . . . . *similis*

Liophryne allisoni, new species

Figure 32

HOLOTYPE: AMNH A81221 (field no. RZ 7890), collected by R. G. Zweifel on July 22, 1968, in Morobe Province, Papua New Guinea, on the road from Wau to Edie Creek, north slope of Mt. Kaindi, elevation 1900 m, about 5 km west and 1 km north of Wau.

Paratypes (all from Papua New Guinea): Eastern Highlands Prov.: AMNH A66710–66718, collected by H. M. Van Deusen (Sixth Archbold Expedition), Oct. 14–24, 1959, at Arau, 1400 m, 22 km E, 9 km S Kainantu. Morobe Prov.: AMNH A83080, AMS 111068, collected by H. G. Cogger (Alpha Helix New Guinea Expedition), Sept. 7, 1969, on the Wau–Edie Creek Road, about 9.7 km from Wau; BPBM 6230, collected by J. L. Gressitt, Sept. 4–6, 1974, 20–25 km ESE Kaisenik, 1700–2000 m; BPBM 6358, collected by A. Allison, June 26, 1974, on Mt. Kaindi, 1800 m, 5 km WNW Wau; BPBM 6417, 6418, collected by T. K. Pratt et al., Oct. 17, 1974, on Mt. Missim, about 10 km NE Wau, 1600 m; BPBM 8475, collected by A. Allison, Jan. 23, 1982, on Mt. Missim, about 1500 m; BPBM 8515, collected by A. Allison, Feb. 19, 1982, on Mt. Missim, 1650 m; BPBM 9359, 9361, 9366, collected by A. Allison, Feb. 16, 1982 on Mt. Missim, Poverty Ck., 1500 m; BPBM 9371, 9374–9376, 9379, collected by A. Allison, Feb. 19, 1983, on Mt. Missim, Coldwater Ck., 1650 m; BPBM 9389, 9390, collected by A. Allison, Feb. 12, 1982, on Mt. Missim, Poverty Ck., 1550 m; BPBM 9408, collected by A. Allison, Feb. 14, 1982, on Mt. Missim, Poverty Ck., 1600 m; BPBM 9550, collected by A. Allison, Apr. 4, 1982, on Mt. Missim, Poverty Ck., 2000 m; BPBM 9554, collected by A. Allison, Feb. 16, 1982, on Mt. Missim, 1990 m; BPBM 9628–9632 (9631 C&S), collected by M. Buka, Apr. 20, 1982, on Mt. Missim, 1950 m; BPBM 9702, collected by A. Allison, May 20, 1982, 5 km NNW Wau, 1800 m.

ETYMOLOGY: The patronym honors Dr. Allen Allison of the Bishop Museum, in recognition of his collections of this species as well as other important contributions to the biology of Papua New Guinea.

DIAGNOSIS: Differs from other species of *Liophryne* in its small size (SVL 30 mm or less) and in the small size and relative obscurity of the ear. *L. dentata* and *L. schlaginhaufeni* just enter maturity at the maximum size of *allisoni*, and *similis* and *rhododactyla* do so at a still larger size.

DESCRIPTION OF HOLOTYPE: Adult male with the following measurements and proportions: SVL 24.6, HW 10.2, TL 12.9, EY 3.0, EN 2.0, IN 3.1, HD 5.8, FT 12.8, third finger disc 0.55, fourth toe disc 1.0, TY 2.0±; HW/SVL 0.415, TL/SVL 0.524, EY/SVL 0.122, EN/SVL 0.081, IN/SVL 0.126, EN/IN 0.645, HD/SVL 0.236, FT/SVL 0.520, FD/SVL 0.022, TD/SVL 0.041.

Head narrower than body, snout bluntly pointed seen from above, rounded and slightly protruding in profile; loreal region a moderately steep slope, scarcely concave; canthus rostralis rounded; nostrils lateral, barely visible from above, a little closer to tip of snout than to eye. Eye moderately large, eyelid about 80% of interorbital space; tympanic annulus scarcely visible. Relative lengths of fingers 3 > 4 = 2 > 1, first more than half length of second, all with grooved terminal discs scarcely or (1st) not broader than penultimate phalanges; subarticular and metacarpal elevations low, rounded. Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, all with grooved terminal discs, those on third and fourth about 2× widths of penultimate phalanges, others progressively narrower; subarticular elevations rounded, slightly prominent; a small, elongate inner metatarsal tubercle, no others. Skin smooth above and below with only a trace of a postocular fold.

The ground color in preservative is tan with small, vague, darker marks and a pair of more prominent, small dark spots in the

TABLE 6
Body Proportions in *Liophryne*

Species	Mean ± σ_m	Range	N	Mean ± σ_m	Range	N
	TL/SVL			HW/SVL		
allisoni	0.515 ± 0.004	0.471–0.547	28	0.393 ± 0.003	0.365–0.418	28
dentata	0.552 ± 0.006	0.516–0.584	13	0.432 ± 0.004	0.399–0.456	13
similis	0.488 ± 0.005	0.461–0.502	8	0.392 ± 0.004	0.382–0.414	11
rhododactyla[a]	0.498 ± 0.007	0.456–0.562	15	0.393 ± 0.005	0.373–0.452	15
rubra	0.566	0.563–0.568	2	0.396	0.392–0.400	2
schlaginhaufeni	0.572 ± 0.007	0.512–0.608	17	0.420 ± 0.004	0.388–0.445	17
	HD/SVL			FT/SVL		
allisoni	0.226 ± 0.002	0.206–0.245	28	0.495 ± 0.004	0.443–0.536	28
dentata	0.224 ± 0.002	0.221–0.228	13	0.514 ± 0.006	0.502–0.522	13
similis	0.247 ± 0.004	0.235–0.275	8	0.488 ± 0.005	0.471–0.513	8
rhododactyla[a]	0.262 ± 0.004	0.231–0.304	15	0.504 ± 0.007	0.468–0.560	15
rubra	0.219	0.216–0.221	2	0.513	0.497–0.528	2
schlaginhaufeni	0.222 ± 0.004	0.188–0.241	16	0.499 ± 0.006	0.442–0.540	18
	EY/SVL			EN/IN		
allisoni	0.124 ± 0.005	0.107–0.223	28	0.661 ± 0.006	0.607–0.754	28
dentata	0.141 ± 0.003	0.112–0.154	13	0.919 ± 0.018	0.733–0.974	13
similis	0.108 ± 0.002	0.103–0.116	8	0.691 ± 0.011	0.660–0.762	8
rhododactyla[a]	0.114 ± 0.002	0.099–0.130	15	0.676 ± 0.009	0.627–0.769	15
rubra	0.109	0.107–0.111	2	0.611	0.571–0.671	2
schlaginhaufeni	0.121 ± 0.001	0.100–0.132	17	0.836 ± 0.010	0.778–0.930	17
	EN/SVL			IN/SVL		
allisoni	0.078 ± 0.001	0.070–0.086	28	0.118 ± 0.001	0.109–0.126	28
dentata	0.100 ± 0.002	0.082–0.108	13	0.109 ± 0.001	0.100–0.116	13
similis	0.073 ± 0.001	0.070–0.080	8	0.106 ± 0.001	0.104–0.111	8
rhododactyla[a]	0.072 ± 0.001	0.066–0.078	15	0.106 ± 0.001	0.099–0.115	15
rubra	0.076	0.075–0.076	2	0.124	0.116–0.131	2
schlaginhaufeni	0.097 ± 0.001	0.091–0.106	17	0.116 ± 0.001	0.109–0.125	17
	FD/SVL			TD/SVL		
allisoni	0.023 ± 0.0005	0.019–0.028	22	0.040 ± 0.0009	0.034–0.049	23
dentata	0.027 ± 0.0004	0.024–0.029	13	0.043 ± 0.0007	0.038–0.048	13
similis	0.028 ± 0.0007	0.026–0.031	8	0.035 ± 0.0014	0.031–0.039	7
rhododactyla[a]	0.024 ± 0.0006	0.018–0.027	13	0.031 ± 0.0008	0.023–0.035	14
rubra	0.027	0.024–0.029	2	0.042	0.038–0.045	2
schlaginhaufeni	0.027 ± 0.0010	0.019–0.033	14	0.045 ± 0.0018	0.029–0.055	14

[a] Type locality and Morobe Prov.

scapular region. The side of the face is dusky, darker below the eye and around the nostril. A narrow, dark brown postocular streak breaks up above the ear and continues in intermittent fashion down to midflank. There are also some dark spots between the ear and front leg. The edge of the chin is dusky with lighter spots. On the throat and chest this gives way to pale brown mottling on the paler background. The abdomen and undersides of thighs are unmarked, the shank and tarsus mottled, and the sole and back of the tarsus nearly uniform dark brown. There is a well-defined, dark brown, triangular subcloacal patch.

In life the dorsal surfaces (head, body, and

Fig. 32. Holotype of *Liophryne allisoni*, AMNH A81221, SVL 21.9 mm.

limbs) are light brown with little pattern except for narrow dark crossbars on the thighs and faintly indicated lumbar ocelli. The postocular and subocular markings are dark brown, the loreal region paler. The chin is grayish white spotted with darker gray. The abdomen has a yellow-gold tint, and the shank has a gray network over the yellowish background.

Variation in Type Series: The largest specimens are a female and a male, both adult, and both measuring 29.6 mm SVL; four other adult females range down to 24.2 mm. Males 18.9 and 19.8 mm SVL appear to lack vocal slits, whereas all specimens 20.1 mm or longer have them, suggesting that males may become mature at about 20 mm SVL. Body proportions are summarized in table 6, and regression statistics are presented in table 7.

The color and pattern description of the holotype fits many of the paratypes almost equally well. Other paratypes vary from this description. These individuals are darker, especially in the head region, have a generally darker ground color on the back, and may have the abdomen mottled rather than clear. Some have additional dark markings, such as a canthal stripe, a W-shaped mark in the scapular region, and spots on the posterior back. Two of the 40 specimens examined

TABLE 7

Regression Statistics of Five Species of *Liophryne*[a]

	α	β	*r*	N	α	β	*r*	N	α	β	*r*	N	α	β	*r*	N	α	β	*r*	N
	TL/SVL				HW/SVL				HD/SVL				FT/SVL				EY/SVL			
allisoni	0.554	0.977	0.952	31	0.479	0.938	0.943	31	0.176	1.076	0.932	31	0.766	0.864	0.949	31	0.329	0.679	0.894	31
dentata	1.111	0.799	0.969	13	0.487	0.965	0.965	13	—	—	—	—	—	—	—	—	0.059	1.249	0.927	13
similis	0.308	1.120	0.996	23	0.522	0.926	0.962	23	0.206	1.048	0.995	23	0.266	1.157	0.995	22	0.271	0.768	0.988	22
rhododactyla[b]	0.307	1.117	0.995	22	0.558	0.909	0.998	22	0.162	1.114	0.991	22	0.340	1.096	0.996	23	0.259	0.775	0.989	23
schlaginhaufeni	0.420	1.088	0.970	23	0.381	1.029	0.976	23	0.130	1.154	0.948	22	0.387	1.072	0.969	22	0.121	1.002	0.902	23
	EN/SVL				IN/SVL				FD/SVL				TD/SVL							
allisoni	0.135	0.830	0.916	31	0.224	0.800	0.948	31	0.038	0.840	0.765	25	0.070	0.829	0.744	26				
dentata	0.078	1.072	0.915	13	0.282	0.727	0.967	13	0.033	0.944	0.926	13	0.097	0.770	0.889	13				
rhododactyla[b]	0.157	0.794	0.995	22	0.172	0.871	0.993	22	0.020	1.033	0.969	18	0.032	0.980	0.962	19				
similis	0.156	0.805	0.993	23	0.170	0.875	0.997	23	0.022	1.061	0.988	23	0.026	1.066	0.980	22				
schlaginhaufeni	0.109	0.968	0.958	23	0.246	0.789	0.926	23	0.006	1.422	0.901	20	0.043	1.020	0.761	20				

[a] Power curves of the form $Y = \alpha X^{\beta}$.

[b] Papua New Guinea: Morobe Prov.

TABLE 8
Call Statistics for *Liophryne allisoni*[a]

Museum no.	Tape no.	SVL, mm	Temp., °C	Call duration, sec		Notes per call		Notes per sec		Dominant, Hz	No. of calls
				Mean	Range	Mean	Range	Mean	Range		
No voucher[b]	192	—	16.5	1.52	1.46–1.53	22.8	22–24	14.6	14.5–14.7	2650	5
BPBM 9359[c]	244	23.4	16.4	1.48	1.41–1.56	24.0	23–25	15.8	15.7–15.9	2950	2
BPBM 9361[c]	244	23.3	16.4	1.55	1.33–1.69	26.1	23–28	16.4	16.1–16.8	2900	7
BPBM 9371[c]	244	19.6	19.6	1.61	1.58–1.65	23.5	23–24	14.1	14.1–14.2	2900	2
No voucher[c]	244	—	19.6	1.28	1.08–1.42	18.2	16–20	14.0	13.0–15.0	2600	11

[a] All recordings made in Morobe Prov., Papua New Guinea.

[b] Edie Ck. Road, Mt. Kaindi.

[c] Mt. Missim.

have a dark-edged, narrow, pale, midvertebral line imposed on the more basic pattern described. Five specimens have a dark figure that involves the top of the head and snout, part of the eyelids, and occupies the middorsal region, where its irregular but well-defined edges set it off abruptly from the paler dorsolateral region. Both polymorphism and individual color change (arrested by preservation) may be involved.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71F; premaxilla, fig. 63E; hyoid, fig. 70; sacral region, fig. 72E; vomer, fig. 65E; skull, fig. 68C; hand and foot, fig. 54B.

CALL: An average call is a train of about 23 short (0.03 sec) notes uttered at 15 per sec over a period of 1.5 sec (fig. 78A, table 8). Individual notes are unpulsed, with an abrupt rise in frequency and a less abrupt fall, with the dominant energy occurring in the region of 2600–2900 Hz. One individual initiated calls at an average interval of 46.8 sec (35.9–58.9, N = 7), another at 35.5 sec (26.7–51.8, N = 4). Temperature was virtually the same in both instances (16.4° and 16.5°C, respectively). There is no indication of an influence of temperature on call characteristics, but the temperature range in the sample is narrow (3.2°C).

COMPARISONS WITH OTHER SPECIES: Details in the Diagnosis should suffice to separate *allisoni* from other *Liophryne*. The more prominent subarticular elevations of *allisoni* and its high TL/SVL ratio will distinguish it from *Austrochaperina* of similar size.

HABITAT AND HABITS: Gressitt and Nadkarni's (1978) description of the vegetation of Mt. Kaindi is illustrated with cross sections of forest at 1790 and 1880 m, within the zone occupied by *Liophryne allisoni*. The forest, on a steep ground with a ground cover of leaves, moss and ferns, has an irregular canopy 27–29 m high. Brass (1964: 201) characterized the forest at Arau as "a transition between mid-mountain fagaceous forest and a lower montane mixed rain forest . . . rich in herbaceous undergrowth."

I found the holotype in the daytime beneath a small log. Frogs tape-recorded by Allen Allison were beneath leaves on the forest floor, and one that I recorded (but that eluded four surrounding herpetologists) was deep in roadside grass. The habitus of this species—especially the long legs and large eyes—suggest that it is more a frog of the leaf litter rather than a truly burrowing form. This is consistent with what is known of other *Liophryne*.

DISTRIBUTION: *Liophryne allisoni* is known from localities in Papua New Guinea spanning 150 km between the eastern edge of Eastern Highlands Province and the vicinity of Wau, Morobe Province (fig. 28). The known range in elevation is 1400–2000 m. The upper limit, at least, may be approximately correct, as this frog has not been taken in the summit region of Mt. Kaindi (2362 m) despite much collecting there. For locality data, see Holotype and Paratypes above.

REMARKS: Members of the Sixth Archbold Expedition (1959) were the first to collect this species. The majority of specimens and tape recordings resulted from the efforts of Allen Allison, working out of the Wau Ecology Institute.

Fig. 33. *Liophryne dentata*, SAMA R11824, SVL 35 mm. J. Menzies photo.

Liophryne dentata (Tyler and Menzies), new combination

Figure 33

Sphenophryne schlaginhaufeni: Zweifel, 1956: 18 (tentative identification of initial specimen of *L. dentata*).

Sphenophryne dentata Tyler and Menzies, 1971: 79 (type locality, ‘‘Alotau, Milne Bay, Territory of Papua’’ [Milne Bay Prov., Papua New Guinea]; holotype SAMA R12063, collected on November 11, 1970, by J. I. Menzies).

DIAGNOSIS: *Liophryne dentata* shares with *L. rubra* and *L. schlaginhaufeni* an intermediate range of adult body size between the smaller *allisoni* (20–30 mm SVL) and the larger *similis* and *rhododactyla* (48–60 mm). The rounded canthus rostralis and sloping loreal region of *dentata* contrasts to the sharp canthus rostralis and nearly vertical lores of *schlaginhaufeni*. Both *rubra* and *schlaginhaufeni* have a straight postocular fold passing diagonally to the flank, whereas *dentata* has a short, curved fold passing down behind the ear, and *rubra* differs in its shorter eye–naris span (maximum EN/SVL 0.076 vs. minimum in *dentata* of 0.082).

MORPHOLOGY: Body size moderately large, up to 38 mm SVL, with long legs (TL/SVL mean, 0.55) and broad head (HW/SVL mean, 0.43) almost as wide as the body. Snout seen from above rounded but not blunt, slightly rounded in profile; nostrils visible from above, closer to tip of snout than to eye; loreal region a gentle, almost flat slope, canthus rostralis rounded. Eyes large, just visible from beneath, eyelid >80% interorbital span; ear distinct, >60% eye diameter. Relative lengths of fingers 3 > 4 ≈ 2 > 1, first finger long, tip reaching to base of disc of second; all fingers with expanded, grooved discs, that of third finger about 1.5× width of penultimate phalanx; subarticular and metacarpal elevations rounded, moderately prominent. Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1; all toes with expanded, grooved discs, that of fourth toe about 2.3× width of penultimate phalanx; subarticular elevations rounded but prominent, a small, elongate inner metatarsal tubercle, no outer. Dorsum rugose; a narrow postocular fold passing down behind ear; a W-shaped fold in scapular region; numerous (1–4 per mm^2) small, conical warts, some running together to form short folds; lateral region with flatter elevations; central dorsal region of thigh and top of shank with warts like those on back; ventral surfaces smooth.

COLOR AND PATTERN: A preserved specimen is brown dorsally with a dark interocular bar and dark pigment associated with the W-shaped scapular fold. There are other indistinct dark marks on the back and legs, and the tiny warts have pale tips. The ear is conspicuously paler than its surroundings. The anterior surfaces of the thighs are dusky but distinctly mottled toward the knee, with the posterior surfaces being dusky with tiny light spots. The throat and chest are lightly mottled with brown, the abdomen is clear, the undersides of the thighs have a few indistinct brown marks, and the shank is more heavily infuscated. A second specimen is paler dorsally with a distinct dark line on the canthus rostralis and postocular fold, and it has a pale midvertebral pinstripe with spotty black border.

Tyler and Menzies (1971) described the dorsal color in life as sandy brown to reddish brown, stippled or mottled with darker and lighter brown, with occasional orange patches irregularly distributed, scapular W-mark occasionally reddish; back of thighs usually gray, finely stippled with white, but sometimes pink; ventral surface white with sparse gray mottling on sides of throat; groin and lower side of hind limbs reddish, sometimes bright red; a light diagonal stripe through ear; iris greenish gold.

VARIATION IN SIZE AND PROPORTIONS: The largest of 13 specimens I measured is a gravid female, 38.0 mm SVL, and the smallest of the six gravid females is 33.6 mm. Tyler and Menzies (1971) gave a slightly narrower range (34.7–37 mm) for a larger series of specimens that included the ones I measured. The size range of adult males has not been determined. Body proportions are summarized in table 6, and regression statistics are presented in table 7.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71H; premaxilla, fig. 63G; sacral region, fig. 72G; vomer, fig. 65G; hand and foot, fig. 54E.

CALL: The advertisement call is a long series of harsh, pulsed notes. The recording available to me begins with 15 sec of notes, with notes being 0.17 sec in duration, uttered at about 1.6 per sec, pulsed at about 225 per sec, and with a dominant frequency of 1600 Hz. There follows a break in the recording, after which the call resumes at a much faster note repetition rate (5 per sec), higher pitch (2600± Hz), faster pulse rate (367 per sec), and shorter note duration (0.08 sec). Toward the end of this 108-sec segment the note repetition rate slows down and becomes more variable, but the other parameters remain much the same. The segment illustrated (fig. 78C) is from the middle part of a call (temperature not noted; recording courtesy of J. Menzies, made at Alotau, voucher UPNG 1727 [paratype], copy on AMNH Herpetology tape no. 253). The variability of this call exceeds anything seen in the other species studied.

COMPARISONS WITH OTHER SPECIES: *Liophryne dentata* most closely resembles *Liophryne schlaginhaufeni*. The two are of similar size and general morphology: large eyes, large and distinct ears, long legs, broad head. They have digital discs of similar size (although those of *schlaginhaufeni* are unusual in being somewhat pointed), long first fingers, and subarticular elevations that are well developed by comparison with other Papuan microhylids. The species are not known to occur in the same region and are readily distinguished by the characters given in the Diagnosis as well as by the well-defined black face mask of *schlaginhaufeni*, the curved postocular fold in *dentata* (straight in *schlaginhaufeni*), the dorsal rugosity of *dentata*, and differences in calls. See account of *L. rubra* for comparison with that species.

As Tyler and Menzies (1971) noted, *L. dentata* bears a striking if superficial similarity to some species of the ranid genus *Platymantis*, more specifically to *P. papuensis*, a common and widely distributed frog of similar habits.

HABITAT AND HABITS: The type series was taken on the floor of well-developed forest on steep, dissected hillsides at elevations of 60 to 150 m in October and November. Of 12 other species of frogs found in the same forest, only 3 (all microhylids) ‘‘appear to occupy exactly the same habitat as *S. dentata*’’: *Hylophorbus rufescens*, *Mantophryne lateralis*, and *Copiula oxyrhina*. ‘‘*Platymantis papuensis* favours the forest floor but at this locality is usually found lower down on the hillsides’’ (Tyler and Menzies, 1971: 83). Another microhylid species at this locality, *Austrochaperina palmipes*, is riparian.

Except for the higher elevation (1550 m), the habitat at the only other known locality for the species, Mt. Dayman, evidently is similar to that described for the type locality, as Brass (1956: 131) wrote of ‘‘steep little gullies’’ and ‘‘gullies and ravines, where mixed rain forest replaced the mid-mountain forest.’’ G. M. Tate found the specimen from this locality under moss on a tree in moist forest.

DISTRIBUTION: The species is known from only the eastern tip of Papua New Guinea at elevations between 60 and 1550 m (fig. 38).

LOCALITY RECORDS AND SPECIMENS EXAMINED: PAPUA NEW GUINEA: Milne Bay Prov.: Near Alotau (AMNH A87205 [paratype], SAMA R11819–11828 [paratypes], R12063 [holotype], UPNG 2641 [paratype, C&S]); north slope, Mt. Dayman, 1550 m (AMNH A56734).

Liophryne rhododactyla Boulenger

Liophryne rhododactyla Boulenger, 1897: 11 (type locality, ‘‘Mount Victoria, Owen Stanley Range, New Guinea’’; syntypes, BMNH 1947.2.12.47–49, formerly 1896.10.31.28–30, collected by A. S. Anthony in 1896).

Sphenophryne rhododactyla: Parker, 1934: 156.

TYPE LOCALITY: A quote from Zweifel (1983: 4) is appropriate here: ‘‘The type locality given in the synonymy is taken from the title of Boulenger's paper, which provides no other information. Wichmann (1912, p. 608) indicates that Anthony collected on Mt. Victoria between April and June 1896, and as Anthony operated out of Port Moresby, it is likely that collections were made on the western rather than the eastern side of the Owen Stanley Range in what is now the Central Province of Papua New Guinea. The title of a paper by Rothschild and Hartert (1896) treating birds collected by Anthony on the same trip (Wichmann, 1912) includes the phrase 'mostly at elevations of from 5000 to 7000 feet.' "

DIAGNOSIS: The largest species of *Liophryne* (adult SVL 48–60 mm), comparable (and possibly identical) in size to *L. similis*, from which it differs in that the male possesses vocal sac apparatus (slits and sac) and in the advertisement call—a single note rather than a series of rapidly repeated notes.

MORPHOLOGY: Head slightly narrower than the rather flat-sided body. Snout rounded to bluntly pointed seen from above, rounded and scarcely projecting in profile; nostrils lateral, barely visible from above, slightly closer to tip of snout than to eye; canthus rostralis angular but not sharp, loreal region nearly vertical, slightly concave. Eyes moderately large, corneal outline visible from below, eyelid about 80% of interorbital span. Tympanum distinct, about 49% of orbit length, closer to eye than its own diameter. Relative lengths of fingers $4 > 3 > 2 > 1$, first finger long, greater than half length of second; all fingers with terminally grooved discs, that of first least developed, others barely broader than penultimate phalanges; subarticular and metacarpal elevations rounded, moderately prominent. Toes unwebbed, relative lengths $4 > 3 > 5 > 2 > 1$, all with terminally grooved discs broader than those of fingers, that of first toe smallest but slightly broader than penultimate phalanx; subarticular elevations rounded, moderately prominent, inner metatarsal elevation rounded, elongate. Skin smooth; indistinct convergent scapular folds sometimes present; a narrow postorbital fold passing across upper edge of tympanum, expanding into a broad, flat region behind tympanum, narrowing again above arm, continuing onto flank as a dorsolateral fold, usually disappearing anterior to groin.

COLOR AND PATTERN: The top of the head and body are moderate to pale brown, sometimes with small, obscure, irregular darker spots. The loreal region, especially near the canthus rostralis, and the area below the postorbital and dorsolateral folds are dark brown, excepting the tympanum, which has the same lighter shade as the dorsum. A thin, pale vertical line on the tip of the snout divides to pass along each canthus rostralis. In some individuals a fairly discrete line continues along the edge of the eyelid, following the postorbital-dorsolateral fold, but in others there is little or no trace of the line posterior to the nostrils. A few specimens have pale eyelids and a swath of the same light pigment between the dorsolateral folds and the remaining light brown of the dorsum. The arms and legs are darker, purplish brown with some light spotting on the arms. The rear of the thigh is unmarked and colored like the middorsal region. The ventral surfaces are brown with numerous small, light irregular spots. In many specimens the light spots are enlarged and coalesce to some extent so that the pale color dominates. The throat and chest are generally somewhat darker than the abdomen.

VARIATION IN SIZE AND PROPORTIONS: The two largest male specimens both measure 52.3 mm SVL; the two largest females are 59.0 and 59.8 mm. Males evidently mature at about 48–49 mm: three measuring 44–47 mm lack vocal slits, whereas two measuring 48.9 mm and four larger specimens have them. Females apparently mature at about the same size as males. A 48.4-mm individual is gravid, as are larger specimens. Body proportions are summarized in table 6, and regression statistics are presented in table 7.

ILLUSTRATIONS: See Boulenger (1897: pl. 2), for illustrations of body form, inside of mouth, and tongue, and Green and Simon (1986) for SEM photographs of the finger discs. For all practical purposes, the illustration of *L. similis* (fig. 31G) will suffice to illustrate the overall appearance. Terminal phalanx of third finger, fig. 71G; premaxilla, fig. 63F; hyoid, fig. 69C; sacral region, fig. 72F; vomer, fig. 65F; skull, fig. 68B; palatal fold, figs. 58, 59. Kuramoto and Allison (1989) illustrated the karyotype.

CALL: Frogs of the presumably disjunct population in mountains southeast of Wau utter a loud, single-note call, being high-pitched for a frog of its size (fig. 77A). I have a recording made by Allen Allison on the Bulldog Road, 2600 m, about 15 km southeast of Wau, Morobe Province, at about 2000 hours on April 30, 1982, copy on AMNH Herpetology tape reel 244. Six calls (notes) average 0.235 sec long (0.22–0.26), with a mean interval between call initiations of 3.98 sec (3.5–5.1). The notes are unpulsed, with the dominant frequency beginning at about 1300 Hz, rising gradually to about 1700 Hz, and descending slightly to the end.

COMPARISONS WITH OTHER SPECIES: Adults of this large species can be confused only with the sibling *Liophryne similis* (see the account of that species for comparisons). Juveniles of *rhododactyla* could be confused with the much smaller but similar sympatric species, *Austrochaperina brevipes* (see the account of that species for comparisons).

HABITAT AND HABITS: Almost nothing is published specifically referring to the habitat and habits of *rhododactyla*. Zweifel and Allison (1982: 9, Allison's observations) referred to *rhododactyla* as a terrestrial species ‘‘that roams the forest floor at night,’’ and Green and Simon (1986) characterized *rhododactyla* as terrestrial. Archbold and Rand (1935) described the forest and terrain near the summit of Mt. Tafa, where *rhododactyla* has been taken.

DISTRIBUTION: Moderately high elevations south of Wau and in the Owen Stanley Mountains (fig. 34). Dr. Allison informed me that he has collected this species as low as 2200 m on Bulldog Road (a World War II supply road, now in disuse, that crossed the divide southwest of Wau), and has heard it at the same elevation south-southeast of Wau. A specimen supposedly from the outskirts of Wau at 1200 m, far below the altitudinal limit otherwise known and in an area where much collecting has produced no other specimens of this species, is almost certainly mislabeled, as presumably is a hylid frog of higher elevations (*Litoria angiana*) bearing the same locality data from the same collector. Undoubtedly the range in the Owen Stanley Mountains, suggested by the area above 2400 m (fig. 34), is much more extensive than the known localities might seem to imply.

LOCALITY RECORDS AND SPECIMENS EXAMINED: PAPUA NEW GUINEA: Central Prov.: Mt. Victoria (BMNH 1947.2.12.47–49, syntypes); Mt. Tafa, 2600 m (BMNH 1935.3.9.123). Morobe Prov.: Bulldog Road, 15–17 km S, about 1 km W Wau, ca. 2400–2700 m (BPBM 6264, 6265, 6325, 6326, 6344, 9641–9643, 9652–9654, 9662, 9793 (C&S); UPNG 4119, 4886, 4887, 5329–5335); Kunai Creek, Wau, 1200 m (BPBM 5520, locality questionable; see above).

REMARKS: *Liophryne rhododactyla* had remained a little known species for the nearly 100 years since its initial description until the activities of collectors and researchers working out of the Wau Ecology Institute provided a generous sample of specimens. The only specimen additional to those of the type series had been one collected by Evelyn Cheeseman on Mt. Tafa in the mid-1930s and reported by Parker (1936).

Liophryne rubra, new species

Figure 35

HOLOTYPE: UPNG 9361 (field no. 97), collected by Tamari Mara on October 3–9, 1995, in Western Highlands Province, Papua New Guinea, about 3 km east of Mt. Opio (5°35′51″S, 144°47′25″E) at an elevation of 2180 m.

PARATYPE: UPNG 4147, collected by G. George in July 1973 in the Kubor Range, Western Highlands Province, Papua New Guinea. No more specific data are available.

ETYMOLOGY: The Latin adjective *rubra* refers to the red color in life.

DIAGNOSIS: A *Liophryne* of moderate size (SVL about 37 mm in two specimens), similar in size to *L. dentata* and *L. schlaginhaufeni* but differing from these in its shorter eye–naris distance (EN/SVL maximum 0.076 vs. minima of 0.082 and 0.091 in *dentata* and *schlaginhaufeni*), wider average internarial span (mean IN/SVL 0.134 vs. maxima of 0.109 and 0.116), and lack of scapular skin folds. *L. dentata* differs additionally in having a postocular skin fold that curves

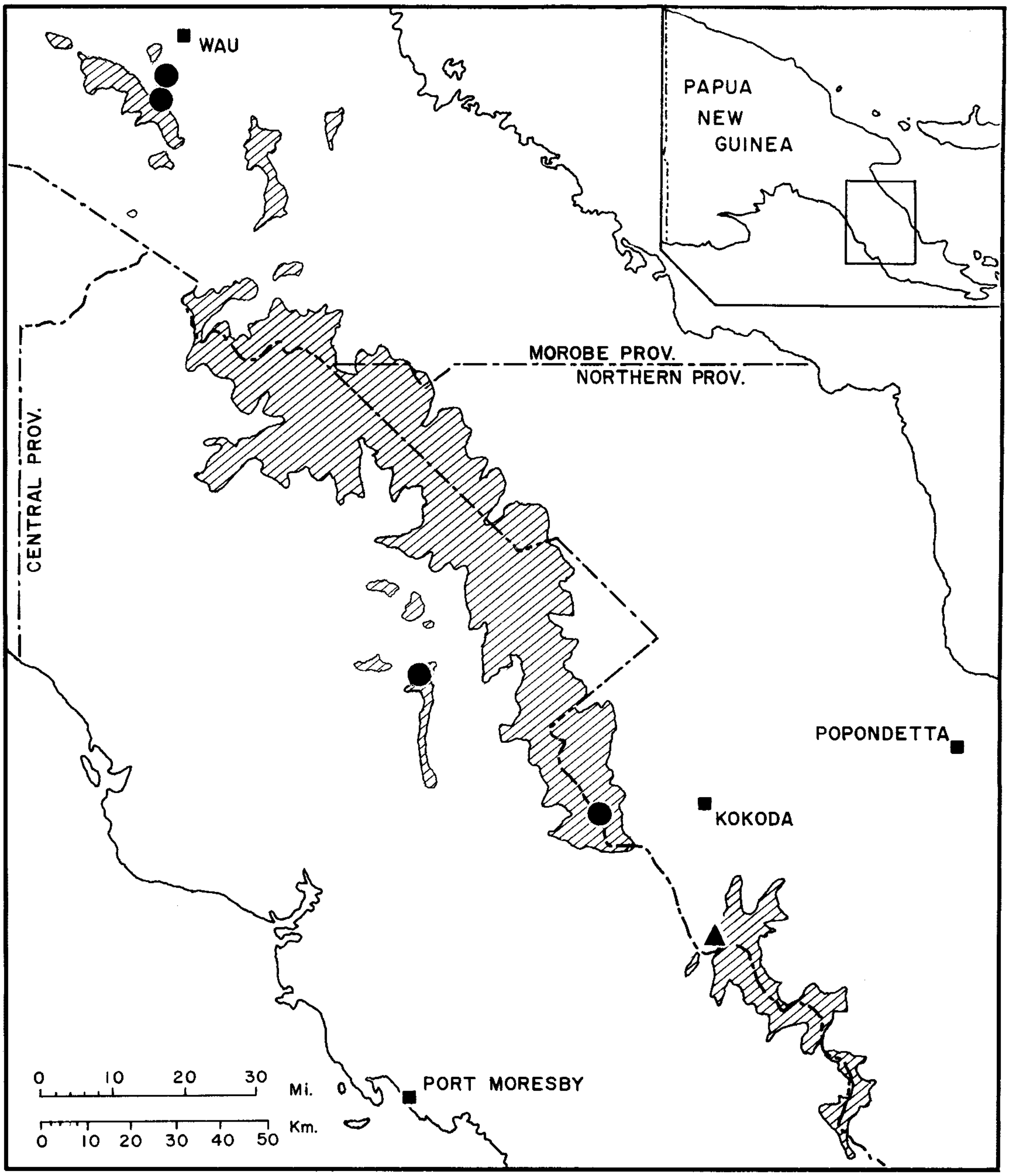

Fig. 34. Distribution of *Liophryne rhododactyla* (circles) and *L. similis* (triangle) in Papua New Guinea. Shaded area is greater than 2400 m elevation.

downward behind the ear rather than continuing straight onto the flank.

Description of Holotype: The holotype specimen is a mature female (2-mm ova), with the following measurements and proportions (those of the single paratype given in parentheses): SVL 37.5 (37.0), HW 15.0 (14.5), TL 21.1 (21.0), EY 4.0 (4.1), EN 2.8 (2.8), IN 4.9 (4.3), TY 3.2 (2.8), HD 8.3 (8.0), FT 19.9 (18.4), disc of third finger 1.1

Fig. 35. Holotype of *Liophryne rubra*, UPNG 9290, SVL 37.5 mm.

(0.09), penultimate phalanx 0.06 (0.05), disc of fourth toe 1.7 (1.4), penultimate phalanx 0.8 (0.08), TY 3.2 (2.8); HW/SVL 0.400 (0.392), TL/SVL 0.563 (0.568), EY/SVL 0.107 (0.111), EN/SVL 0.075 (0.076), IN/SVL 0.131 (0.116), EN/IN 0.571 (0.651), HD/SVL 0.221 (0.216), FT/SVL 0.528 (0.497), FD/SVL 0.029 (0.024), TD/SVL 0.045 (0.038).

Head narrower than the rather robust body, snout bluntly pointed seen from above, rounded and slightly projecting in profile; nostrils lateral, barely visible from above, slightly closer to eye than to tip of snout; canthus rostralis distinct, slightly rounded; loreal region steep, nearly flat. Eyes moderate in size, corneal outline visible from beneath, interorbital span about 1.5× width of eyelid. Tympanum relatively large and smooth. Relative lengths of fingers $4 > 3 > 2 > 1$, first relatively long, reaching to base of disc of second, all with discs broader than penultimate phalanges; subarticular elevations moderately prominent, rounded. Relative lengths of toes $4 > 3 > 5 > 2 > 1$, first short, reaching base of subarticular elevation of second, all with discs broader than penultimate phalanges, disc of fourth toe about 1.5× width of that of third finger; subarticular elevations moderately prominent, rounded; inner metatarsal elevation low, rounded. A straight fold of skin passing from posterior corner of eye diagonally on flank where it fades out; skin otherwise smooth with no dorsal tubercles or scapular folds. There appear to be small maxillary teeth.

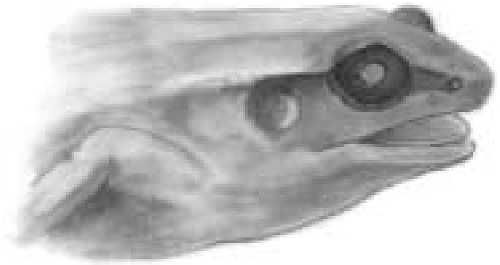

Fig. 36. Holotype of *Liophryne rubra*, UPNG 9290.

Shortly after being preserved, the specimen was ‘‘bright chestnut red’’ in color (J. Menzies, personal commun.); the dorsal surfaces (head, body, legs, and feet) have since faded to pale yellowish tan, unmarked except for a white vertebral hairline. A dark streak passes from nostril to eye and resumes at the posterior corner of the eye to include much of the ear before terminating (fig. 36). The streak is sharply defined at the canthus rostralis, less so along its lower edge; the upper lip is pale. The ventral surfaces are pale and unmarked from chin to hind legs. There are a few dark marks on front and rear surfaces of the front legs, an irregular longitudinal dark streak on the anterior side of each thigh, and a poorly defined dark streak on the posterior side. The palms and soles have some dark pigment but are not wholly dark.

VARIATION IN TYPE SERIES: The paratype resembles the holotype in all pertinent characters, most notably the relatively short eye–naris span, absence of convergent scapular folds, and color pattern. Body proportions are summarized in table 6.

REFERRED SPECIMEN: A specimen of *Liophryne*[9] from the Baiyer River region some

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[9] SAMA R23853, collected by Thomas Burton Jan. 3, 1982, at Trauna Ridge, 1750 m, 13 km E Baiyer River Wildlife Sanctuary, Western Highlands Prov., Papua New Guinea.

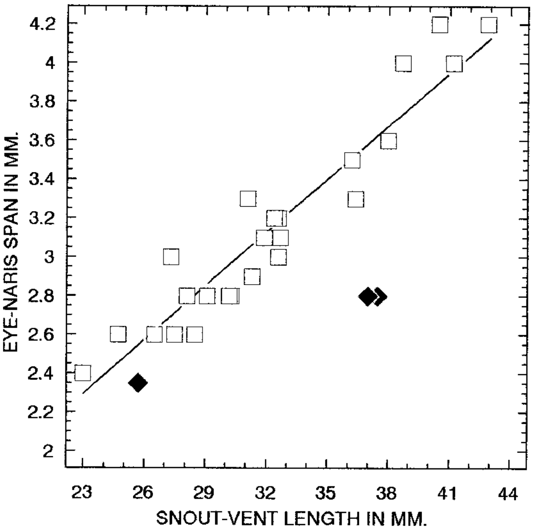

Fig. 37. Comparison of relative eye–naris span in *Liophryne schlaginhaufeni* (squares and regression line) and *L. rubra* (diamonds). The diamond at approximately 26 mm SVL represents a specimen tentatively referred to *rubra*; see text.

75 km west-northwest of the type locality of *L. rubra* and at a lower elevation (1750 m) may represent this species. It is a male, maturity not determined, but at SVL 25.7 mm it is smaller than the known size of maturity of male *schlaginhaufeni* (29 mm). Thomas Burton (personal commun.) described the living frog as rich reddish brown above and orange below (deepest in the throat region) with white flecking and white spots edging the mandible. This specimen also has a pale midventral hairline intersected by a similar line running between the arms. In the critical EN measurement it falls outside the range of *schlaginhaufeni* of similar size and in the same direction as the holotype (fig. 37). I tentatively regard this specimen as *rubra*, but do not accord it paratype status as I have not compared it directly with the holotype and paratype, and hence it does not contribute to my characterization of the new species.

ILLUSTRATIONS: Hand and foot, fig. 54A. Burton's (1986: figs. 7C, 11D, 21C) illustrations of throat and jaw musculature and anterior view of mandibles of *Sphenophryne schlaginhaufeni* may represent *L. rubra* (see Remarks, below).

CALL: The call has not been described.

COMPARISONS WITH OTHER SPECIES: In most respects the proportions of this species are within the range of variation of *Liophryne schlaginhaufeni* of similar size, but there is a significant exception, the eye–naris distance being much shorter than in *schlaginhaufeni* (fig. 37). If the absence of convergent scapular folds proves to be consistent, this too will be diagnostic. Also, *schlaginhaufeni*, recorded from about 400–1550 m, is not known from such a high elevation (2180 m; but see Referred Specimen). *L. dentata* differs from *rubra* in the same way in eye–naris proportions and in its curved rather than straight postocular fold.

HABITAT AND HABITS: Nothing is on record for the holotype. Thomas Burton (in litt.) reported finding the referred specimen under leaf litter and another, larger male accompanying eggs.

DISTRIBUTION: This species is known from the central ranges of Papua New Guinea—the type locality in the Bismarck Range, the Kubor Mountains, and possibly from a locality about 75 km west-northwest of the type locality in the highlands of Papua New Guinea (fig. 38).

Liophryne schlaginhaufeni (Wandolleck), new combination

Sphenophryne schlaginhaufeni Wandolleck, 1911: 5 (type locality, "Oberlauf des Rienjamur 650–700 m üb. Meer, 15. Sept." [1909, Torricelli Mtns., West Sepik Prov., Papua New Guinea]; 2 syntypes, MTKD D2212 [destroyed in World War II: Obst, 1977], collected by Otto Schlaginhaufen on Sept. 15 [year?]). Parker, 1934: 154 (*klossi* synonymized with *schlaginhaufeni*).

Sphenophryne klossi Boulenger, 1914: 251 (type locality, "Launch Camp, Setekwa R.," Irian Jaya; syntypes, BMNH 1947.2.12.45 and 1947.2.12.46, formerly 1913.11.1.140 and 1913.11.1.141, collected on the Wollaston Expedition, probably by C. Boden Kloss on September 12, 1912.[10] Van Kampen, 1923: 107. Nieden, 1926: 46.

Sphenophryne macrorhyncha: van Kampen, 1923: 107 (*schlaginhaufeni* referred with question to the synonymy of *macrorhyncha*).

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[10] Wollaston (1916: 3) cited Kloss as being responsible for the zoological and botanical collections, and (p. 5) described a brief excursion on the Setekwa River on this date.

S[phenophryne]. basipalmata: Nieden, 1926: 46 (*schlaginhaufeni* referred with question to the synonymy of *basipalmata*).

TYPE LOCALITY: I cannot place the "upper course of the Rienjamur" with certainty, but from a map published by the collector (Schlaginhaufen, 1914, fig. 1) it is likely that this is the river now known as the Drinumor (Suain Quadrangle, sheet 7491, Papua New Guinea 1:100,000 topographic survey). This would place the type locality about 29 km south and 25 km east of Aitape.

TYPE MATERIAL: Although the type specimens of *schlaginhaufeni* have been destroyed, there is no reason to question associating this name with the specimens I examined. Not only did Wandolleck provide an adequate description that mentions several pertinent characters, but Parker (1934: 154) examined one of the syntypes and compared it with the types of *klossi*. Inasmuch as there are no outstanding biological problems complicating the taxonomy, a neotype need not be designated.

DIAGNOSIS: Distinguished from *Liophryne allisoni* by larger adult size (SVL ≥ 30 mm) and from *L. similis* and *L. rhododactyla* in being smaller than adults of these two, which are ≤45 mm SVL. *L. schlaginhaufeni* has a sharply defined canthus rostralis (rounded in *dentata*), nearly vertical loreal region (sloping in *dentata*), and a straight postocular-supratympanic skin fold (curved down behind the ear in *dentata)*. See the account of *L. rubra* for diagnostic comparison with that species.

MORPHOLOGY: Body size moderately large, up to about 43 mm SVL, with the longest legs (TL/SVL mean, 0.57) and almost the broadest head (HW/SVL mean, 0.42) in the genus. Snout as seen from above nearly truncate, obtusely angled, slightly projecting in profile; nostrils lateral, scarcely visible from above, much closer to snout tip than to eye; loreal region flat, nearly vertical, sloping only a little outward to lip; a sharp angle along canthus rostralis between loreal region and flat top of snout. Internarial distance relatively broad (IN/SVL mean, 0.12), eye–naris distance slightly less than eye diameter (EN/EY mean, 0.80). Eyes moderately large (EY/SVL mean, 0.12), laterally placed and visible from beneath, interorbital span broader than an upper eyelid. Tympanum large and distinct, horizontal diameter about half that of eye. Relative lengths of fingers $3 > 4 = 2 > 1$, first little shorter than second; all fingers with small, somewhat pointed discs with circum-marginal grooves, disc of third finger about 1.5× width of penultimate phalanx and narrower than disc of fourth toe; subarticular and inner and outer metacarpal tubercles moderately prominent. Relative lengths of toes $4 > 3 > 5 > 2 > 1$, all unwebbed with grooved, somewhat pointed discs, that of fourth toe about twice width of penultimate phalanx; subarticular tubercles moderately prominent, an elongate inner metatarsal tubercle but no outer. Dorsal surface of body finely tuberculate; a pair of angular, convergent folds in the scapular region; a narrow lateral fold commences at the posterior corner of the eye and passes diagonally to the flank, crossing the upper edge of the tympanum; several transverse ridges on the hind limbs and pointed tubercles on the heel and edge of tarsus; ventral surfaces of body and limbs smooth.

COLOR AND PATTERN: Preserved specimens are pale tan to dark gray-brown dorsally, often with the area between and posterior to the scapular folds a deeper tone. Indistinct darker spotting may be present over the dorsal surfaces, and there may be small, paired black spots centered on pale tubercles. Occasional specimens show a narrow vertebral light line. The side of the head is dark brown, darkest and sharply bounded at the canthus rostralis and postocular fold, fading somewhat toward the upper lip. The anterior and posterior surfaces of the thighs are dusky, largely unmarked or with indistinct spotting or mottling. A dark, triangular "seat patch" has its apex at the cloaca. The soles of the feet and rear of the tarsus are dark brown. The ventral surfaces may appear pale with sparse melanic pigmentation visible only on close examination, but in a darker phase light spots contrast with a darker background, especially on the throat.

James Menzies (personal commun.) described specimens from the Adelbert Mountains: dorsally bright yellow (grayish on the head), or reddish fawn, or mottled fawn and brown; sides of head black, continuing to

TABLE 9

Call Statistics for *Liophryne schlaginhaufeni*[a]

Museum no.	Tape no.	Temp., °C	Call duration, sec	Note duration,[b] sec Mean	Note duration,[b] sec Range	Notes/call	Notes/sec	Dominant, Hz
UPNG 7245	286	—	10.7	0.093	0.074–0.106	17	1.51	2200
No voucher	286	—	6.0	—	—	11	1.70	2400
UPNG 7246	286	18.4	10.3	0.130	0.113–0.159	20[c]	1.99	2350

[a] Recordings made by J. Menzies at Mabimap Village, Adelbert Mtns., Madang Prov., Papua New Guinea, Feb. 1987.

[b] N = 10 notes measured.

[c] Initial one or two notes missing from recorded call.

midbody but broken; ventrally white with all over dark reticulation, limbs included; soles and anal region black.

VARIATION IN SIZE AND PROPORTIONS: The largest among 23 specimens examined is a female, SVL 42.9 mm. The smallest evidently mature female, 30.3 mm, has ova 2.5 mm in diameter. Mature males (vocal sac openings present) range from 29.1 to 38 mm. The number of specimens is inadequate to investigate geographic variation. Statistics on proportions are summarized in table 6, and regression data are presented in table 7.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71I; premaxilla, fig. 63H; sacral region, fig. 72H; vomer, fig. 65H; hand and foot, fig. 54D. Mahony et al. (1992) illustrated the karyotype. Boulenger (1914: pl. XXVII, figs. 3, 3a, 3b) has excellent drawings of a syntype of *S. klossi*. Bickford (1999) has a color photograph of a male *schlaginhaufeni* transporting several young.

CALL: G. P. Opit (note on BPBM field tag, specimen from Adelbert Mountains) stated: "Calls both day and night; several loud, high-pitched, very bird-like chirps." James Menzies has provided me with recordings of three frogs made near Mabimap Village, Adelbert Mountains, Madang Province, Papua New Guinea. The call lasts roughly six to 11 sec and consists of a series of 11 to about 20 pulsed, chirplike notes, averaging about 0.09 sec in one frog and 0.13 sec in another (table 9, fig. 79A). The dominant frequency is 2200–2400 Hz.

COMPARISONS WITH OTHER SPECIES: The only species that much resemble *schlaginhaufeni* are *L. dentata* and *L. rubra*. The first two are closely similar in size and proportions but are readily distinguished by the characters given in the Diagnosis and additionally by the dark face mask of *schlaginhaufeni*. So far as is known, their geographic ranges are widely separated. *L. rubra* occurs closer to *schlaginhaufeni* although probably at higher elevations. See the account of *rubra* for morphological comparisons.

HABITAT AND HABITS: I have had no field experience with this species and there is nothing pertinent in the literature. G. B. Opit (notes on field tags, BPBM specimens) found *schlaginhaufeni* active both by day and night on leaf litter in primary forest in the Adelbert Mountains. Bickford (1999) reported that the male broods the eggs and carries the newly hatched young on its back and sides for up to 8 days.

DISTRIBUTION: Although recorded from few localities, *Liophryne schlaginhaufeni* evidently has a rather extensive distribution at middle elevations (about 400–1550 m, but one record as low as 15 m). It has not yet been taken on the Huon Peninsula or on the eastern tail of Papua New Guinea (fig. 38). Published records for the species in the latter region were based on a specimen of *S. dentata* (Zweifel, 1956; see the account of *dentata*) and on misidentified *Cophixalus cheesmanae* (Room, 1974: 440; MCZ specimens examined by me).

LOCALITY RECORDS AND SPECIMENS EXAMINED: IRIAN JAYA: Launch Camp, Setekwa River (BMNH 1947.2.12.45–46, syntypes of *Sphenophryne klossi*); 18 km SSE Timeka Airport, 15 m (BPBM 13859). PAPUA NEW GUINEA: Western Prov.: Derongo, 550 m (MCZ A80000). West Sepik Prov.: Mt. Hunstein, 1200 m (AMNH A77589–77591); Mt. Nibo, Torricelli Mtns., 700–1550 m (AMNH A78182–78184). East Sepik Prov.: Upper

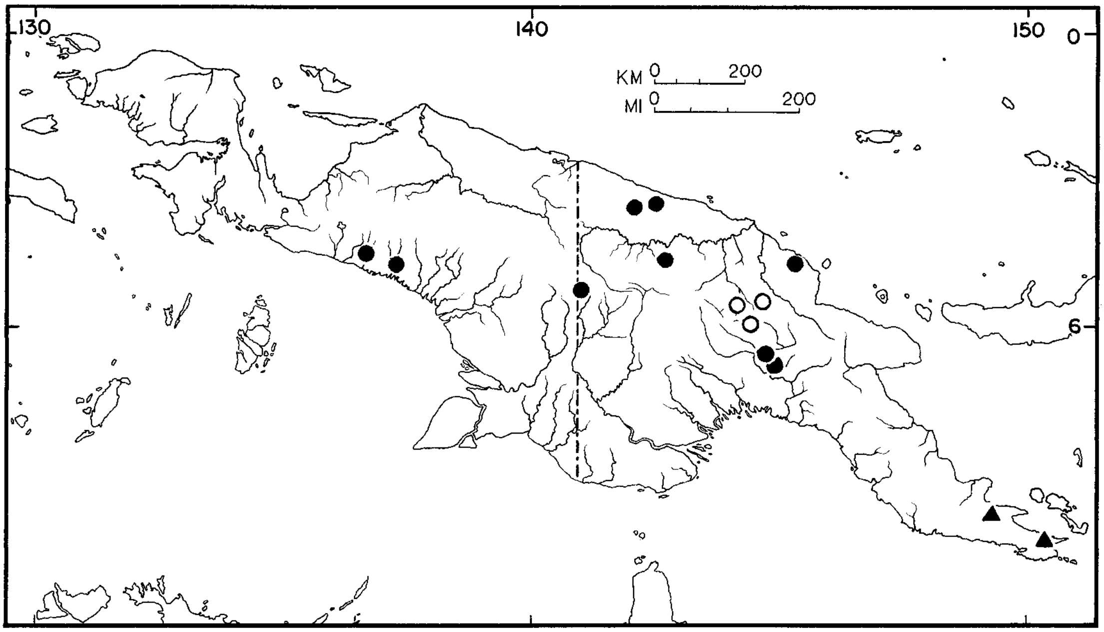

Fig. 38. Distribution of *Liophryne schlaginhaufeni* (closed circles), *L. rubra* (open circles), and *L. dentata* (triangles) in New Guinea. The westernmost locality for *rubra* marks the referred specimen (see text).

course of the Reinjamur, Torricelli Mtns., 650–700 m (Wandolleck, 1911; type locality–see comments above). Simbu Prov.: Diodo, 1200 m, 144°50′E, 6°30′S (AMS R133043, 133044); Weiana, 8 km S, 1 km E Soliabedo, 460 m (MCZ A111929); between Camp III, 13.5 km S, 1 km E Soliabedo, and Weiana, 8 km S, 1 km E Soliabedo, 420–730 m (MCZ A111928); Soliabedo, 550 m (MCZ A111927, 111931). Madang Prov.: Adelbert Mtns., vic. of Wamambre, about 15 km NE Wanuma, 1300 m (BPBM 5676); Adelbert Mtns., Mt. Mengam about 21 km NNW Wanuma, 1500 m (BPBM 5690, 5691, 5785, 5786); Adelbert Mtns., vic. of Hinihon, about 22 km NNW Wanuma, 1300 m (BPBM 5702); Adelbert Mtns., Mabimap, 1500 m (J. Menzies, personal commun.).

Remarks: In the years since its description by Wandolleck (1911) and redescription as *Sphenophryne klossi* by Boulenger (1914), *schlaginhaufeni* has rarely been collected or mentioned in the literature. Van Kampen (1923: 107) recognized *klossi* and placed *schlaginhaufeni* with question in the synonymy of *Sphenophryne macrorhyncha*. Nieden (1926: 46) also recognized *klossi* but referred *schlaginhaufeni* to the synonymy of *Sphenophryne basipalmata*, also with question. Parker (1934: 154) examined syntypes, resurrected *schlaginhaufeni* and synonymized *klossi*. Loveridge (1948: 421) misidentified two specimens of *Copiula* as *schlaginhaufeni* (see Zweifel, 1956: 19); Zweifel (1956: 18) did the same with the first specimen of *L. dentata*; Room (1974) confused *Cophixalus cheesmanae* with *schlaginhaufeni* (see above). A specimen utilized by Burton (1986) may be *L. rubra* rather than *schlaginhaufeni* (see account of *rubra*). Possibly the only correct attributions of new specimens in the literature are a passing mention of *schlaginhaufeni* from Mt. Hunstein in Zweifel (1967a: 6) and a citation of voucher specimens for a karyological study (Mahony et al., 1992).

Liophryne similis, new species

Figure 31G

Holotype: AMNH A130570 (field no. RZ 13518), collected by Richard G. Zweifel and Laurence T. Penny on August 10, 1987, at Myola Guest House, 2080 m, 7 km south, 6 km west of Mt. Bellamy, Northern Province, Papua New Guinea.[11]

PARATYPES: AMNH A130561–130565, A130567–130569, A130571–130578, A130580, A130581, UPNG 8274, collected at the type locality by Fred Parker, R. Zweifel, and L. Penny on Aug. 8–10, 1987; UPNG 7080–7082, collected by James I. Menzies at the type locality in March 1986.

ETYMOLOGY: The Latin adjective *similis* refers to the morphological resemblance of this species to *Liophryne rhododactyla*.

DIAGNOSIS: Morphologically identical to *Liophryne rhododactyla* except for the lack of vocal slits and sac in the adult male. The call is a series of rapidly repeated notes rather than the single note of *rhododactyla*.

DESCRIPTION OF HOLOTYPE: Adult male (calling when captured) with the following measurements and proportions: SVL 49.7, HW 19.3, TL 22.9, EY 5.1, EN 3.5, IN 5.2, TY 3.5, HD 12.0, FT 24.3, disc of third finger 1.55 (penultimate phalanx 1.1), disc of fourth toe 1.95 (1.25); HW/SVL 0.388, TL/SVL 0.461, EY/SVL 0.103, EN/SVL 0.070, IN/SVL 0.105, EN/IN 0.673, HD/SVL 0.241, FT/SVL 0.489, FD/SVL 0.031, TD/SVL 0.039.

Head slightly narrower than the somewhat flat-sided body. Snout bluntly pointed seen from above, rounded and slightly projecting in profile; nostrils lateral, scarcely visible from above, slightly closer to tip of snout than to eye; canthus rostralis relatively sharp, straight; loreal region nearly vertical, concave. Eyes moderately large, corneal outline visible from beneath, eyelid almost as wide as interorbital space. Tympanum distinct, relatively large, 69% of orbit, its diameter greater than distance from eye. Relative lengths of fingers $3 > 4 > 2 > 1$, first finger long, nearly equal to second, all fingers with rounded discs bearing terminal grooves, disc of first finger not enlarged, those of other fingers wider than penultimate phalanges; subarticular and metacarpal elevations moderately prominent, rounded. Toes unwebbed, relative lengths $4 > 3 > 5 > 2 > 1$, all with terminally grooved discs broader than those on fingers, that of first toe smallest but broader than penultimate phalanx; subarticular and inner metatarsal elevations moderately prominent, rounded. Skin fairly smooth except for indistinct, convergent scapular folds and narrow postocular fold passing across upper edge of tympanum, broadening into an elevated triangular area, narrowing again above front leg, and becoming obscure on midflank.

There are neither vocal slits nor (of course) a vocal sac.

In preservative, the dorsal surfaces of head and body are medium brown with faint, indefinite smaller spots. The front legs and hind legs are a deeper plumbeous shade, with pale spots prominent on the front legs and hands. The posterior thigh surface is colored like the dorsum of the body but is unmarked. A pale vertical line on the tip of the snout bifurcates, passing along the canthus rostralis and edge of eyelid and following the postorbital-dorsolateral fold. The line is obscure in places. The area below the pale line (loreal region, flanks) is darker brown, but the tympanum bears the paler dorsal shade. The lips are light spotted. The ventral surfaces of body and legs are brown with pale irregular spots, smallest on the chin.

VARIATION IN TYPE SERIES: The largest male in the series is 49.7 mm SVL. Because of the lack of vocal slits in this species, I cannot infer the size at male sexual maturity. The largest females are gravid at 51.9 and 49.0 mm, whereas one of 39.6 mm appears to be immature. Body proportions are summarized in table 6, and regression statistics are presented in table 7.

Inasmuch as the species is known only from a single locality, nothing can be said of geographic variation. Occasionally the scapular folds are more evident than in the holotype, and there are traces of short folds and tubercles on the back. The dorsolateral fold may extend almost to the groin.

Most specimens closely resemble the holotype in color and pattern. Exceptions include two specimens with more pale pigment on the snout and eyelids instead of its restriction to the canthal-dorsolateral line, one specimen that is much paler all over (above and below), one specimen with an asymmetrical dark area in the anterior dorsal region, and one specimen with a dark-edged dorsal region and a pale band above the dorsolateral fold. A midvertebral pale hairline is more ev-

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[11] See footnote 4 for location of Myola Guest House.

ident in living specimens. The colors in life are not greatly different from those of the preserved specimens except for their relatively greater brightness.

HABITAT AND HABITS: The habitat of *Liophryne similis* at Myola Guest House is heavily mossed forest (mapped by Paijmans, 1975, as Lower Montane Forest) bordering a grassy meadow (see Zweifel and Parker, 1989: fig. 7). We found most of our specimens by day beneath surface cover. One discovered at night was active on the surface of the leaf litter (see also under Call, below).

A male *L. similis* of 29 mm SVL (AMNH A130565, fig. 11) was associated with a group of 24 eggs (AMNH 130565) with capsular diameters of 6–7 mm and connected by peduncles of about the same length. Judged from the size at maturity of *L. rhododactyla*, a *similis* of this size would not be mature, so the association probably was fortuitous. However, the large clutch size and relatively large size of the eggs favors the identification of the eggs as those of *L. similis*, unless there is a large terrestrial microhylid present that we did not find.

ILLUSTRATIONS: Hand and foot, fig. 54C.

CALL: I recorded the call at the type locality in August 1987 (AMNH Herpetology tape reels 252 and 253). It is a series of 7–10 clear, moderately loud piping notes, each about 0.06 sec long delivered over the space of 0.75– 1.24 sec (fig. 77B). Notes are unpulsed and frequency is modulated, with an initial rapid rise of the dominant frequency from about 540–600 Hz to a peak of 680–720 Hz and then a lesser, slower descent. Four calls of the holotype recorded in the field at an air temperature of 12.8°C averaged 1.20 sec long (1.09–1.24) with a rate of 7.65 (7.6–7.7) notes per sec. Intervals of almost exactly 1 min separated the four calls. Another recording involved several frogs in a collecting bag, at least two of which called at 15.5°C. The anticipated correlations with higher temperature are confirmed in the data for these eight calls: shorter call length (mean 0.98, range 0.75–1.17 sec) and faster note repetition rate (mean 8.5, range 8.2–8.8 notes per sec). Only *L. similis* were in the bag, so there is no question of the association of species and call.

The holotype was calling from among the prop roots of a pandanus at about 2300 hours following an afternoon rain. It was on the surface, not hidden in the litter.

COMPARISONS WITH OTHER SPECIES: In all but the call and morphological features associated with vocalization, this species appears to be identical to *L. rhododactyla*. This is emphasized by the extreme closeness (identical means in two instances) of the various morphological ratios of adults (table 6), and by the similarity of ontogenetic trends revealed by the regressions (table 7). In addition to the clearcut character of the presence or absence of vocal sac and slits, there may be a specific difference in the size of the tympanum of adults. Regression lines for tympanum diameter relative to snout–vent length diverge notably, with *similis* having the larger tympanum. There is broad overlap in tympanum size, however, and the sample is not adequate for determining a possible influence of sexual dimorphism.

Juvenile *L. similis* may be confused with the much smaller, sympatric *Austrochaperina brevipes*, as is discussed in the account of that species.

DISTRIBUTION: Known only from the type locality (fig. 34). See Holotype and Paratypes for details.

REMARKS: Evidence provided by the calls strongly indicates that *L. rhododactyla* and *L. similis* are different species, their close morphological similarity notwithstanding. Differences between the calls may be explained by (1) functionally different calls (e.g., territorial and mate-attracting) that were recorded for the same species, or (2) the samples represent sibling species. With respect to the first possibility, I heard the sort of call recorded at Myola on several nights and did not hear the other call there. Allen Allison has had much field experience with *L. rhododactyla*, and reported to me (personal commun.), ‘‘I have never heard anything else from this species and have heard this species calling practically every time that I visited Bulldog Road.’’ He listened to a playback of the *similis* call and assured me that he had not heard that call before. This information, coupled with the single morphological difference (vocal slits and sac present in *rhododactyla*, absent in *similis*) leads me to conclude that two species should be recognized.

The type locality of *Liophryne rhododactyla*, Mt. Victoria, is much closer to Myola Guest House (38 km) than to the region southeast of Wau (about 190 km) where recordings of *rhododactyla* were made. Presumably at least three disjunct populations are involved (fig. 34)—two of *rhododactyla* and one of *similis*. On the basis of proximity, one might expect the frogs at Mt. Victoria and Myola to represent the same species, with the disjunct northern population near Wau requiring a new name. Countering this interpretation is the morphological evidence of the vocal sac apparatus, intimately associated with the difference in calls. Verification of the call of *rhododactyla* at the type locality is much desired.

A striking, parallel geographic situation exists in the microhylid genus *Aphantophryne* (Zweifel and Parker, 1989). This genus has the same basic distribution as *L. rhododactyla* and *L. similis*—high elevations near Wau and in the Owen Stanley Mountains. *Aphantophryne pansa* occurs with *L. rhododactyla* near Wau and both inhabit high elevations in the central Owen Stanley Range. At Myola Guest House, *Aphantophryne sabini*, a sibling of *A. pansa* distinguished mainly by its call, occurs with *L. similis*.

Genus *Oxydactyla* van Kampen

Oxydactyla van Kampen, 1913: 464. Type species (by monotypy) *Oxydactyla brevicrus* van Kampen, 1913: 465.
Sphenophryne: Parker, 1934: 152 (*Oxydactyla* referred to synonymy of *Sphenophryne*).

CONTENT: Five species: *Oxydactyla alpestris*, new species; *Oxydactyla brevicrus* van Kampen; *Oxydactyla coggeri*, new species; *Oxydactyla crassa* (Zweifel); *Oxydactyla stenodactyla*, new species.

DIAGNOSIS: A genus of genyophrynine microhylid frogs (sensu Zweifel, 1971, and Burton, 1986) with the following combination of morphological characters: clavicles long and slender, reaching from scapula almost to midline of pectoral girdle; legs short, maximum TL/SVL = 0.395; tips of fingers narrow and rounded, or, if slightly flattened, not disclike and with terminal grooves lacking or only weakly indicated on fingers 2–4.

MORPHOLOGY: These are small, short-legged frogs, with a maximum known SVL of 32 mm and mature males as small as 19 mm SVL in one species. Mean TL/SVL ratios range from 0.294 to 0.366, a range that excludes almost all other species with the primitive pectoral girdle. The situation with respect to small foot size is similar: mean FT/SVL 0.338–0.399, with just one other species having a mean in this range. The hands are small, with the range of means HD/SVL (0.199–0.213) falling within the lower 30% of the total range for all genyophrynine species with the primitive pectoral girdle. The fingertips show little or no trace of the expanded, flattened discs with prominent terminal grooves seen in other species with the primitive pectoral girdle. The species pair *alpestris* + *stenodactyla* has the most derived condition, with no trace of fleshy expansion or grooving (fig. 49) and with the underlying terminal phalanges having slightly constricted tips much narrower than the base of the bone (fig. 71A, B). In other species of *Oxydactyla* the tips may be slightly flattened but with no more than a faint terminal groove on fingers 2–4, and the terminal phalanges (where known) are bluntly T-shaped with the tip not or scarcely wider than the base (fig. 71C, D). The toe tips of *alpestris* and *stenodactyla* resemble those of the fingers externally, although the terminal phalanges have slightly more of a T shape. Toe tips in the other *Oxydactyla* are less extremely modified from the common slightly expanded disc with T-shaped phalanges. The tympanic annulus is not well defined externally, but the ear is not notably reduced in size. Mean eye size is small to moderate (EY/SVL 0.093–0.117). These frogs have the morphology commonly associated with cryptic, terrestrial habits, which fits well with what is known of their ecology. See table 10 for body proportions of the species and table 11 for regression statistics.

DISTRIBUTION: The genus is montane and confined to high elevations, with records ranging from 1800 to 4000 m. One species is in the central ranges of Irian Jaya, three in the highlands of Papua New Guinea, and one far to the southeast on the eastern tail of Papua New Guinea.

KEY TO *OXYDACTYLA*

1. Tips of fingers *and* toes narrow, rounded, not flattened (fig. 53A, B) 2
   Fingertips as above, or slightly flattened, terminal grooves absent or weak; tips of toes flattened or disclike 3
2. EY/SVL ≤ 0.105 and TL/SVL usually <0.31 (fig. 46) . . . . *stenodactyla*
   EY/SVL ≥ 0.105 and TL/SVL ≥ 0.31 . . . . *alpestris*
3. Toe tips flattened but not distinctly disclike, lacking terminal grooves . . . . . . *brevicrus*
   Toe tips disclike with terminal grooves . . . 4
4. IN/SVL < 0.100 and EY/SVL ≥ 0.110 (fig. 40) . . . . *coggeri*
   IN/SVL ≥ 0.100 and EY/SVL ≤ 0.110 . . . . *crassa*

Oxydactyla alpestris, new species

Figure 39

Sphenophryne brevicrus: Zweifel, 1956: 10 (part, specimens from Mt. Hagen). Tyler, 1963: 18 (part?).

HOLOTYPE: AMNH A76584 (field no. Fred Parker 293), collected on April 17, 1965, by Fred Parker at Gomgale Pass, elevation about 2400 m, approximately 17 km south and 15 km west of Kundiawa, Simbu Province, Papua New Guinea.

PARATYPES: All from Papua New Guinea. Eastern Highlands Prov.: AMNH A76585, MCZ A59653–59663, collected by Fred Parker, Oct. 3, 1965, at Daulo Pass, 2480 m, 5 km N, 18 km W Goroka; AMNH A66240, A66335, collected on the Sixth Archbold Expedition, Aug. 7–9, 1959, at Kotuni, S slope Mt. Otto, 2100–2440 m; MCZ A59616, collected by Fred Parker, Feb. 21, 1966, at Kotuni, 1800 m. Simbu Prov.: MCZ A59667–59673, collected by Fred Parker, Apr. 17, 1965, at Gomgale Pass, 2400 m, 17 km S, 15 km W Kundiawa; AMNH A76582, A76583, and MCZ A59626–59647, collected by Fred Parker, Mar. 29, 1965, at Sikuri Pass, 4 km S, 13 km E Kundiawa; MCZ A68349, collected by Fred Parker, June 4, 1967, at Tuna Pass, 2600 m; MCZ A59617–59625, 64294, 64295, collected by Fred Parker, Nov. 30, 1965, and Aug. 21, 1967, at Dumun, 2300–2400 m, 6 km S, 8 km E Kundiawa; MCZ A59649–59652, collected by Fred Parker, Jan. 1, 1965, at Masul, 8 km S, 10 km E Kundiawa; MCZ A59648, collected by Fred Parker, Sept. 26, 1965, at Mintima, 4 km N, 6 km W Kundiawa; MCZ A59674–59681, collected by Fred Parker, Nov. 15, 1965, at Derim, Kwi Valley; MCZ A59682–59695, collected by Fred Parker, Nov. 26, 1965, at Agakamatasa; MCZ A59664–59666, collected by Fred Parker, July 28, 1965, on the southern slope of Mt. Kerigomna, 2590–2890 m; MCZ A80001, 80002, collected by Fred Parker, Nov. 13, l965, on the southwest slope of Mt. Kerigomna, 2590 m. Western Highlands Prov.: AMNH A65304–65308, collected on the Spalding–Peterson Expedition, Aug. 10, 1959, on the Wahgi Dividing Range near Nondugl, 2440 m; AMNH A65281–65301, 65303, collected on the Spalding–Peterson Expedition, Aug. 6, 1959, on Mt. Pollam, Wahgi Dividing Range near Nondugl, 2490 and 2740 m; AMNH A56272, A58171–58174, collected by E. T. Gilliard in 1950 or 1952 on Mt. Hagen, 2440 m; BPBM 3008, 3014, 3305, collected by J. Sedlacek, May 24, 1963, and MCZ A64088–64097, collected by Fred Parker, Mar. 24, 1967, at Tomba, 2450 m, 3 km N, 23 km W Mt. Hagen town.

ETYMOLOGY: The specific name, a Latin adjective meaning ‘‘living in high mountains,’’ is appropriate for this species.

DIAGNOSIS: Differs from other *Oxydactyla* except *O. stenodactyla* in that the toe tips as well as fingertips are rounded, not expanded or flattened, and lack terminal grooves. The eyes of *alpestris* are relatively larger and the legs relatively longer than those of *stenodactyla* (see Comparisons).

DESCRIPTION OF HOLOTYPE: Adult female (ova up to 2 mm in diameter) with the following measurements and proportions: SVL 22.7, HW 8.6, TL 8.2, EY 2.6, EN 1.4, IN 2.2, TY, 1.1, HD 4.8, FT 8.8; TL/SVL 0.361, HW/SVL 0.379, EY/SVL 0.114, EN/SVL 0.062, EN/IN 0.636, IN/SVL 0.097, HD/SVL 0.211, FT/SVL 0.388.

A stout, short-legged frog, body wider than head; snout rounded in dorsal aspect, slightly more flattened in profile and scarcely projecting beyond the mouth; nostrils easily visible from above, closer to end of snout than to eye, appearing nearly terminal in pro-

TABLE 10
Body Proportions in *Oxydactyla*

Sample	Mean ± σ_m	Range	N	Mean ± σ_m	Range	N
	TL/SVL			HW/SVL		
alpestris[a]	0.326 ± 0.003	0.304–0.348	14	0.376 ± 0.003	0.360–0.395	14
alpestris[b]	0.326 ± 0.003	0.307–0.361	23	0.365 ± 0.002	0.337–0.379	23
alpestris[c]	0.339 ± 0.004	0.309–0.373	17	0.354 ± 0.004	0.330–0.382	17
brevicrus	0.347 ± 0.007	0.317–0.375	7	0.385 ± 0.007	0.364–0.417	7
coggeri	0.366 ± 0.003	0.330–0.395	35	0.394 ± 0.002	0.364–0.422	35
crassa	0.361 ± 0.004	0.336–0.380	12	0.394 ± 0.006	0.346–0.426	12
stenodactyla[d]	0.299 ± 0.003	0.265–0.337	25	0.362 ± 0.004	0.333–0.408	25
stenodactyla[e]	0.288 ± 0.003	0.268–0.311	24	0.368 ± 0.002	0.347–0.392	24
stenodactyla[a]	0.295 ± 0.006	0.285–0.320	5	0.347 ± 0.007	0.326–0.366	5
	HD/SVL			FT/SVL		
alpestris[a]	0.200 ± 0.002	0.192–0.212	14	0.362 ± 0.004	0.333–0.383	14
alpestris[b]	0.199 ± 0.002	0.185–0.214	23	0.365 ± 0.003	0.337–0.395	23
alpestris[c]	0.206 ± 0.003	0.191–0.230	17	0.367 ± 0.005	0.342–0.402	17
brevicrus	0.213 ± 0.006	0.200–0.239	6	0.369 ± 0.012	0.327–0.398	6
coggeri	0.202 ± 0.002	0.181–0.224	35	0.388 ± 0.003	0.350–0.431	35
crassa	0.210 ± 0.003	0.192–0.224	12	0.399 ± 0.005	0.362–0.420	12
stenodactyla[d]	0.213 ± 0.002	0.196–0.233	25	0.350 ± 0.004	0.312–0.384	25
stenodactyla[e]	0.206 ± 0.003	0.171–0.231	24	0.327 ± 0.004	0.289–0.354	24
stenodactyla[a]	0.209 ± 0.003	0.199–0.214	5	0.340 ± 0.002	0.335–0.345	5
	EY/SVL			EN/IN		
alpestris[a]	0.108 ± 0.001	0.100–0.114	14	0.759 ± 0.014	0.674–0.878	14
alpestris[b]	0.110 ± 0.001	0.103–0.115	23	0.719 ± 0.010	0.636–0.818	23
alpestris[c]	0.110 ± 0.001	0.097–0.118	17	0.727 ± 0.007	0.694–0.796	17
brevicrus	0.116 ± 0.004	0.102–0.128	7	0.750 ± 0.024	0.667–0.864	7
coggeri	0.117 ± 0.001	0.110–0.127	35	0.784 ± 0.006	0.727–0.878	35
crassa	0.109 ± 0.002	0.100–0.127	12	0.722 ± 0.014	0.667–0.808	12
stenodactyla[d]	0.094 ± 0.001	0.083–0.103	25	0.698 ± 0.015	0.560–0.857	25
stenodactyla[e]	0.091 ± 0.001	0.080–0.105	24	0.776 ± 0.011	0.682–0.895	24
stenodactyla[a]	0.090 ± 0.003	0.082–0.097	5	0.701 ± 0.014	0.653–0.731	5
	EN/SVL			IN/SVL		
alpestris[a]	0.069 ± 0.001	0.061–0.078	14	0.091 ± 0.001	0.084–0.094	14
alpestris[b]	0.066 ± 0.001	0.061–0.073	23	0.092 ± 0.001	0.084–0.099	23
alpestris[c]	0.067 ± 0.001	0.061–0.071	17	0.093 ± 0.001	0.084–0.100	17
brevicrus	0.070 ± 0.002	0.064–0.076	7	0.093 ± 0.002	0.088–0.099	7
coggeri	0.072 ± 0.001	0.063–0.081	35	0.092 ± 0.001	0.083–0.098	35
crassa	0.077 ± 0.001	0.071–0.089	12	0.107 ± 0.002	0.098–0.116	12
stenodactyla[d]	0.057 ± 0.001	0.051–0.064	25	0.083 ± 0.001	0.069–0.094	25
stenodactyla[e]	0.061 ± 0.001	0.054–0.067	24	0.078 ± 0.001	0.065–0.085	24
stenodactyla[a]	0.059 ± 0.002	0.053–0.062	5	0.084 ± 0.002	0.075–0.089	5
	FD/SVL			TD/SVL		
coggeri	0.021 ± 0.0004	0.016–0.025	33	0.031 ± 0.0006	0.023–0.036	34
crassa	0.021 ± 0.0007	0.018–0.025	11	0.029 ± 0.0007	0.026–0.033	11

[a] Wahgi Dividing Range, Western Highlands Prov., PNG.

[b] Porol Ranges, Simbu Prov., PNG.

[c] Tomba and Mt. Hagen, Western Highlands Prov., PNG.

[d] Mt. Wilhelm, Simbu Prov., PNG.

[e] Mt. Otto, Eastern Highlands Prov., PNG.

TABLE 11

Regression Statistics for Eight Samples of *Oxydactyla*[a]

	α	β	r	N	α	β	r	N	α	β	r	N	α	β	r	N	α	β	r	N
	TL/SVL				HW/SVL				HD/SVL				FT/SVL				EY/SVL			
alpestris[b]	0.933	0.670	0.923	27	0.580	0.863	0.966	27	0.307	0.868	0.965	27	1.032	0.673	0.941	27	0.325	0.652	0.921	27 0
alpestris[c]	0.767	0.720	0.970	41	0.482	0.912	0.983	41	0.322	0.848	0.964	41	0.730	0.782	0.968	41	0.280	0.704	0.947	41
alpestris[d]	1.411	0.522	0.915	18	0.530	0.874	0.920	18	0.778	0.586	0.849	18	1.176	0.636	0.901	18	0.198	0.814	0.897	18
brevicrus	0.429	0.934	0.960	9	0.557	0.886	0.969	9	0.020	1.724	0.780	6	0.080	1.478	0.786	6	0.236	0.780	0.928	9
coggeri	0.761	0.768	0.956	43	0.411	0.987	0.980	43	0.362	0.815	0.938	43	0.655	0.834	0.960	43	0.234	0.780	0.957	43
crassa	0.738	0.784	0.803	12	1.653	0.564	0.571	12	0.189	1.031	0.801	12	0.414	0.989	0.812	12	0.531	0.519	0.526	12
stenodactyla[e]	0.703	0.744	0.972	54	0.800	0.763	0.959	54	0.286	0.910	0.973	54	0.616	0.830	0.950	54	0.303	0.650	0.946	54
stenodactyla[f]	0.547	0.808	0.980	51	0.580	0.865	0.987	51	0.312	0.877	0.961	51	0.522	0.861	0.960	51	0.343	0.602	0.912	51
	EN/SVL				IN/SVL				FD/SVL				TD/SVL							
alpestris[b]	0.099	0.884	0.905	27	0.368	0.560	0.944	27	—	—	—	—	—	—	—	—				
alpestris[c]	0.120	0.812	0.959	41	0.188	0.773	0.953	41	—	—	—	—	—	—	—	—				
alpestris[d]	0.115	0.831	0.944	18	0.203	0.756	0.939	18	—	—	—	—	—	—	—	—				
brevicrus	0.024	1.332	0.959	8	0.128	0.901	0.962	8	—	—	—	—	—	—	—	—				
coggeri	0.116	0.847	0.937	43	0.183	0.781	0.955	43	0.019	1.043	0.862	40	0.024	1.078	0.833	40				
crassa	0.363	0.531	0.552	12	0.251	0.742	0.660	12	0.003	1.556	0.715	11	0.006	1.469	0.844	11				
stenodactyla[e]	0.159	0.697	0.947	54	0.282	0.632	0.881	54	—	—	—	—	—	—	—	—				
stenodactyla[f]	0.142	0.745	0.958	51	0.259	0.639	0.946	51	—	—	—	—	—	—	—	—				

[a] Power curves of the form $Y = \alpha X^{\beta}$.

[b] Wahgi Dividing Range, Western Highlands Prov., PNG.

[c] Simbu Prov., PNG.

[d] Tomba and Mt. Hagen, Western Highlands Prov., PNG.

[e] Mt. Wilhelm, Simbu Prov., PNG.

[f] Mt. Otto, Eastern Highlands Prov., PNG.

Fig. 39. Holotype of *Oxydactyla alpestris*, AMNH A76584, SVL 22.7 mm.

file; canthus rostralis rounded, loreal region sloping, flat; eyes relatively large, corneal margin barely visible from beneath, interorbital space about 1.5× width of an upper eyelid; tympanic annulus indistinct, tympanum separated from posterior corner of eye by about its own diameter. Relative lengths of fingers 3 > 2 = 4 > 1, first well developed, more than half length of second, tips narrow, rounded, not flattened, no trace of terminal groove (fig. 53B); subarticular elevations virtually nonexistent, inner and middle metacarpal elevations indistinct, low and rounded. Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, first small, less than half length of second, tips and subarticular elevations as on hands, inner metatarsal elevation small, low, rounded, no outer elevation. Body surfaces smooth dorsally and ventrally; no skin folds or wartiness.

The dorsal ground color is medium brown. The side of the head and the eyelids are darker, almost black, with a few light flecks on the upper lips. A dark brown streak begins behind the eye, broadens as it passes above and behind the tympanum, and fades into the ground color as it extends diagonally down the midflank region. The upper edge of this streak is clearly defined only anteriorly. The middorsal region shows only a few obscure hints of darker markings. The upper surfaces of the limbs are similar but with markings more obvious, especially on the arms. The immediate region of the cloacal opening is pale, surrounded by a black ring. The anterior surfaces of the thighs are brown with indistinct lighter spots; the posterior surfaces have a pale tan ground color mostly obscured by darker pigment in no definite pattern. The ground color of the undersides is pale tan. The border of the lower jaw is dark with a few light spots. Irregular clumps of dark pigment on the throat and chest are less dense on the abdomen but again dominant on the undersides of the hind legs. The sole is dark with a few light flecks.

VARIATION IN TYPE SERIES: The largest specimens are two females from Tomba measuring 27.8 mm SVL. The largest males are two from Agakamatasa measuring 26.6 and 26.9 mm. Both males and females are unusually large in comparison with frogs from other samples, where the largest male is 24.7 mm and females rarely attain 26 mm. Females mature at about 20 mm. See table 10 for variation in body proportions and table 11 for regression data.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71B; premaxilla, fig. 63B; sacral region, fig. 72B; vomer, fig. 65B; hand and foot, fig. 53B.

CALL: The call has not been described.

COMPARISONS WITH OTHER SPECIES: The species with which *O. alpestris* is most likely to be confused are *O. coggeri* and *O. stenodactyla*. Known localities for *alpestris* are remote from those for *coggeri*, but if the species should be found together (for example, in eastern Enga Province), the presence of grooved, disclike toe tips in *coggeri* provides adequate distinction.

The habitat of *stenodactyla* appears to be generally at higher elevations than that of *alpestris*, but the two species evidently occur together on the Sepik-Wahgi Dividing Range. Although there is overlap between the two species in ranges of all the standard ratios (table 10), the means are well separated, and combining two ratios (TL/SVL and EY/SVL) achieves a nearly complete division (fig. 46). Specimens of *stenodactyla* from the sympatric sample fall within the area of the *stenodactyla* sample in figure 22.

HABITAT AND HABITS: Tyler (1963), in reporting studies made on the Sepik-Wahgi Dividing Range, published the only information that may pertain to *alpestris* (as *Sphenophryne brevicrus*). Both *alpestris* and *stenodactyla* occur in the region where Tyler worked, but judged from the range of elevations cited (specimens taken on saturated ground beneath moss at 1800–2400 m), his observations on habitat, reproduction (egg-brooding observed, but adult sex not noted), and food habits (one found eating an earthworm) most likely apply to *alpestris*.

DISTRIBUTION: *Oxydactyla alpestris* occurs at elevations of 1800–2740 m in Western Highlands, Simbu, and Eastern Highlands Provinces of Papua New Guinea (fig. 41). The known range spans 160 km from Mt. Hagen east to Mt. Otto, although large areas—most notably the entire Kubor Range—are as yet unrepresented by specimens. See Holotype and Paratypes for localities and specimens examined.

Oxydactyla brevicrus van Kampen

Oxydactyla brevicrus van Kampen, 1913: 465 (type localities ''Hellwig-Gebirge, ± 2500 m . . . . [and] Wichmann-Gebirge, ± 3000 m.''; lectotype ZMA 5714 from the Hellwig Mountains designated by Daan and Hillenius [1966], collected by H. A. Lorentz in October 1909).

Sphenophryne brevicrus: Parker, 1934: 158 (first use of combination). Zweifel, 1956: 10 (part).

TYPE LOCALITIES: The type localities are in the central mountainous region of Irian Jaya, south-southeast of Peak Trikora (Mt. Wilhelmena) at about 4°20′35″S, 138°20′35″E (Wichmann) and 4°30′10″S, 138°40′10″E (Hellwig). The choice of the lectotype was dictated by its being the individual illustrated by van Kampen as well as being the only adult in the type series.

DIAGNOSIS: Differs from its congeners in that the tips of the toes are somewhat flattened rather than narrow and rounded, but not disclike with terminal grooves.

MORPHOLOGY: A rather chunky bodied, relatively short-legged frog. Head slightly narrower than body. Snout rounded as seen from above and in profile; nostrils readily visible from above, slightly closer to tip of snout than to eyes; loreal region a gentle slope, almost flat; canthus rostralis rounded, not distinct. Eyes large, corneal outline just visible from beneath, eyelid about 80% of interorbital span. Tympanum almost completely hidden. Relative lengths of fingers, 3 > 2 = 4 > 1 (or 4 > 2), first more than one-half length of second; tips rounded, not disclike, third finger with possibly a trace of a terminal groove (fig. 53C); subarticular elevations very low, rounded. Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, tips somewhat flattened but not distinctly disclike, not expanded, no distinct terminal grooves (fig. 53C); subarticular elevations scarcely evident, inner metatarsal elevation elongate, low and rounded. A weak postorbital-supratympanic fold, skin otherwise smooth dorsally and ventrally.

COLOR AND PATTERN: The dorsal ground color in preservative is tan. A narrow dark brown canthal line continues postorbitally, broadening on the flank, but there it is almost lost in an abundance of irregular brown spots. Such spots are present middorsally, on the flanks, the head and facial region, and legs. They are largest on the back and legs. The posterior of the thigh bears small, irregular dark spots, some of which run together, on a pale tan background. The lower jaw is edged with a band of brown, irregular on its inner margin, whereas the rest of the chin is pale with a few small darker spots. The chest and abdomen are pale with irregular, indistinct spotting, not greatly different from the chin.

The preceding account of morphology and color pattern describes the best preserved specimen (MZB 448). Several of the remaining specimens available to me are somewhat desiccated, so the character of the digital tips cannot adequately be assessed. However, one specimen in reasonably good condition has the digits as described above, and the original description stressed the lack of adhesive discs. The described specimen is the most boldly marked one examined. The others are more like the illustration in the original description (van Kampen, 1913, pl. 11, fig. 8), with dark facial region and flanks, and the dorsum only obscurely marked.

VARIATION IN SIZE AND PROPORTIONS: Females evidently mature at about 24–25 mm SV, and the largest specimen is a female of 27.2 mm. A male measures 24.2 mm; I have not determined the size at maturity. See table

10 for statistics on proportions and table 11 for regression data.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71C; hand and foot, fig. 53C.

CALL: The call is unknown.

COMPARISONS WITH OTHER SPECIES: *Oxydactyla brevicrus* has been confused with high montane species of Papua New Guinea that have either less (*alpestris, stenodactyla*) or greater (*coggeri*) development of toe discs. The only somewhat similar species known in the mountains of Irian Jaya is *Austrochaperina kosarek*, which has well-developed toe discs and longer legs (TL/SVL = 0.409).

HABITAT AND HABITS: There is nothing specific published concerning this species. Archbold et al. (1942: 258–266) described in detail the region in which the AMNH specimens were collected, an area of steep mountain slopes and valleys, with tall forests where not disrupted by native agricultural practices.

DISTRIBUTION: *Oxydactyla brevicrus* is known from elevations of 2200–3000 m in a restricted region of the central dividing range of Irian Jaya (fig. 10). Published records for *brevicrus* 600 km or more to the east in Papua New Guinea are based on other species (see *O. coggeri*, *O. alpestris*, and *O. stenodactyla*).

LOCALITY RECORDS AND SPECIMENS EXAMINED: IRIAN JAYA: Hellwig Mtns., 2500 m (ZMA 5714, lectotype); Wichmann Mtns., 3000 m (ZMA 5715, 5716, lectoparatypes); 9 km NE Lake Habbema, 2800 m (AMNH A43696, A43698); Bele River, 2200 m, 18 km N Lake Habbema (AMNH A43761–43763); Doorman River, ca. 2400 m (MZB 448, one of several specimens under this number, the remainder are *Oreophryne* sp.).

Oxydactyla coggeri, new species

Sphenophryne brevicrus: Bulmer and Tyler, 1968: 342. Menzies and Tyler, 1977: 457.

HOLOTYPE: AMS R22851, obtained by Papuan collectors for Harold G. Cogger in the vicinity of Fungoi, Kaironk Valley, 2000 m elevation, about 3 km north, 6 km west of Simbai, Madang Province, Papua New Guinea, between Dec. 15, 1963, and Jan. 2, 1964.

PARATYPES: All specimens from Papua New Guinea. Madang Prov.: AMNH A140871–140874 (the last C&S), same data as holotype; AMS R22647, R22815–22817, 22819–22821, 22823–22837, 22839–22850, R22852–22857, R22860, R22861, R22863–22880, R23121, R23182–23184, R23207, same data as holotype; AMS 32116–23118, Bismarck Range, 2200 m, north of Fungoi, collected by H. G. Cogger, Dec. 28, 1963; UPNG 837, 838, collected by J. Menzies, Aug. 30, 1969 at Kaironk, Schrader Range, 2300 m. Southern Highlands Prov.: UPNG 5559, collected by J. Menzies, July 9, 1976, at 16 km north of Mendi, 2400 m.

ETYMOLOGY: This species is named for Dr. Harold Cogger of the Australian Museum in recognition of his important contributions to Australasian herpetology, among them collecting the initial specimens of the species.

DIAGNOSIS: Distinguished from other *Oxydactyla* except *O. crassa* in that the fingertips are rounded to slightly flattened but not clearly disclike, and the toe tips are disclike with terminal grooves but not or scarcely broader than the penultimate phalanges. The vocalizations of *crassa* and *coggeri* differ, the former having a single-note call, the latter a call of similar quality but with several notes uttered in rapid succession. See Comparisons for other morphological differences.

DESCRIPTION OF HOLOTYPE: Adult male (vocal slits present) with the following measurements and proportions: SVL 23.5, HW 9.4, TL 8.4, EY 2.65, EN 1.65, IN 2.2, HD 4.6, FT 8.6, tip of third finger 0.55 (penultimate phalanx 0.525), disc of fourth toe 0.7 (0.65); HW/SVL 0.400, TL/SVL 0.357, EY/SVL 0.113, EN/SVL 0.070, IN/SVL 0.094, EN/IN 0.750, HD/SVL 0.196, FT/SVL 0.366, third finger tip/SVL 0.023, fourth toe disc/SVL 0.030

Head slightly narrower than body. Snout rounded viewed from above, rounded and scarcely projecting in lateral view; nostrils visible from above; loreal region a flat, gentle slope, canthus rostralis not well defined. Eyes relatively large, corneal outline visible in ventral view, eyelid almost as wide as interorbital space. Tympanic annulus inconspicuous. Relative lengths of fingers $3 > 4 > 2 > 1$, first about one-half length of second; tips of fingers rounded to slightly flattened, not clearly disclike, minutely broader than penultimate phalanges, only third with faint terminal groove (fig. 53D); subarticular and metacarpal elevations low, rounded, inconspicuous. Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, first short, its tip barely reaching to subarticular elevation of second; tips of second to fourth flattened with terminal grooves but little or no wider than penultimate phalanges, first and fifth less flattened, fifth sometimes weakly grooved (fig. 53D); subarticular elevations low, rounded, inner metatarsal elevation low, elongate, rounded. Dorsal region with many small, inconspicuous tubercles but no folds; a weak postocular-supratympanic fold curving downward behind ear; venter smooth.

The color in preservative is various shades of brown. The facial region is purple-brown, being more concentrated in the canthal area. The area behind the eye is dark, bordered above on a diagonal line directed to the insertion of the arm. A dark postocular streak extends posterior from the eye as a dark band passing above the foreleg and then discontinuously to the groin. The region beneath this band is vaguely mottled brown, paler than the postocular streak. A pale vertebral hairline passes from the snout to just anterior to the cloaca, where it divides and runs along the rear of the thigh and weakly onto the shank. On the back, a narrow streak of dark brown borders the hairline and is in turn bordered by a wider swath of lighter brown, slightly darker than the side of the body below the dark dorsolateral streak. A prominent black spot lies just anterior to the cloaca. The upper sides of the legs are brown with darker spotting, and the back of the thigh below the light line is indistinctly mottled dark and light brown. The chin and chest bear dense, even melanic stippling, which gives way abruptly on the abdomen to a sparser stipple, often with scattered dark spots.

VARIATION IN TYPE SERIES: See table 10 for variation in proportions and table 11 for regression data. The largest specimen is a female, 28.2 mm SVL. The size of females at maturity is about 20–21 mm, as three frogs 19.3–20.6 mm appear to be immature, whereas two at 20.6 mm are gravid. The range in size of mature males (vocal slits present) is 19.0–26.7 mm SVL.

The back may be unicolor, may have small dark spots, and may have, as does the holotype, a light, midvertebral hairline. Nearly half the specimens tabulated (15 of 38) show at least a trace of the vertebral hairline, which is not always as well developed as described for the holotype.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71D; premaxilla, fig. 63C; sacral region, fig. 72C; vomer, fig. 65C; skull, fig. 67B; hand and foot, fig. 53D.

CALL: James I. Menzies recorded this species at an elevation of 2300 m at Kaironk where the frog (UPNG 837) called from the leaf litter at noon. The two recorded calls each have 11 pure-toned, unpulsed musical notes given over about 2.3 sec at a rate 4.4–4.5 notes per second (fig. 78B). Notes are 0.04–0.05 sec long and are slightly frequency modulated, dropping about 50 Hz from an initial 900 Hz. Menzies and Tyler (1977) published an audiospectrogram of part of one of these calls in connection with a discussion of vocalization of burrowing microhylids.

COMPARISONS WITH OTHER SPECIES: *Oxydactyla coggeri* is distinguished from the other species of *Oxydactyla* known in the same general area of New Guinea—*alpestris* and *stenodactyla*—in possessing toe discs. Similar in morphology, although widely separated geographically, *coggeri* and *crassa* differ in advertisement calls and sufficiently in certain proportions to permit correct assignment of a large majority of specimens in a mixed sample without reference to geography (fig. 40).

HABITAT AND HABITS: Dr. Harold Cogger (personal commun.) reported finding this species under logs at 2200 m just inside primary rainforest (above grassland).

DISTRIBUTION: *Oxydactyla coggeri* is known only from two regions. All but one specimen came from the Kaironk Valley–Schrader Mountains area of Madang Province, Papua New Guinea, at the northern edge of the highlands region. A single specimen is from near Mendi, Southern Highlands Province, 120 km to the southwest. Possibly the species may have an extensive range in Enga Province, west of the Schrader Range and north of Mendi, where there has been little collecting (fig. 41). See Holotype and Paratypes for localities and specimens examined.

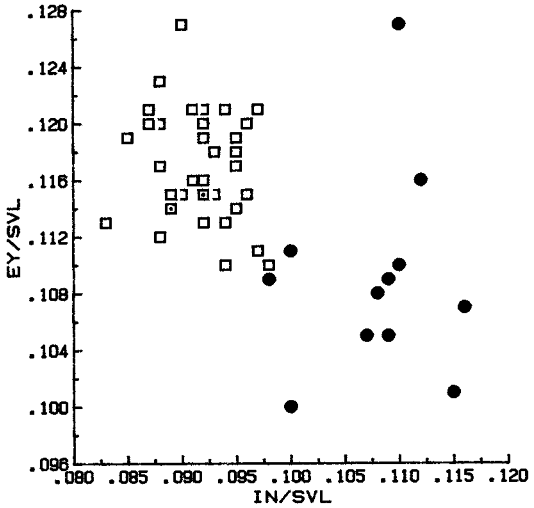

Fig. 40. Comparison of relative eye size and internarial span in *Oxydactyla crassa* (circles) and *O. coggeri* (squares). Adult individuals only plotted; symbols enclosing dots represent two specimens with identical ratios.

Oxydactyla crassa (Zweifel), new combination

Sphenophryne crassa Zweifel, 1956: 11 (type locality, "north slope of Mt. Dayman, Maneau Range, Territory of Papua [Milne Bay Province, Papua New Guinea], at an elevation of 2230 meters"; holotype, AMNH A56803, collected by G. M. Tate on the Fourth Archbold Expedition to New Guinea, May 25, 1953).

DIAGNOSIS: Distinguished from other *Oxydactyla* (except *O. coggeri*) in that the fingertips are rounded to slightly flattened but not clearly disclike and the toe tips are disclike with terminal grooves but not (or scarcely) broader than the penultimate phalanges. Differs from *coggeri* in the advertisement call (see diagnosis of *coggeri*) and in certain proportions (see Comparisons with Other Species).

MORPHOLOGY: The holotype, a female with ova 3 mm in diameter, is described in Zweifel (1956); its measurements and proportions

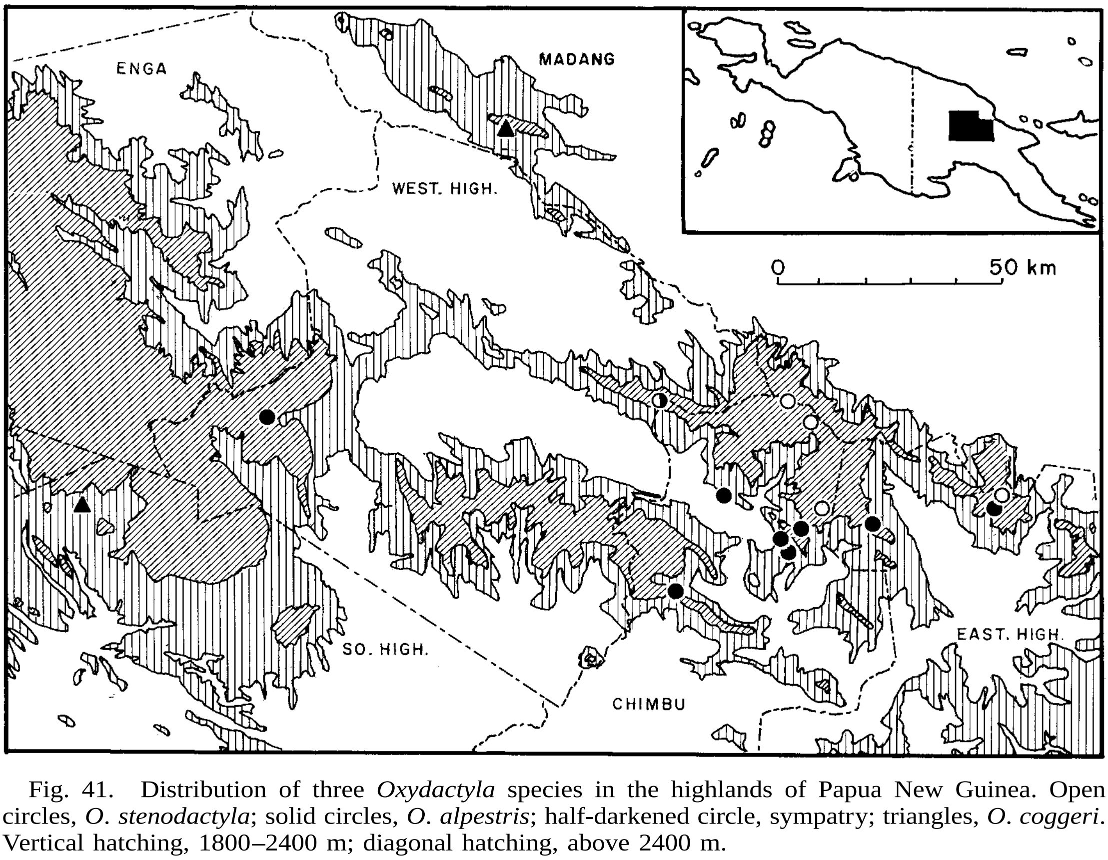

Fig. 41. Distribution of three *Oxydactyla* species in the highlands of Papua New Guinea. Open circles, *O. stenodactyla*; solid circles, *O. alpestris*; half-darkened circle, sympatry; triangles, *O. coggeri*. Vertical hatching, 1800–2400 m; diagonal hatching, above 2400 m.

are: SVL 28.6, HW 10.7, TL 9.6, EY 3.0, EN 2.2, IN, 2.9, HD 5.5, FT 10.6, FD of 0.6, TD 0.8; TL/SVL O.336, HW/SVL 0.374, HD/SVL 0.210, FT/SVL 0.399, EY/SVL 0.105, EN/SVL 0.077, IN/SVL 0.107, EN/IN 0.722, FD/SVL 0.021, TD/SVL 0.029.

This is a small (up to 30 mm), chunky, short-legged species. Snout bluntly pointed as seen from above, rounded and projecting slightly in profile; nostrils lateral, just visible from above, slightly closer to snout tip than to eye but in lateral view nearly terminal; loreal region flat, moderately steeply sloping, canthus rostralis abrupt but not sharp. Eyes relatively small (EY/SVL 0.109), eyelid width equals about 60% of interorbital distance. Tympanum relatively large (<75% of EY) but scarcely distinct externally. Relative lengths of fingers 4 > 3 > 5 > 2 > 1, first more than half length of second; tips not disclike, rounded, equal to or slightly broader than penultimate phalanges, terminal groove not (or but faintly) present; subarticular and metacarpal elevations low, rounded. Toes unwebbed, relative lengths 4 > 3 > 5 > 2 > 1, tips flattened and broadened into small but distinct discs with terminal grooves; subarticular and inner metatarsal elevations low, rounded; no outer metatarsal tubercle. A weak, diagonal postocular fold. Back with numerous short skin folds and indistinct rugosities; a ><-shaped pair of folds in the scapular region; hind legs somewhat rugose. Ventral surfaces smooth.

COLOR AND PATTERN: In preservative, the dorsum is light brown with indistinct, random, tiny darker spots and some larger spots on the flanks. Lumbar eyespots are more or less evident. The loreal region is slightly duskier than the back. A narrow dark band passes from the tip of the snout through the nostril to the eye and resumes at the posterior corner of the eye, following the postocular fold across the upper edge of the tympanum. This band may terminate anterior to the arm or may continue as a series of spots or as a stripe for a short distance above and past the arm. The venter is pale with relatively large, irregular dark spots, larger on the chin than on the abdomen. The anterior and posterior surfaces of the thighs have dark, splotchy markings, and the posterior surface has an ill-defined, dark triangular seat patch. The undersides of the thighs are pale with obscure dusky markings, whereas the shanks are marked more like the abdomen. The palms are pale with dark markings, the soles the reverse.

Brass (1956: 130) called these frogs ‘‘reddish brown’’; I have not examined living individuals.

VARIATION IN SIZE AND PROPORTIONS: Nothing can be said of geographic variation, as the few specimens all come from the same mountain. The smallest of the 12 specimens (SVL 23.7 mm) is at or close to maturity, as it has ova >1 mm in diameter; I cannot be sure of the sex of the largest specimen (SVL 30.1 mm). Proportions are summarized in table 10, regression data are presented in table 11.

ILLUSTRATIONS: Hand and foot, fig. 53E.

CALL: Brass (1956: 130) characterized the sound of a chorus of these frogs as ‘‘like concerted cackling in a distant fowl-yard.’’

James Menzies recorded three individuals at Betamin, Mt. Dayman, 2050 m, in July 1984. The note is a soft ‘‘coo’’ lasting about 0.35 sec (0.26–0.41, N = 9; see fig. 77C) and repeated about every 16 sec (13–18, N = 5 intervals). I have recordings of four notes of one frog, three of another, and two of a third. The unpulsed note is finely tuned in all instances and maintained at a frequency of 900 Hz. One individual consistently initiated each of four notes with a brief (0.05 sec) segment at 1050 Hz before dropping to 900 Hz. This was not true of the other frogs.

Menzies (personal commun.) recorded one frog at between noon and 1300 hours, the others at about 2100 hours. One frog was found calling from the ground beneath a leaf, whereas the others were deeper in the substratum and were not captured. Menzies recorded the body temperature of a calling frog as 17°C where the ground was 13.2°C.

COMPARISONS WITH OTHER SPECIES: No other *Oxydactyla* is known from the area in which *crassa* occurs. *Austrochaperina brevipes*, a species of similar size and habitus, occupies much the same habitat in the Owen Stanley Mountains to the northwest. If questionable specimens are captured in an intermediate region and vocalizations are not known, such specimens should be diagnosed especially on the basis of the nature of the

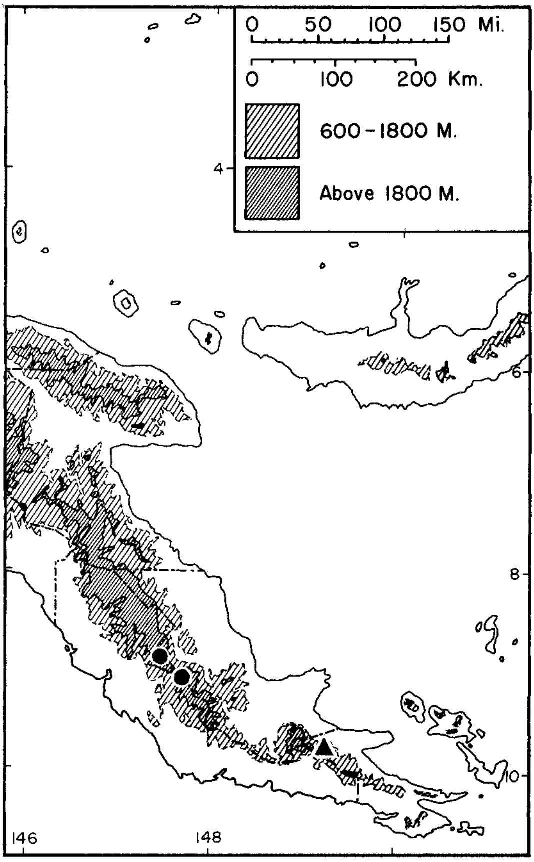

Fig. 42. Distribution of *Austrochaperina brevipes* (circles) and *Oxydactyla crassa* (triangle) in Papua New Guinea.

fingertips (much more disclike in *brevipes*), leg length (longer in *brevipes*), and dorsal rugosity (greater in *crassa*). See account of *O. coggeri* for a comparison with that similar but geographically remote species.

Habitat and Habits: Brass (1956: 110) called the vegetation at the type locality "mossy forest" and provided a detailed description and photograph (pl. 16, fig. 1). He stated that "several specimens were uncovered from under about 10 cm. of loose, somewhat peaty humus in raspberry tangles bordering the forest."

Distribution: This species is known only from high elevations (2050–2230 m) on Mt. Dayman, whose highest point is on the border between Milne Bay and Central provinces in the southeastern tail of New Guinea (fig. 42). Mt. Suckling, Mt. Dayman and Mt. Simpson form the core of a highland region somewhat distinct from the main mass of the Owen Stanley Mountains, and *O. crassa* may prove to be restricted to this area.

Locality Records and Specimens Examined: PAPUA NEW GUINEA: Milne Bay Prov.: north slope of Mt. Dayman, 2230 m (AMNH A56803 [holotype], A56805, A56865, A57424, A57425, A57441–57443 [paratypes]; BMNH 1956.1.1.18 [paratype]; MCZ A28495 [paratype]); Betamin, Mt. Dayman, 2050 m (PNGM 20888 [2 specimens]).

Remarks: Tape recordings of this form made by James Menzies that provide good evidence of its specific status were particularly welcome in view of the somewhat equivocal nature of the morphological characters.

Oxydactyla stenodactyla, new species

Figures 43, 44

Sphenophryne brevicrus: Loveridge, 1948: 422.

Holotype: AMNH A66047, collected by Hobart M. Van Deusen on the Sixth Archbold Expedition, June 21, 1959, at Piunde-Aunde Lakes, Mt. Wilhelm, 3570 m, Simbu Province, Papua New Guinea.

Paratypes (all from Papua New Guinea): Simbu Prov.: AMNH A66040–66046, A66048–66054, A92799–92801 (C&S), A92802, A135269, A135271–135310, A135313–135333, collected by the Sixth Archbold Expedition at the type locality, June 13–28, 1959; AMNH A78909, collected by L. K. Wade at the type locality, June 5, 1966; AMS R68908–R68924, collected on Mt. Wilhelm by J. Hope; BPBM 5302, collected by G. A. Samuelson, June 12, 1967, and 13430–13033, collected by R. C. A. Rice, Sept. 22, 1968, at the type locality; MCZ A64308, 64310–64336, 64338, collected by Fred Parker, June 10, 1967, and MCZ A111896–111900, 111967–111977, collected by Fred Parker at the type locality; RMNH 16765, 16766, 16769, 16671–16678, collected by M.M.J. van Balgooy, May 5, and June 4, 1965, at the type locality; BPBM 1049, collected by J. L. Gressitt, June 3, 1955, at Denglagu, Mt. Wilhelm, 2500 m; BPBM 2898, 2899, collected by J. Sedlacek, July 3, 1963, on Mt. Wilhelm, 3800 m;

Fig. 43. *Oxydactyla stenodactyla*, MCZ F21761 (specimen not located) from Mt. Otto, Eastern Highlands Prov., Papua New Guinea. Fred Parker photo.

BPBM 5353, collected by J. L. Gressitt, Aug. 2, 1969, on Mt. Wilhelm, 4000 m; MCZ A25920–25929 + 3 untagged specimens, collected by P. J. Darlington in 1944 on Mt. Wilhelm, 3050–3660 m; MCZ A64296, collected by Fred Parker, June 10, 1967, on Mt. Wilhelm, 2900–3050 m; RMNH 16763, 16768, collected by M.M.J. van Balgooy, June 15 and Apr. 21, 1965, at Kombugomambuno, 3300 m, Mt. Wilhelm; RMNH 16762, collected by M.M.J. van Balgooy, June 14, 1965, south of Lake Aunde, 3900 m, Mt. Wilhelm; RMNH 16770, collected by M.M.J. van Balgooy, Apr. 26, 1965, northeast of Lake Aunde, 3600 m; MCZ A111932, 111933, collected by Fred Parker, Nov. 13, 1965, on the southwest slope of Mt. Kerigomna, 2900 m. Eastern Highlands Prov.: AMNH A76580–76581, A76587–76589, A137304–A137307 (137306 C&S), MCZ A53083–53095, 53097, A111934–111966, and SAMA R6582, R16629, collected by Fred Parker, July 25, 1964, and Oct. 11, 1965, on Mt. Otto, 3540 m. Western Highlands Prov.: AMNH A65276–65280, A65302, collected on the Spalding-Peterson Expedition, Aug. 6, 1959, on Mt. Pollam, Wahgi Dividing Range, 2740 and 2490 m.

ETYMOLOGY: The specific name derives from the Greek *stenos* (narrow) and *dactylos* (digit), and is used as an adjective.

DIAGNOSIS: *Oxydactyla stenodactyla* differs from other *Oxydactyla* except *alpestris* in that the toe tips are narrow, not widened or flattened, and lack terminal grooves. The larger eye size of *alpestris* (mean EY/SVL > 0.33) will alone properly segregate most *alpestris* from *stenodactyla* (mean EY/SVL < 0.30), and combining the greater leg length of *alpestris* along with eye size (fig. 46) affords nearly complete separation.

DESCRIPTION OF HOLOTYPE: Adult female (gravid) with the following measurements and proportions: SVL 30.4, HW 10.6, TL 9.2, EY 2.9, EN 1.6, IN 2.5, HD 6.2, FT 10.2, TY 1.6; HW/SVL 0.349, TL/SVL 0.303, EY/SVL 0.095, EN/SVL 0.053, IN/SVL 0.082, EN/IN 0.640, HD/SVL 0.204, FT/SVL 0.336.

Head narrower than rotund, short-legged body. Snout rounded as seen from above and laterally, scarcely projecting; nostrils easily visible from above, about equidistant from eye and tip of snout; loreal region a flat, gentle slope, canthus rostralis rounded, barely distinguished. Eyes relatively small, corneal outline just visible from beneath if eyes fully protruded, eyelid about 75% of interorbital span. Tympanum small, well separated from eye, tympanic annulus barely visible. Relative lengths of fingers $3 > 4 > 2 > 1$, first more than half length of second; tips rounded, not disclike, no terminal grooves; subarticular and metacarpal elevations scarcely evident. Toes not webbed, relative lengths $4 > 3 > 5 > 2 > 1$, first less than half length of second, tips rounded, not disclike, no terminal grooves; subarticular and inner metatarsal elevations scarcely evident. A postocular skin fold curving downward behind tympanum, becoming indistinct at foreleg insertion; skin otherwise smooth dorsally and ventrally.

All dorsal surfaces are mottled in two shades of brown, with small areas of paler ground color occasionally showing through. The ventral surfaces are pale yellow-brown with a few indistinct marks on the lower lip and scattered dark spots on the abdomen. The posterior of the thigh is largely pale, with a few dark spots.

VARIATION IN TYPE SERIES: Body proportions of adult frogs in three samples are in table 10 and regression data for the two principal samples in table 11. The largest male *stenodactyla* measures 30.8 mm and the largest female 31.9 mm. Judged from the presence vocal slits, males mature at about 22–23 mm. Females 25–26 mm and larger are

Fig. 44. *Oxydactyla stenodactyla*, AMNH A135272, SVL 26 mm from Mt. Wilhelm (type locality), Simbu Prov., Papua New Guinea.

mature; a large (SVL 30 mm) specimen from Mt. Otto contained 23 ova about 3 mm in diameter.

Variation in the color pattern of this species has individual, ontogenetic, and geographic components. Adult frogs from Mt. Wilhelm are quite variable, but generally show modifications of the theme described for the holotype—mottling of two shades of brown on a paler ground color. At the darkest extreme, only small, vermiform spots of the pale ground color may show, or at the other extreme large areas of the back may be occupied by pale ground color alone. Dark mottling may be fine or coarse. Some individuals have moderately well-developed lumbar ocelli and a pale postorbital-dorsolateral streak (fig. 44). The ventral surfaces range from immaculate to heavily spotted, with no obvious anterior-posterior differentiation (fig. 45). Small frogs tend to show a dark postorbital streak that broadens and extends along the flank, sharply defined from the paler and largely unmarked dorsum. Traces of the dark lateral area persist in some adults.

In contrast to frogs from Mt. Wilhelm, most from the summit of Mt. Otto are quite uniform in dorsal color pattern, being unmarked light brown (fig. 43). Juveniles, like those on Mt. Wilhelm, may have a dark postocular streak that expands to cover the flank, and this pattern persists faintly in some adult frogs. Dark or light markings in the flank region may hint at the contrasting patterns seen in Mt. Wilhelm frogs, but they rarely approach this degree of patterning even in the least developed pattern. Ventral coloration is variable: A rather uniform brown color with no macroscopic pattern is the mode, but this may be broken up by pale splotches of various sizes, or the venter may be pale with coarse, irregular dark marks.

The sample of one juvenile and five adult frogs from the Wahgi Dividing Range presents a third facies. The dorsal pattern in these resembles the juvenile pattern at the other localities. The dorsum from snout to cloaca is largely unmarked, pale tan, or has faint, indistinct darkening. Two specimens show an indistinct pale vertebral hairline, and all show dark marks in the lumbar region. A dark streak passes from the tip of the snout along the canthus rostralis and the edge of the eyelid, and from there toward the groin, usually becoming ill defined posteriorly. The facial region and the area below the streak posterior to the tympanum are more or less darkened, almost as dark as the streak in some instances and almost as pale as the back in others. The ventral pattern shows the sort of variation described for the Mt. Wilhelm frogs. Two adult specimens from Mt. Kerigomna resemble those from the Sepik-Wahgi Divide, but differ in having a pale inner edge to the canthal-dorsolateral streak.

The foregoing descriptions all refer to preserved specimens. Notes by M.M.J. van Balgooy on RMNH specimens from Mt. Wilhelm stated: ‘‘Orange with black markings darker above than below,’’ and ‘‘dark grey above with orange markings, below light orange with grey spots.’’ Color transparencies of a frog from Mt. Otto (fig. 43) show a deep gray dorsal color, with markings of a similar shade on a dull orange ventral background.

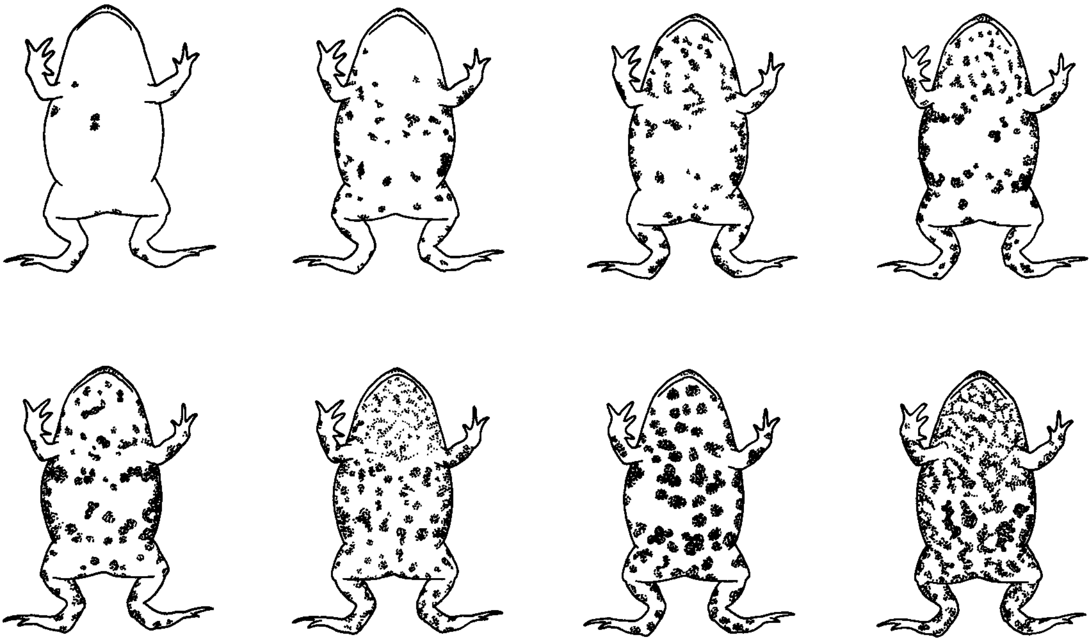

Fig. 45. Ventral surfaces of *Oxydactyla stenodactyla* from Mt. Wilhelm showing variation in amount of dark spotting.

Illustrations: Ventral pattern, fig. 45; 3rd finger terminal phalanx, fig. 71A; tip of 3rd finger, fig. 49; premaxilla, fig. 63A; hyoid, fig. 69A; sacral region, fig. 72A; vomer, fig. 65A; skull, fig. 67A; hand and foot, fig. 53A; jaw musculature, figs. 74, 78A.

Call: I have no recording of the call, which Loveridge (1948: 422, citing information from P. J. Darlington) described as ‘‘woodeny croaking.’’ M.M.J. van Balgooy (collector’s notes accompanying RMNH specimens) stated: ‘‘Its sound, a soft chirping ‘krrr, krrr’ not unlike that of a cricket, can be heard all day.’’ Hobart M. Van Deusen, who collected this species on Mt. Wilhelm on the Sixth Archbold Expedition, wrote in the field catalog: ‘‘Call note a single short ‘enh,’ rapidly repeated (40 or 50 in 30 seconds).’’

Comparisons with Other Species: Only *O. alpestris* could be confused with this species (see Diagnosis).

Habitat and Habits: The principal habitat of this species is alpine grassland, although the elevations at which some specimens were taken suggest that it may also occur in subalpine forests. Brass (1964) described in detail the cold, wet habitat at the type locality. Wade and McVean (1969: 31) stated that these frogs form ‘‘an extensive network of burrows in the tussock grassland.’’ Notes by R. Rice accompanying a BPBM specimen stated: ‘‘Very sluggish species. Sit in shallow holes in soil and duff of tussocks and clumps of vegetation.’’ In notes accompanying RMNH specimens, M.M.J. van Balgooy characterized *stenodactyla* as ‘‘a very common species in the alpine region where it hides away in hollows in the soil, under shrubs and grass-tussocks from 3300–4000 m.’’ P. J. Darlington found one, together with 14 eggs, in moss under a tussock (Loveridge, 1948). The foregoing notes all refer to Mt. Wilhelm.

Distribution: This species is known from elevations of 2490 to 4000 m in the central highlands of Papua New Guinea in Western Highlands, Simbu and Eastern Highlands Provinces (fig. 41). Populations in the four major areas of distribution—the Sepik Wahgi Divide, Mt. Wilhelm, Mt. Otto, and Mt. Kerigomna—probably are disjunct from one an-

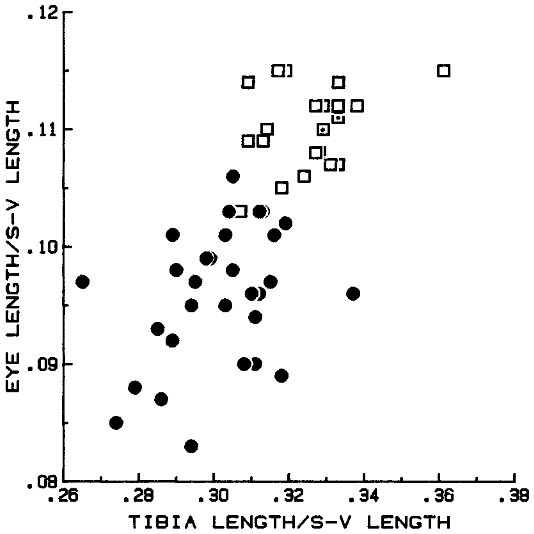

Fig. 46. Comparison of relative eye size and tibia length in *Oxydactyla stenodactyla* from Mt. Wilhelm (circles) and *O. alpestris* (squares) from the Porol Ranges. Adult individuals only plotted; symbols enclosing dots represent two specimens with identical ratios.

other. See Holotype and Paratypes for localities and specimens examined.

REMARKS: It is evident from the description of variation that frogs from at least the three principal population samples (excluding Mt. Kerigomna, with only two specimens available) are quite distinctive in color pattern. A large majority could be assigned correctly geographically on the basis of color pattern alone. One could argue not unreasonably for separate specific (or at least subspecific) status for each population. I regard the morphological similarity (other than color pattern) of the three populations as compelling evidence for conspecific status, although I would welcome the opportunity to test this hypothesis against information from advertisement calls. Naming the known populations as subspecies would, in my opinion, serve no particularly useful service, because knowledge of the variation and distribution of the species most likely is far from complete.

P. J. Darlington, who climbed Mt. Wilhelm during World War II, was the first to collect this species. Loveridge (1948) referred the specimens to *Sphenophryne brevicrus*, a name that as used in the past included four species by my present reckoning.

Genus *Sphenophryne* Peters and Doria

Cornufer Tschudi, 1838: 28, 71, part; see Zweifel (1967b) for disposition of this name.

Sphenophryne Peters and Doria, 1878: 430. Type species (by monotypy),

Sphenophryne cornuta Peters and Doria, 1878: 430.

DIAGNOSIS: A genus of genyophrynine microhylid frogs (sensu Zweifel, 1971 and Burton, 1986) with the following combination of morphological characters: clavicles long and slender, reaching from scapula almost to midline of pectoral girdle; frontoparietal region of skull short and wide, mean ratio of braincase to skull length, 0.56; diapophyses of sacral vertebra broadly expanded, mean ratio of anterior-posterior distance to lateral span, 0.47 (table 14); first finger short, less than half length of second; tips of fingers (except 1st) and toes broadened into flattened discs with terminal grooves, disc on third finger broader than that on fourth toe; terminal phalanges with the tip broadly T-shaped, span of tip of phalanx of third finger averages 2× width of base of phalanx.

CONTENT: The genus is monotypic.

MORPHOLOGY: See species account.

DISTRIBUTION: See species account.

REMARKS: Superficially, *Sphenophryne* may be distinguished from other genyophrynine genera by the presence of a small dermal appendage on each eyelid. Proportions of the skull and sacral vertebra set it apart from the other genera with the primitive pectoral girdle, as do the short first finger and the relative sizes of finger and toe discs.

Sphenophryne cornuta Peters and Doria

Figures 31A, 47

Cornufer unicolor Tschudi, 1838: 28, 71, part (based on two specimens, only one of which is *S. cornuta*; see Zweifel, 1967b).

Sphenophryne cornuta Peters and Doria, 1878: 430 (type locality, "presso il fiume Wa Samson nella Nuovo Guinea settentrionale" ["near the Wa Samson River in northern New Guinea"; this river is on the northwestern edge of the Vogelkop Peninsula, Irian Jaya, Indonesia, with its mouth about 20 km east-northeast of Sorong]; holotype, MSNG 29479, collected by O. Beccari in 1875).

Fig. 47. *Sphenophryne cornuta*, AMNH A83051, SVL 38.5 mm.

Chaperina ceratophthalmus van Kampen, 1909: 43 (type localities, ''Noord-Fluss bei Geitenkamp'' [Geitenkamp, Lorentz River] and ''Resi-Gipfel'' [Resi Peak], Irian Jaya, Indonesia; syntypes, ZMA 5777 [Geitenkamp], collected by H. A. Lorentz, July 2, 1907, and ZMA 5778, 5779 [Resi Peak], collected by Lorentz on August 20 and September 9, 1907).

TYPE MATERIAL: The holotype is a small individual (SVL 21.8 mm), presumably immature (not sexed), in ''Discrete condizioni'' (fairly good condition: Capocaccia, 1957: 220). In all pertinent characters it agrees with the following composite description.

DIAGNOSIS: The presence of a small but distinct, pointed tubercle on each eyelid distinguishes this species from all other Papuan microhylids. (The large-mouthed, squat *Asterophrys turpicola* has elongate warts on the eyelids, but not a single slender tubercle.) Equally distinctive are the combination of flat, vertical loreal region and flat upper surface of the snout, and the large finger discs, that of the third finger being broader than that of the fourth toe.

MORPHOLOGY: Males and females mature at about 29 mm SVL. Among 106 specimens measured, the largest male measures 37.4 mm and the largest individual, probably a female, 41.4 mm. The largest specimen whose sex was determined, a female, measured 40.0 mm. Head and body relatively slender, HW/SVL about 0.35 in adults. Snout subacutely pointed as seen from above; nostrils lateral, much closer to tip of snout than to eye; loreal region vertical and flat, distinctly set off from flat upper surface of snout. Internarial distance relatively broad (mean IN/SVL, 0.12), eye–naris distance usually slightly less than eye diameter, rarely a little greater. Eyes moderate, laterally oriented, EY/SVL about 0.11 in adults, eyelid with a small but distinct pointed tubercle near its free margin. Tympanum distinct, horizontal diameter about 63% that of the eye, no sexual dimorphism. Hind legs relatively long, TL/SVL average about 0.49 in adults. Relative lengths of fingers $3 > 4 > 2 > 1$, first quite short; terminal disc of first finger scarcely if at all expanded, without a distinct groove, discs of other fingers well developed with terminal grooves, disc of third finger averages 2.3× width of penultimate phalanx (fig. 52). Relative lengths of toes $4 > 3 > 5 > 2 > 1$, all with grooved terminal discs, that of fourth toe about 1.7× width of penultimate phalanx and about 82 % of width of third finger disc. Fingers and toes with low, rounded subarticular areas; no palmar or plantar elevations evident. Toes free or with sparse basal webbing (fig. 52). Body generally smooth above and below, but with rows of widely spaced tubercles on dorsal and ventral surfaces; similar tubercles on dorsal surfaces of hind limbs; usually a tubercle on heel and others along outer edge of tarsus.

COLOR AND PATTERN: Preserved specimens are brown or gray-brown above, virtually patternless or with rather indistinct markings. Variations include a darker central figure (fig. 47), a pale vertebral hairline, and faint lighter spots. Tubercles are typically light-tipped. The dorsal surface of the thigh usually has a

TABLE 12
Body Proportions of *Sphenophryne cornuta*

Ratio	Mean ± σ_m	Range	N
TL/SVL	0.481 ± 0.003	0.436–0.522	61
HW/SVL	0.347 ± 0.002	0.313–0.376	60
HD/SVL	0.252 ± 0.004	0.226–0.282	21
FT/SVL	0.421 ± 0.004	0.382–0.452	21
EY/SVL	0.107 ± 0.001	0.096–0.126	60
EN/IN	0.850 ± 0.006	0.732–0.941	60
EN/SVL	0.102 ± 0.001	0.086–0.110	60
IN/SVL	0.120 ± 0.001	0.107–0.131	60
FD/SVL	0.054 ± 0.0012	0.037–0.071	35
TD/SVL	0.043 ± 0.0010	0.029–0.058	34

TABLE 13
Regression Statistics for *Sphenophryne cornuta*[a]

Ratio	α	β	*r*	N
TL/SVL	0.735	0.880	0.956	60
HW/SVL	0.376	0.978	0.969	53
EY/SVL	0.215	0.800	0.925	59
EN/SVL	0.162	0.866	0.943	59
IN/SVL	0.212	0.839	0.958	59
HD/SVL	0.174	1.107	0.967	25
FT/SVL	0.296	1.101	0.982	25
FD/SVL	0.023	1.237	0.876	40
TD/SVL	0.036	1.050	0.818	39

[a] Power curves of the form $Y = \alpha X^{\beta}$.

thin, longitudinal light line, and light lines of the same width diagonally cross the anterodorsal surface of the thigh and the dorsal surfaces of the lower leg segments in many individuals. The posterior of the thigh is slightly darker than the dorsal surface with tiny light spots. The ventral surfaces are almost completely pale in some specimens, but in others there is heavy dark mottling, especially on the chin and chest.

I recorded the following colors in life for the specimen illustrated (fig. 31A, evidently it had paled slightly when photographed): a dark reddish brown middorsal band not sharply defined from lighter reddish brown ground color of head and rest of dorsal surfaces; anterior and posterior surfaces of thighs grayish brown with numerous minute yellowish white flecks; chin and chest brighter reddish brown than dorsum, with gray-brown mottling; paired tubercles on chest and anterior part of abdomen tipped with white, a similar row of tiny white tubercles margined with black along lateral surface of body; iris grayish gold. A frog from Western Province had a golden line along the canthus rostralis reaching to the spike on the eyelid and a pale vertebral hairline in addition to the dorsal line on the thigh; chin and chest gray with splotches of orange; iris grayish gold with a red streak before and behind the pupil. Another specimen from the same region was largely gray beneath with a white midventral hairline and no red streak in the grayish gold iris.

Menzies (1976, pl. 12d) illustrated in color a specimen of much grayer aspect than those described, and (p. 61) mentioned one specimen whose ‘‘ventral side was bright red all over.’’ Brongersma and Venema (1962: 104) stated ‘‘it has a brown back and a rusty-red belly.’’

VARIATION IN SIZE AND PROPORTIONS: Parker (1934: 154) gave the maximum length as 41 mm. The largest specimen I measured is 41.5 mm SVL (ZMA, uncataloged from Heuvelbivak, Lorentz River, Irian Jaya, probably female but not sexed). A female syntype of *Chaperina ceratophthalmus* (ZMA 5779) measures 40.0 mm. Males reach at least 37.4 mm (ZMA 5777, syntype of *C. ceratophthalmus*; RMNH 16641, one of several with this number), but few males attain 36 mm whereas many females do. I measured and sexed 61 specimens (RMNH) from Mabilibol, Sibil Valley, Star Mountains, Irian Jaya. Males mature at about 28 mm and females at only a slightly larger size: The smallest males with vocal slits are that size; females of about 27–28 mm have apparently immature ova, whereas enlarging ova are present at 29 mm SVL.

Variation in proportions among adults in the large sample from the Sibil Valley region of West Irian is set forth in table 12, and regression statistics are presented in table 13. I detect no geographic trends in size or proportions in this widespread species. Measurements of individuals in scattered, smaller samples fall within the ranges set by the Sibil specimens.

ILLUSTRATIONS: 3rd finger terminal phalanx, fig. 71M; premaxilla, fig. 64D; sacral region, fig. 73; vomer, fig. 65P; skull, fig. 66; hand and foot, fig. 52; mandibular musculature, fig. 75B.

CALL: Menzies (1976: 61) described the call as ''a long rattling chuckle lasting about one second and so loud that it can be heard from several hundred metres distance.'' I heard this call near Tabubil but was unable to record it. However, a recording by Ian Redmond made available through the courtesy of Mr. Redmond and the British Library of Wildlife Sounds is available for analysis (fig. 76B). The calls (N = 4 from one individual, BMNH 1980.673) are 1.9–3.1 sec in length (mean 2.4) and consist of 42–67 notes (mean 52.2), each note comprised of 2 or 3 (rarely 4) discrete pulses. There is a dominant frequency at 3000 Hz and a slightly lesser peak at 1200 Hz. The note repetition rate is 21.6–23.0 notes per second (mean 22.1), with no obvious change in rate over the course of a call. Temperature was not noted.

In addition to the call described above, the species also has another that is possibly territorial in function. This call includes one to three brief (0.03–0.05 sec) pulsed notes with several emphasized harmonics. Single- and double-note calls are in the majority; triple-note calls are infrequent. Single or initial notes are more rapidly pulsed than second or third notes and include a more nearly complete set of harmonics (fig. 76A). In one recorded instance, a frog called 18 times in the space of 3 min 49 sec (average, once every 12.7 sec). Many of these calls (10 of 19) appeared to elicit responses from, or were in response to, similar calls from an individual nearby.

COMPARISONS WITH OTHER SPECIES: *Sphenophryne cornuta* is that rare creature, a Papuan microhylid that readily can be identified to genus and species without resorting to dissection or call analysis. No other species shares its combination of a small dermal appendage on the eyelid, fingers with enlarged discs larger than those on the toes, and vertical loreal region. Scansorial species of *Cophixalus* and *Oreophryne* may be similar in size and general morphology, but none has the eyelid appendage.

HABITAT AND HABITS: My field experience with this species is limited to two areas—the Adelbert Mountains in coastal Madang Province, and the vicinity of Tabubil, Western Province. At an elevation of 670 m in the former region, I found individuals at night at heights of less than 2 m on vegetation beside a stream in rainforest regrowth. They shared this habit and habitat with two other microhylids of similar size, *Cophixalus biroi* (Méhelÿ) and *C. cheesmanae* Parker. These two were calling, whereas I heard no calls from *cornuta*. Near Tabubil, frogs gave possibly territorial calls (see above) from perches 1–2 m up in shrubs, saplings, or tangled vegetation not close to any running water.

Menzies (1976: 60–61) remarked that ''calling males seem to be well spaced out for I have never found, or heard, two close together,'' and added that *cornuta* ''is probably as much terrestrial as scansorial although males, at least, do climb about on low vegetation.'' I find nothing else in the literature on the ecology of this species.

DISTRIBUTION: On the north coast of New Guinea, *Sphenophryne cornuta* has been found at low to moderate elevations from near the tip of the Vogelkop Peninsula eastward to the Adelbert Mountains north of Madang. Records on the south coast extend from the Bomberi Peninsula in Irian Jaya eastward to slightly east of Port Moresby (fig. 48). Spotty but fairly intensive collecting on the Huon Peninsula and eastward on the north coast has produced no *cornuta*. Elevations of collection range from virtually sea level, as at Kerema and Katau, to 2600 m in the Hellwig Mountains of Irian Jaya, though most localities lie between about 400 and 1250 m. There are no insular records.

LOCALITY RECORDS AND SPECIMENS EXAMINED: IRIAN JAYA: Bomberi (BPBM 5290); Camp VI, Utakwa River (BMNH 1913.11.1.139); foot of Charles Lewis Mtns. (BMNH 1897.3.23.5); Geitenkamp, Lorentz River (ZMA 5777, syntype of *Chaperina ceratophthalmus*); Hellwig Mtns., 2600 m (ZMA, unnumbered); Heuvelbivak, 800 m, Lorentz River (ZMA, unnumbered); Mt. Kohari, between Modder-lust and Kasawari (MCZ A7611); Launch Camp, Setekwa River (BMNH 1913.11.1.136–138); near the Wa Samson River, about 20 km ENE Sorong (MSNG 29479, holotype); Peramelesbivak, Lorentz River (ZMA unnumbered); Resi Peak, Lorentz River (ZMA 5778, 5779, syntypes of *Chaperina ceratophthalmus*); Sabang, Lorentz River (ZMA, unnumbered);

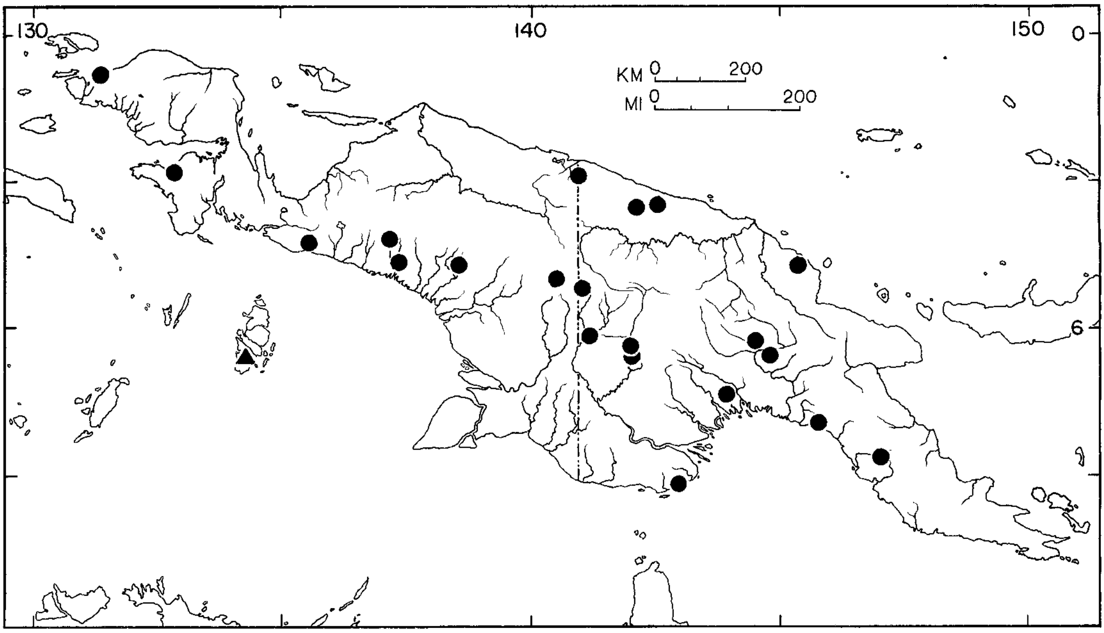

Fig. 48. Distribution of *Sphenophryne cornuta* (spots) in New Guinea and *Microbatrachus pusillus* (triangle) on the Aru Islands.

Sibil Valley, 1250 m (AMNH A84503; BPBM 1045–1047, 3167, 3171, 3173, 3175); Mabilibol (RMNH 16607, 16609 [4], 16613 [2], 16636 [2], 16637 [2], 16638 [20], 16641 [8], 16642, 16644 [12], 16647 [2], 16654 [2], 16659; Sibil Valley; Sibil (RMNH 16663 [3]). PAPUA NEW GUINEA: Central Prov.: Vikaiku, Angabunga (St. Joseph) River (MSNG 29929); Bellavista, via Fane, 1460 m (PNGM, James Menzies, personal commun.; not examined by author); Musgrave River, 18 km E Sogeri, 460 m (MCZ A88020). Gulf Prov.: Gihiteri Village, Omati River (Schultz-Westrum 350 [ZSM]); Kerema (UPNG 3666–3668, 3670, 3671); Weiana, 8 km S, 1 km E Soliabedo, 460 m (MCZ A64105, 64106); Camp III, Nimi River, 13.5 km S, 1 km E Soliabedo, 430 m (MCZ A64111–64114); Uraru, Purari River 90 m (MCZ A64108, 64115). Madang Prov.: Wanuma, Adelbert Mtns., 670 m (AMNH A83048–83052); Wanuma, 1000 m (BPBM 1203). Simbu Prov: Bomai area (AMNH A76586), Bomai, Tive Plateau, 1070 m (MCZ A59696–59701); Karimui, 1100 m (AMNH A77101; MCZ A64104, 64109, 68338–63341); Camp II, Pio River, 6.5 km S, 1 km E Soliabedo, 300 m (MCZ A64110). Western Prov.: Derongo, 400 m (AMNH A82286; MCZ A80006, 81231–81234); Megalsimbip (UPNG 6731–6733); Imigabip, 1280 m (MCZ A80995–80997); Menemsorae (MCZ A80005); Bolangon, 1280 m (MCZ A80998); Yongtau No. 1, 240 m (MCZ A80993, 80994); Haidauwogam, 240 m, 27 km S, 5 km E Tabubil (AMNH A130542–130544); Finalbin, 840 m, 5 km N, 2 km W Tabubil (AMNH A130545, A130546, A130548, A130549, UPNG 8275); Katau (MSNG 29480); junction of Strickland and Rentoul rivers (BMNH 1980.673); junction of Strickland and Tomu rivers (BMNH 1980.674); Kiunga (MCZ A80003, 80004; USNM 203856); Emeti, Bamu River (MCZ A87269, 87270). West Sepik Prov.: Upper course of the Reinjamur, Torricelli Mtns., 650–700 m (south of Paup; Wandolleck, 1911: 4); Mt. Somoro, Torricelli Mtns., 730–1420 m (AMNH A78145–78149); Mt. Nibo, Torricelli Mtns., 700–1550 m (AMNH A78150–78155, A92803–92804 (C&S), A135334–135369 (the last C&S), A135334–135339; Lumi, 530 m (AMNH A78156, A78157).

NOMINA DUBIA

Microbatrachus Roux 1910

Microbatrachus Roux, 1910: 228. Type species (by monotypy) *Microbatrachus pusillus* Roux 1910: 228.

Sphenophryne: Tyler, 1978: 459 (*Microbatrachus* considered a junior synonym of *Sphenophryne*).

Microbatrachus pusillus Roux

Microbatrachus pusillus Roux, 1910: 228 (type locality, ''Pobdjetur, Terangan,'' Aru Islands, Indonesia; holotype, NMBA 2732, collected Feb. 6, 1908, by H. Merton and J. Roux). Van Kampen, 1923: 121. Nieden, 1926: 50. Parker, 1934: 179. Forcart, 1946: 135.

Sphenophryne pusilla: Tyler, 1978: 459.

TYPE MATERIAL: The type specimen is a juvenile 7 mm SVL that ''has been extensively dissected . . . and very badly damaged in the process'' (Tyler, 1978: 457).

DIAGNOSIS: The condition and immaturity of the type specimen allow diagnosis of neither the species nor of the genus of which it is the type species.

MORPHOLOGY: The following description is from van Kampen (1923: 121) and evidently is his paraphrase of the original description, as he did not examine the type specimen: ''Tongue large, subtriangular, about half free behind. Head nearly as long as broad; snout broadly truncated, as long as the eye; no canthus rostralis; nostril in the middle between the orbit and the tip of the snout; interorbital space 1 times the width of the upper eyelid; tympanum hidden. Fingers obtuse; second to fifth toe with very feebly dilated tips; fingers very short, first shorter than second, which is shorter than fifth; no subarticular or metatarsal tubercles; the heel reaches the posterior border of the eye.''

''Skin smooth.''

Roux (1910: 228) stated: ''Sternal apparatus cartilaginous, extremely simple. Sternum a narrow plate. Coracoid and procoracoid present. No clavicle, no omosternum.'' Tyler (1978) noted that as tiny a bone as the clavicle of specimen of this size might easily have been overlooked or lost in dissection. Except for the peculiar *Genyophryne*, no genyophrynine frog possesses a procoracoid but lacks the clavicle.

COLOR AND PATTERN: ''Upper parts brown, darker on the head and the anterior part of the back; fore limbs greyish white, hind limbs yellowish brown; lower parts yellowish white, the throat a little darker, with small lighter dots. Length 7 mm'' (van Kampen, 1923: 121–122).

ILLUSTRATIONS: Roux (1910: pl. 14) illustrated the body in dorsal aspect (fig. 6), open mouth (fig. 6a), and pectoral girdle (fig. 6b).

HABITAT AND HABITS: ''We took this tiny amphibian from wet soil at the edge of a stream'' (Roux, 1910: 229).

DISTRIBUTION: This species is known only from the type locality (fig. 48).

REMARKS: The systematic position of *Microbatrachus pusillus* has elicited comments from most authors dealing with the species: ''Perhaps a young *Sphenophryne* or *Oreophryne* sp.'' (van Kampen, 1923: 122); ''almost certainly the young of an *Oreophryne*'' (Dunn, 1928: 4); ''This genus may . . . prove to have been founded on an immature *Oreophryne* or *Sphenophryne*, more probably the latter'' (Parker, 1934: 179). Only Tyler (1978), who placed *Microbatrachus* in the synonymy of *Sphenophryne*, has gone into the matter in detail, including examination of the type specimen. With allowance for the poor condition of the specimen, Tyler made a strong case for eliminating *Cophixalus* and *Oreophryne* from consideration, leaving *Sphenophryne* as the most likely candidate. The possibility that *Microbatrachus* represents a valid genus was given little credence by these authors.

Tyler's (1978) allocation of *Microbatrachus* as a junior synonym of *Sphenophryne* was reasonable at the time, but with *Sphenophryne* (sensu Parker, 1934) now sundered into four genera, the status of *Microbatrachus* is more obscure than ever. In nomenclatural priority, *Microbatrachus* (1910) stands ahead of *Austrochaperina* (1912) and *Oxydactyla* (1913). The last is a genus of montane frogs most unlikely to be found on the Aru Islands. *Austrochaperina*, however, might well occur there, and I have commented elsewhere (Zweifel, 1985b: 285) that *pusillus* may be a senior synonym of *A. adelphe* (Australian) or *A. gracilipes* (Australian and Papuan), either of which lowland species may occur on the Aru Islands.

My present view is that because of the

paucity of the description and poor condition of the juvenile holotype, *Microbatrachus pusillus* cannot be identified with any known genus and species, and that future taxonomic stability will be enhanced if the name is set aside as a nomen dubium.

MORPHOLOGY

BODY FORM AND PROPORTIONS

SEXUAL DIMORPHISM: Typically the sexes cannot be distinguished externally. The male subgular vocal sac is not evident except when the frog is calling. The only male external secondary sexual character, found in a some species of *Austrochaperina*, is a tendency for an elongation of the snout that is paler than the dorsal surface of the head. Females grow slightly larger than males. In 25 species the largest males average 90% of the SVL of the largest females, (range 81–100%). In only one species with an adequate sample (i.e. *Liophryne allisoni*) are the largest male and female of equal size.

HANDS AND FEET: Hands range in size from about 19% to 27% of SVL. Smaller hands appear to be associated with secretive or burrowing habits, whereas scansorial species are at the high end of the range.

Relative sizes of feet in different species range more widely than do those of hands, from about 33% to 51% of SVL. As would be expected, the burrowing and litter-dwelling species fall at the lower end of the range, roughly 40% of SVL, whereas species known to be active on the forest floor have the relatively longest feet. The lengths, both relative and absolute, of the tibia and foot (and presumably other leg segments not measured) are typically similar, but some exceptions are notable.

The relative finger lengths are the same in all species: $3 > 4 > 2 > 1$. The first finger is typically long; only in *Sphenophryne cornuta* is it conspicuously reduced (fig. 52). The toe lengths of all species show no variation from the presumably primitive order $4 > 3 > 5 > 2 > 1$, and most are webless. Only one species, *Austrochaperina palmipes*, has moderately webbed toes (fig. 56D), while one other, *A. basipalmata*, has basal webbing (fig. 56C). A slight trace of webbing appears in some *A. derongo*.

The fingertips and toe tips may be narrow and rounded with no trace of expansion or of terminal grooves, or they may be broadened into adhesive organs up to more than twice the width of the penultimate phalanx and with a prominent terminal groove, or any degree in between (figs. 49, 51). Intermediate conditions include discs present on toes but not on fingers, but never the reverse, or discs on toes and longer fingers only. The adhesive pad cells of one species, *Austrochaperina derongo* (fig. 50), are perhaps more similar to the cuboidal cells of terrestrial *Liophryne rhododactyla* (Green and Simon, 1986: fig. 8) than to those of scansorial *Cophixalus riparius* (Green and Simon, 1986: fig. 9).

Most species have discs on fingers and toes, typically with those of the toes being distinctly larger. For comparative purposes I use the discs on the third finger and fourth toe, which normally are the largest. Two species, *S. cornuta* and *A. palmipes*, have the largest finger discs. In *S. cornuta* the finger disc is markedly wider than the toe disc by about 1.2×. The finger disc of *A. palmipes* is virtually the same size (relative to body size) as that of *S. cornuta*, but in contrast the toe disc is also large, usually almost equal to the finger disc.

There is a clear correlation between the state of the digital tips and habits. The species with the largest discs (and most pronounced T-shaped terminal phalanges; see Osteology) are, so far as their habits are known, scansorial: *S. cornuta* climbs into shrubs or low into trees when active at night; *A. basipalmata*, *A. palmipes*, *A. rivularis*, and *A. macrorhyncha* are riparian forms with need for adaptation to traversing slick, sometimes steep rock surfaces. Those species with small to intermediate degrees of expansion are terrestrial, active on and within the leaf litter and in some cases doing limited climbing. The narrow, rounded tips seen in *Oxydactyla alpestris* and *O. stenodactyla* are associated with a burrowing mode of life.

Most species have subarticular elevations

Fig. 49. SEM photographs of tip of third finger of *Oxydactyla stenodactyla* AMNH A135289 in palmar (left) and end-on views. Scale line spans 400 μm.

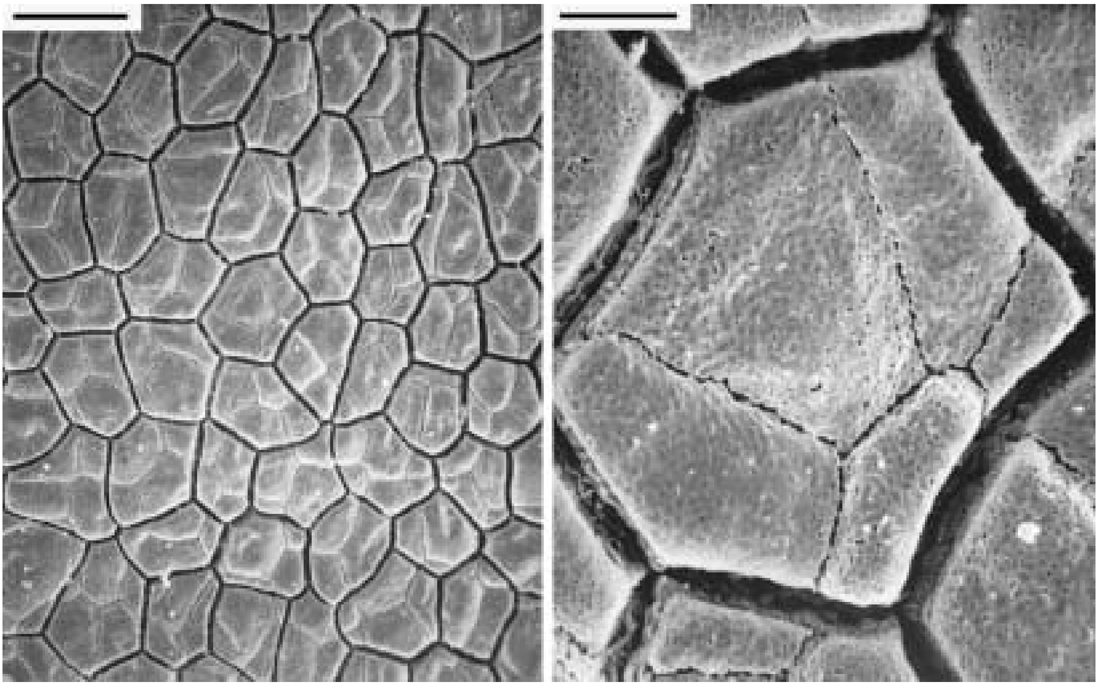

Fig. 50. SEM photographs of lower surface of disc of third finger of *Austrochaperina derongo* AMNH A145507. Left scale line spans 20 μm, right 4 μm.

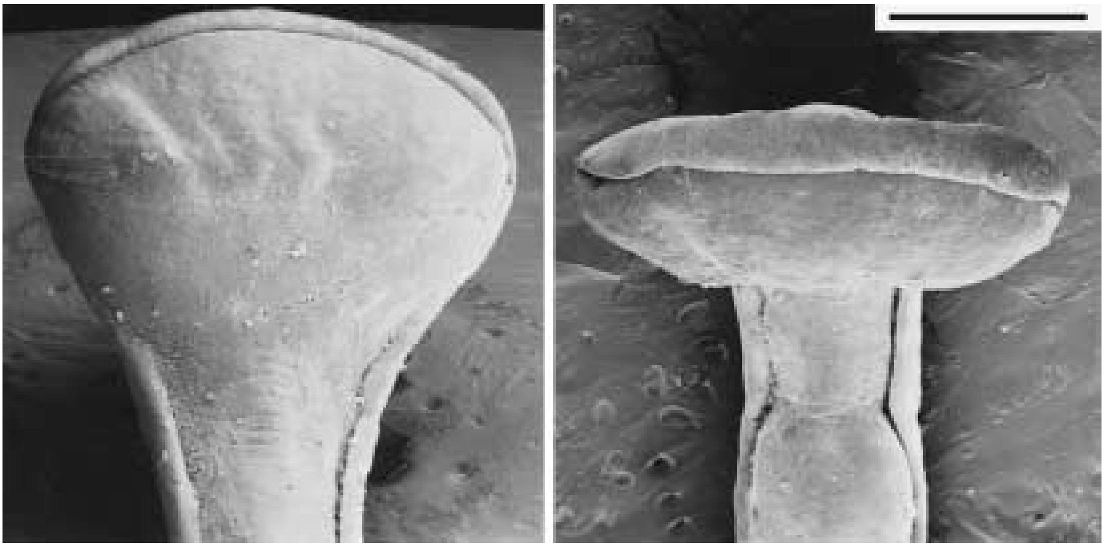

Fig. 51. SEM photographs of tip of third finger of *Austrochaperina palmipes* AMNH A60178 in palmar (left) and end-on views. Scale line spans 800 μm.

that are low, rounded, and inconspicuous, sometimes virtually absent, with none deserving the common appellation ''subarticular tubercle.'' This group include scansorial, litter-dwelling, and burrowing forms. The six species of *Liophryne* have subarticular elevations of a more angular, protruding nature (fig. 54A–E; *similis* identical to *rhododactyla*). Elevations on the palms and soles are inconspicuous in all species. The inner metatarsal elevation is usually elongate and rounded, and there is no outer metatarsal elevation. None of the Australopapuan microhylids possesses a prominent, compressed outer metatarsal tubercle such as is seen in some genera of microhylids in all other parts of the world inhabited by the family. Presumably the scant development of the tubercle is related to head-first as opposed to feet-first burrowing (Menzies and Tyler, 1977).

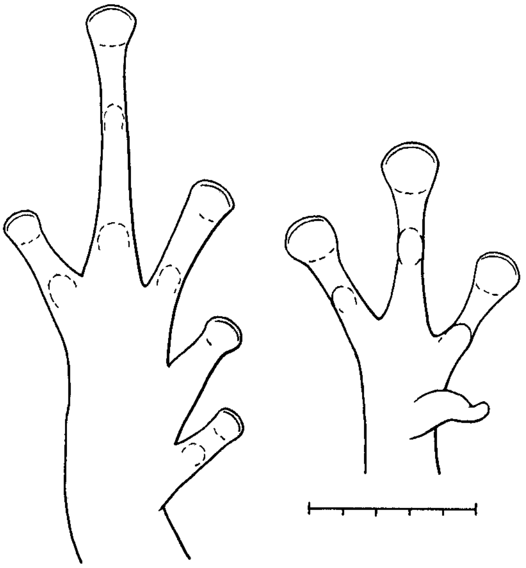

Fig. 52. Lower surfaces of foot and hand of *Sphenophryne cornuta*, AMNH A130546. Scale bar marked in 1-mm intervals.

Pharyngeal Folds: The presence of one to (rarely) three smooth, lobate or serrate transverse folds or ridges across the palate just anterior to the pharynx is common to most genera and species of microhylids and is ''almost diagnostic of the group'' Parker (1934: 6). The exceptions that lack folds are three genera of the Melanobatrachinae (of Madagascar, Parker, 1934) and four genera of Cophylinae (also of Madagascar, where two genera have folds; Parker, 1934). This feature remains undescribed for three cophyline genera of Madagascar. Given the frequency of lack of folds in microhylids of Madagascar, it is curious that the only literature reference to lack of folds in a species of microhylid

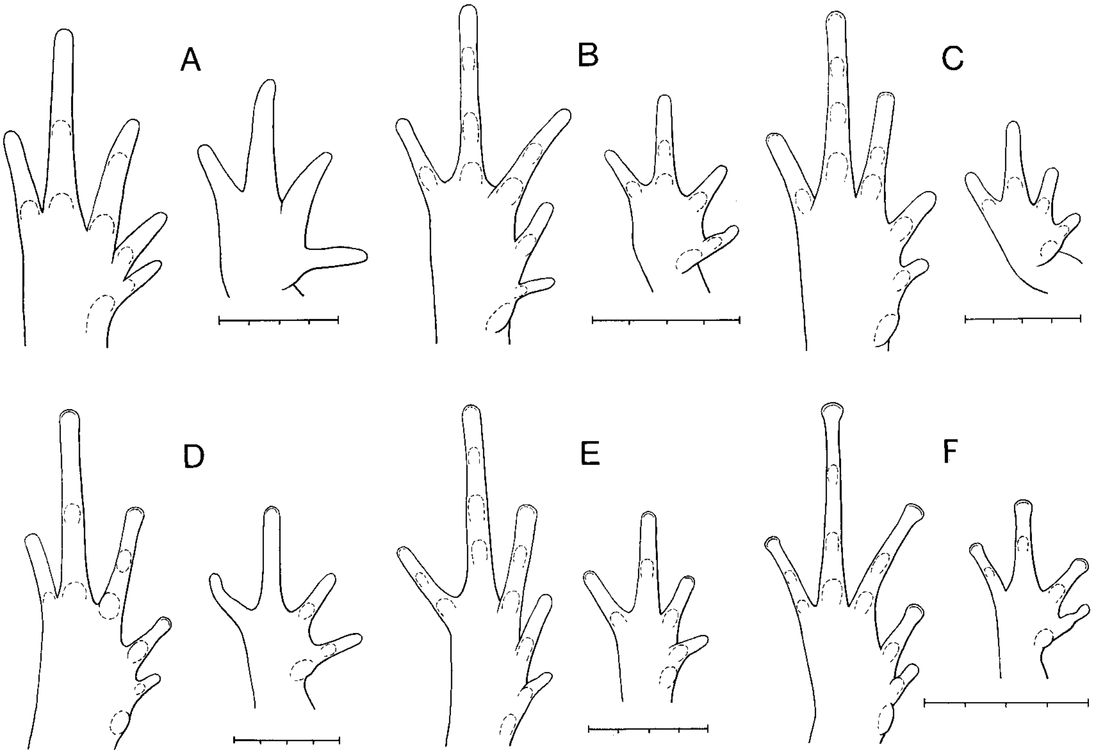

Fig. 53. Lower surfaces of feet and hands of *Oxydactyla* and *Austrochaperina*. **A.** *O. stenodactyla*, AMNH A66046. **B.** *O. alpestris*, AMNH A76584. **C.** *O. brevicrus*, AMNH A43761. **D.** *O. coggeri*, AMNH A140871. **E.** *O. crassa*, AMNH A57424. **F.** *A. kosarek*, MZB 3561. Scale bars marked in 1-mm intervals.

elsewhere is for the North American *Gastrophryne carolinensis*, for which Roux (1944: 12) stated that folds ‘‘are entirely absent.’’ Parker included *Gastrophryne* within *Microhyla*, which he characterized as having folds. A specimen of *G. carolinensis* that I examined has a short fold that does not protrude and could easily be overlooked. A specimen of the presumably related *Hypopachus variolosus* has a single protruding, smooth fold.

As the genyophrynine frogs possess pharyngeal folds and thus conform to the mode for the Microhylidae, I see no utility for the folds at the systematic level of the present work. However, as the structures have not been illustrated in detail, I present SEM photographs (figs. 58, 59) of those of *Liophryne rhododactyla*, which species is typical of many species in having a smooth anterior fold and a longer, denticulate posterior one. The denticulate structures are not, as might be supposed, soft and flexible, but are quite firm. As they point posteriorly, they could serve to interfere with movement out of the mouth by soft-bodied prey such as earthworms. However, the role of a lesser, smooth fold is not subject to such facile explanation.

EYES: All species that I have seen in life and, insofar as can be told from preserved specimens, all Australopapuan microhylids have pupils with horizontal orientation when contracted. Relative eye size among the species studied here ranges in mean EY/SVL from 0.092 to 0.141. There is a tendency for small eyes to be associated with cryptic habits (e.g., *O. stenodactyla*, mean 0.093) and large eyes with surface activity (*L. dentata*, 0.141), but the correlation is not strong.

EARS: The ears of some of the species studied are of moderate size with the annulus externally well defined and with the covering skin smooth and distinct from the surround-

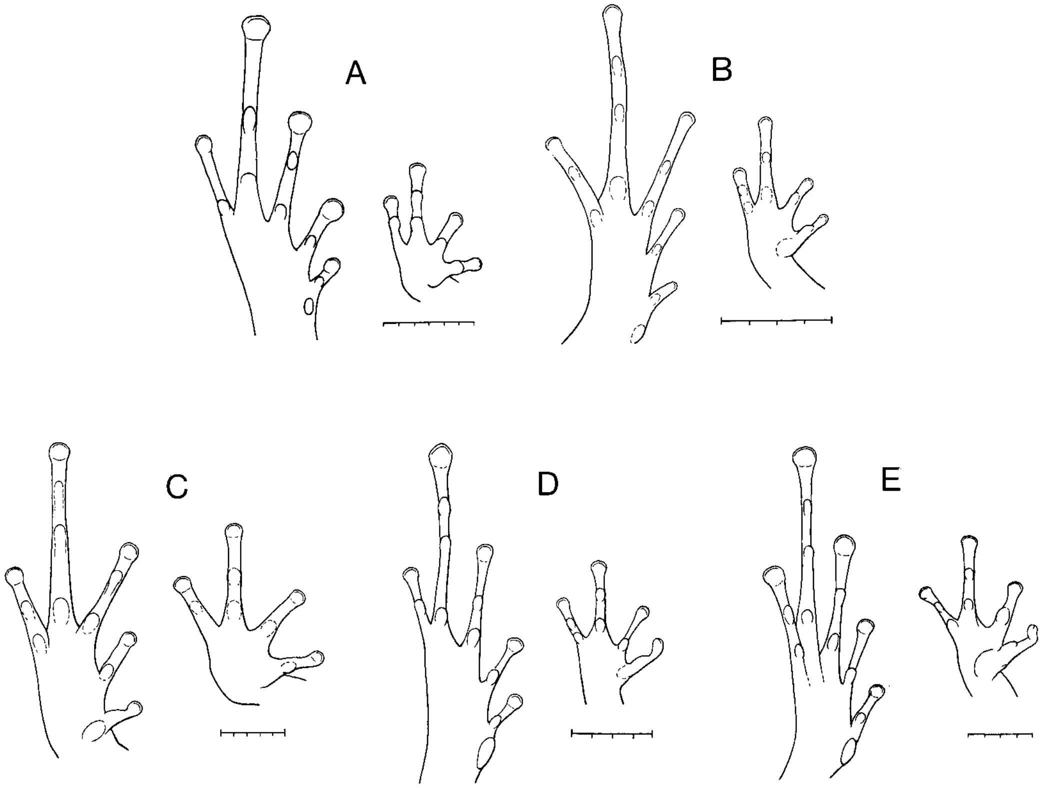

Fig. 54. Lower surfaces of feet and hands of *Liophryne*. **A.** *L. rubra*, UPNG 9290. **B.** *L. allisoni*, AMNH A81221. **C.** *L. similis*, AMNH A130577. **D.** *L. schlaginhaufeni*, AMNH A77589. **E.** *L. dentata*, AMNH A87205. Scale bars marked in 1-mm intervals.

ing skin. More often the annulus is indistinct and the covering skin undifferentiated. In a semiaquatic, riparian species *Austrochaperina palmipes* there is no external sign of the ear. I noted no sexual dimorphism of tympanum size in the species studied for this report, but Tyler et al. (1991) reported that females of an Australian species, *A. adelphe*, have a strikingly larger tympanum than do the males. This is unusual because where dimorphism is present in frogs, the male typically has the larger tympanum.

External appearance and variation in the relative size of the tympanic annulus notwithstanding, the ear in the 13 species dissected (including examples of all four genera) is complete, with the tympanum distinct from the overlying skin (fig. 60). Wever (1985) examined four species of three microhyline genera: *Gastrophryne carolinensis*, *G. olivacea*, *Hypopachus variolosus* (''*cuneus*''), and *Kaloula pulchra*. He found that ''All four are closely similar in general ear structure, lacking a true tympanic membrane but with an effective substitute in the form of a cartilaginous plate (the pars externa of the columella in a flattened form) located immediately beneath the skin.'' Earlier authors (e.g. Parker, 1934) have generally referred to these species as having a ''hidden tympanum.'' Presumably the condition Wever described is derived.

Thirteen species treated in the present study that I dissected share the primitive structure of a true, albeit concealed, tympanum, and probably the rest do, too. But Wever's description suggests that, in comparative studies of other genera and subfamilies, examination of the ears should be more than skin deep. For example, Smirnov (1986, fig. 1) illustrated the middle ear apparatus of five species of *Microhyla*: three with a tympanum

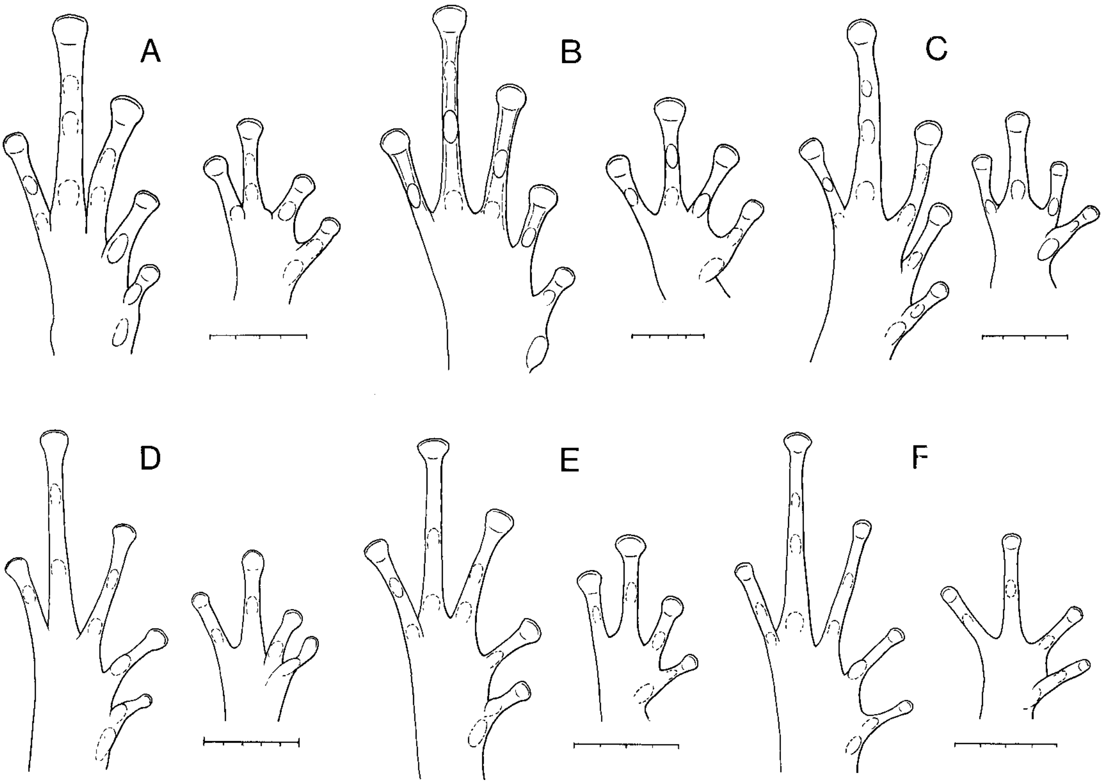

Fig. 55. Lower surfaces of feet and hands of *Austrochaperina*. **A.** *A. derongo*, AMNH A79975. **B.** *A. guttata*, MCZ A92812. **C.** *A. archboldi*, AMNH A66719. **D.** *A. hooglandi*, AMNH A77592. **E.** *A. adamantina*, AMNH A78185. **F.** *A. aquilonia*, AMNH A78186. Scale bars marked in 1-mm intervals.

(*berdmorei*, *pulchra*, *ornata*) and two without (*heymonsi* and *butleri*). All five are characterized in the literature as "tympanum hidden."

ONTOGENETIC CHANGE IN PROPORTIONS

As mentioned in the introductory section on Methods, body proportions typically change with growth. I present here some examples from species treated in this monograph, using nine standard measurements. I have chosen five species, with the choice having been determined by availability of samples of adequate size and range of body sizes and by their different ecologies: (1) *Oxydactyla stenodactyla*, a high montane burrower in grass clumps; (2) *Austrochaperina derongo*, a streamside-associated species; (3) *Sphenophryne cornuta*, a scansorial form that calls from shrubs and low trees; (4) *Liophryne schlaginhaufeni*, a terrestrial, surface-active species sometimes out in daytime; and (5) *Austrochaperina palmipes*, a more highly adapted semiaquatic species.

Relative tibia length generally decreases slightly with growth (that of *O. stenodactyla* the most), but *L. schlaginhaufeni* goes counter to this trend (fig. 61A). Adult head width is relatively narrower in all but *schlaginhaufeni*, too (fig. 61B), and the same trend appears in eye size and eye–naris distance (fig. 61C). Internarial span decreases in all five species (fig. 61D). Hand size increases in three species and decreases in two, whereas foot length increases in two and decreases in three (fig. 62A, B). Among the four species with digital discs, three show some increase in the finger disc whereas *derongo* does not (fig. 62C). One species, *cornuta*, shows a slight increase in toe disc size whereas the other three do not (fig. 62D).

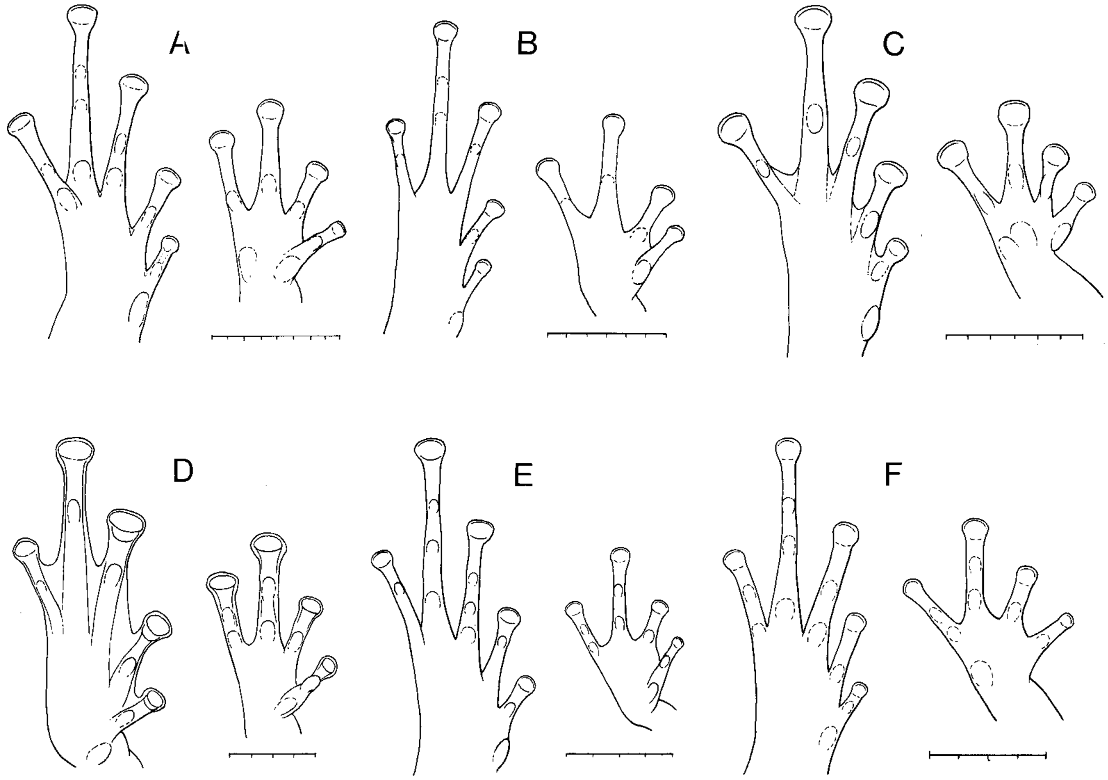

Fig. 56. Lower surfaces of feet and hands of *Austrochaperina*. **A.** *A. rivularis*, AMNH A77576. **B.** *A. macrorhyncha*, BPBM 13860. **C.** *A. basipalmata*, AMNH A78167. **D.** *A. palmipes*, AMNH A81210. **E.** *A. parkeri*, MCZ A89220. **F.** *A. blumi*, MZB 3562. Scale bars marked in 1-mm intervals.

The most striking ontogenetic change in *O. stenodactyla* is the relative narrowing of the head. Head-first burrowing through tightly packed grass may put a premium on maintaining a narrow prow.

Austrochaperina derongo has proportions that I associate with leaf-litter species, in the midrange of the other species and paralleling the growth changes of most others.

Sphenophryne cornuta is notable for its ontogenetic increase in relative hand size, foot length, and disc size. These tendencies must be related to its scansorial habits. The increase in foot length coupled with a decrease in tibia length is especially notable, for in most species these two are directly correlated both in trend direction and amount.

Liophryne schlaginhaufeni has the longest legs and feet, and both measurements increase relatively with growth, in marked contrast to the other species (but see *cornuta*, above). This elongation of limb segments provides an efficient jumping mechanism in a surface-active species, and the maintenance of relative eye size rather than relative decrease may be related to surface activity, too. The increase in the size of the small finger discs is not explicable as a direct adaptation, but may merely accompany the significant increase in hand size.

Increase in hand size is presumably a scansorial adaptation in *A. palmipes*, although in this instance the climbing is done on stream-associated rocks rather than in bushes. The digital discs are large and either increase slightly (fingers) or maintain their relative size (toes).

OSTEOLOGY

A thorough description of the osteology is not possible owing to lack of appropriate material of about 40% of the species studied. I have examined cleared-and-stained (bone, or

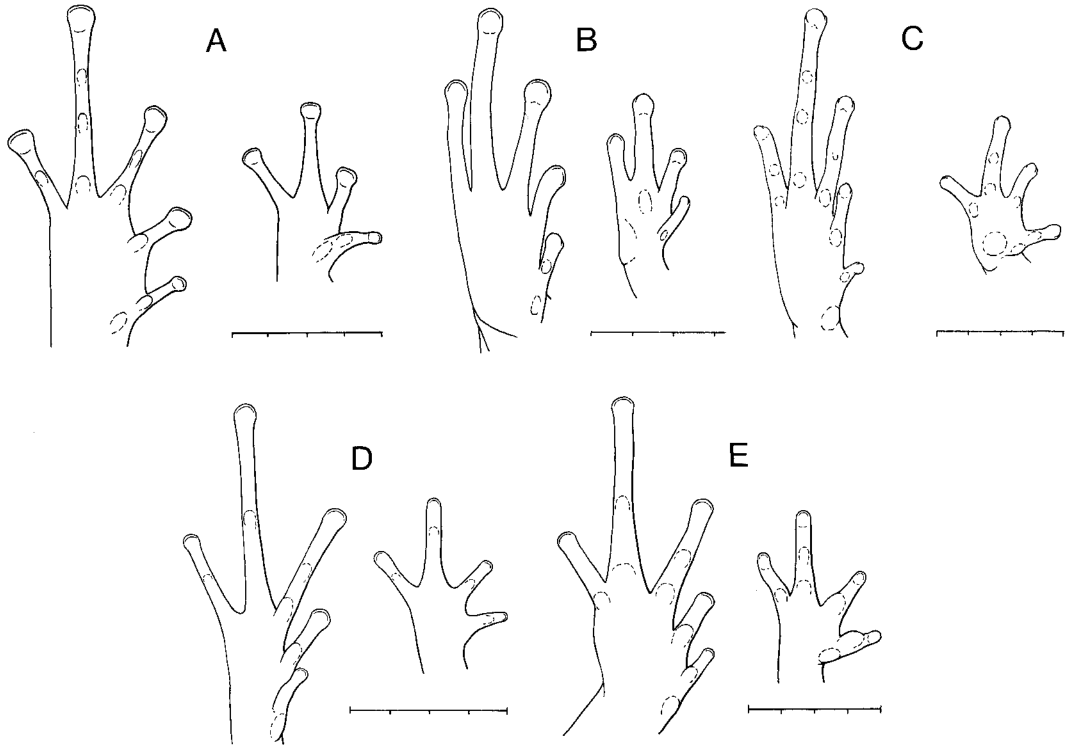

Fig. 57. Lower surfaces of feet and hands of *Austrochaperina*. **A.** *A. yelaensis*, AMNH A135406. **B.** *A. novaebritanniae*, AMS R29351. **C.** *A. gracilipes*, AMS R62053. **D.** *A. mehelyi*, UPNG 7241. **E.** *A. brevipes*, AMNH A120523. Scale bars marked in 1-mm intervals.

bone and cartilage) preparations of 20 species, including three Australian endemics, and three additional dried skeletons of one of the 20, a total of 38 specimens.[12] I do not attempt to describe and compare all features of the skeletal anatomy, but concentrate on those that seem to offer some utility in assessing relationships.

SKULL

As is the case in other genyophrynine genera, the skulls of the species considered here are generally sturdy, well-ossified structures, even in species of rather small adult size (figs. 66–68).[13] The skull is typically broader than long, with the width/length being ≥1.1 (as high as 1.5) in all specimens except single individuals of two small species, *Austrochaperina gracilipes* (0.982) and *A. novaebritanniae* (0.915). The nasals are large and scarcely separated from each other and from the frontoparietals. The quadratojugal is consistently present.

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[12] *Austrochaperina basipalmata* (2), *A. blumi, A. brevipes, A. derongo* (6), *A. fryi, A. gracilipes, A. kosarek, A. novaebritanniae, A. palmipes* (3 + 3 dried), *A. pluvialis, A. rivularis, A. robusta, Liophryne allisoni, L. dentata, L. rhododactyla, L. schlaginhaufeni, Oxydactyla alpestris, O. coggeri, O. stenodactyla* (6), *Sphenophryne cornuta* (3).

[13] In addition to those presented here, illustrations of the skulls of genyophrynine genera may be found in the following works: Burton, 1986 (*Cophixalus, Genyophryne*); Fry, 1912 (*Austrochaperina*); Fry, 1916 (*Aphantophryne*); Méhelÿ, 1901 (*Austrochaperina* as *Chaperina*; *Copiula*; *Cophixalus* as *Phrynixalus biroi*; *Oreophryne* as *Sphenophryne biroi*); Zweifel, 1971 (*Genyophryne*); Zweifel, 1985b (*Cophixalus*; *Austrochaperina* as *Sphenophryne*); Zweifel and Parker, 1989 (*Aphantophryne* and *Cophixalus*). Wandolleck (1911) illustrated disarticulated skull bones of *Sphenophryne, Liophryne* (as *Sphenophryne schlaginhaufeni*), and *Oreophryne* (as *Mehelyia*).

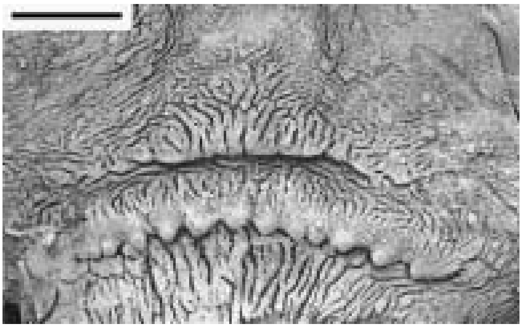

Fig. 58. SEM photograph of palatal folds of *Liophryne rhododactyla* BPBM 9793, anterior to top of figure. Scale line spans 2 mm.

FRONTOPARIETALS: In most species these are somewhat parallel-sided bones, flaring posteriorly and in some with lateral margins converging slightly anteriorly (figs. 66–68). Exceptions are *A. blumi*, *A. gracilipes*, and *A. novaebritanniae*, in which the lateral margins diverge gradually before flaring (see Zweifel, 1985b: fig. 45, for *gracilipes)*. There is considerable interspecific variation in the width of the braincase relative to the width of the skull, with the ratio ranging from 0.209 to 0.455. Two small species, *A. gracilipes* (0.429) and *A. novaebritanniae* (0.444), and *Sphenophryne cornuta* (mean 0.376 [0.336–0.455], N = 3) have the widest braincases. The frontoparietal region is unusually short in *cornuta* where the ratio of braincase length to skull length averages 0.559 (0.526–0.580, N = 3). The lowest such ratio in all other specimens is 0.631 in one of five *Oxydactyla stenodactyla*.

PREMAXILLAE: The premaxillae of 15 species are illustrated in figures 63 and 64, where ventral views emphasize the shape of the premaxillary shelf. Interspecific variation in the shelf involves its length (relative to the width of the bone) and the degree of emargination of the posterior edge. The relatively longest bones are seen in *O. alpestris* and *O. stenodactyla*, with *O. coggeri* approaching these two in length. The first two also show the least emargination. Inasmuch as these (and *coggeri*) are secretive species and probably are head-first burrowers in litter and grass clumps, the relatively robust bones may serve a strengthening function.

Another variable in premaxillae is the extent to which the ascending process slopes forward. In species with snouts that project notably beyond the lip, such as *A. palmipes* and *A. rivularis*, the ascending process is conspicuous in ventral view, whereas processes that are essentially vertical cannot be seen (*O. alpestris*, *O. coggeri*). The variation shown in the drawings should not be taken

Fig. 59. SEM photographs, enlarged views of conical projections of posterior palatal fold shown in fig. 58. Left scale line spans 100 μm, right 20 μm.

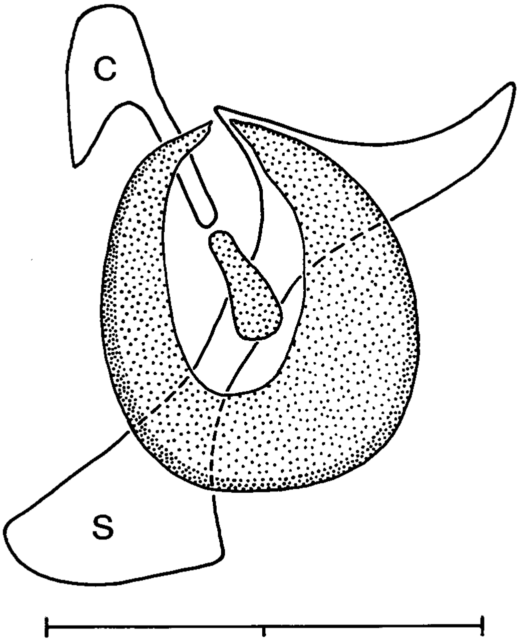

Fig. 60. Lateral view of right ear of *Austrochaperina brevipes* (AMNH A130527, anterior to right). Cartilage stippled, bone clear; c = columella, s = squamosal; scale line spans 2 mm.

too literally, as accurate depiction depends on having the premaxillary shelf exactly horizontal when drawn, an ideal not readily achieved with such tiny bones.

The presence or absence of teeth or serrations on the labial margin of the premaxillae is discussed in the following section on dentition.

I regard the elongate shelf with little emargination and vertical ascending processes as derived features indicative of a close relationship between *O. alpestris* and *O. stenodactyla*. No such clear relationships appear in the apparently plesiomorphic features of the premaxillae of the other species, although *O. coggeri* is suggestively closer in morphology to *alpestris* and *stenodactyla* than to the others.

DENTITION: Parker (1934: 3) stated that in the Microhylidae, maxillary "teeth may be present or absent, but when present are usually well developed and of the normal Salientian pattern; in *Sphenophryne cornuta* alone have they been discovered in a vestigial condition." Those microhylids that possess "normal" teeth include all members of the Dyscophinae (Madagascar and southeast Asia) and most species of Cophylinae (Madagascar). In these groups there often are teeth on the vomer as well.

Typical maxillary and premaxillary frog teeth are elongate, tubular structures with a basal pedicel and a distal crown attached to the lingual surface of the bone in pleurodont fashion (Parsons and Williams, 1962: figs. 3–4, 7). Teeth of no genyophrynine microhylid match this description, but in several species studied here, as well as in some *Cophixalus* (Zweifel, 1985b) there are toothlike maxillary and premaxillary structures. Any such structures on the vomer are more clearly odontoids or serrations.

Among cleared-and-stained specimens of 19 species I examined, 11 have smooth-edged maxillary and premaxillary bones with no trace of teeth: *Austrochaperina basipalmata, A. blumi, A. derongo, A. fryi* (Australian), *A. gracilipes, A. novaebritanniae, A. palmipes, A. pluvialis* (Australian), *A. rivularis, A. robusta* (Australian), and *Liophryne rhododactyla*. The remaining eight have toothlike irregularities along the edges of the bones: *Austrochaperina brevipes, Liophryne allisoni, L. dentata, L. schlaginhaufeni, Oxydactyla alpestris, O. coggeri, O. stenodactyla*, and *Sphenophryne cornuta*. In addition, *L. rubra* apparently has tiny teeth.

The toothlike structures are not uniform among species, but range from being relatively large, almost fanglike, to fine serrations, with the variation having no particular correlation with the size of the frog. Some of the finer structures (but not all) appear most toothlike. Thus, it is likely that the various structures are not homologous—some may be true tooth vestiges (e.g., those of *S. cornuta* and *L. dentata*), and others, especially the grosser serrations in such species as *A. brevipes*, may be neomorphs and not necessarily homologous among species. Illustrations in Wandolleck (1911: figs. 3, 12) contrast the more toothlike structures of *S. cornuta* with the serrations of *L. schlaginhaufeni*. The question of the nature of the toothlike structures is of consequence for determining polarities, for if true (albeit vestigial) teeth are present, this would represent the plesiomorphic state, whereas the absence

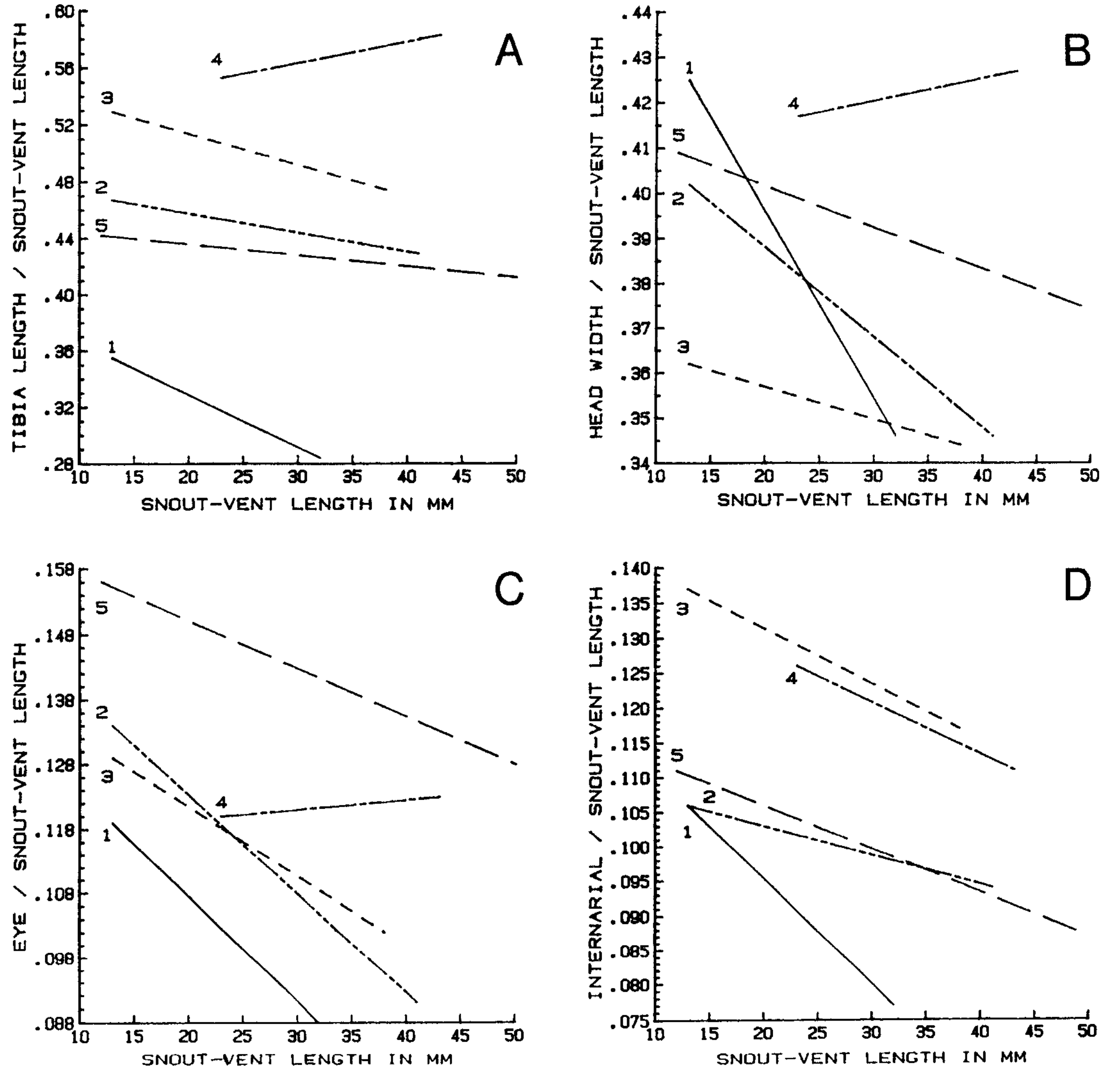

Fig. 61. Changes of proportions relative to body size in five species: 1, *Oxydactyla stenodactyla*; 2, *Austrochaperina derongo*; 3, *Sphenophryne cornuta*; 4, *Liophryne schlaginhaufeni*; 5, *Austrochaperina palmipes*.

of teeth or presence of serrations would be apomorphies, possibly either sequential or independent.

VOMER: This is a complex bone that may derive from vomerine and palatine precursors, but whose developmental history remains to be clarified (Trueb, 1973; de Sá and Trueb, 1991). I use the term vomer without prejudice as to the bone's true nature. In most species studied (including three Australian species not illustrated here, but see Zweifel: 1985b, fig. 47), a lateral arm of bone extends from the midline of the palate to the maxilla (or almost so), and an anterior arm passes medial to the internal naris, in most instances sending a branch laterally along the anterior border of the naris (fig. 65). The exceptional species is *Austrochaperina novaebritanniae* (fig. 65J), in which there are separate anterior and posterior bones, and the lateral arm stops short of the maxilla. This may represent a pedomorphic state. In *Sphenophryne cornuta* the lateral arm also tapers out short of the maxillary shelf while the prenasal branch is

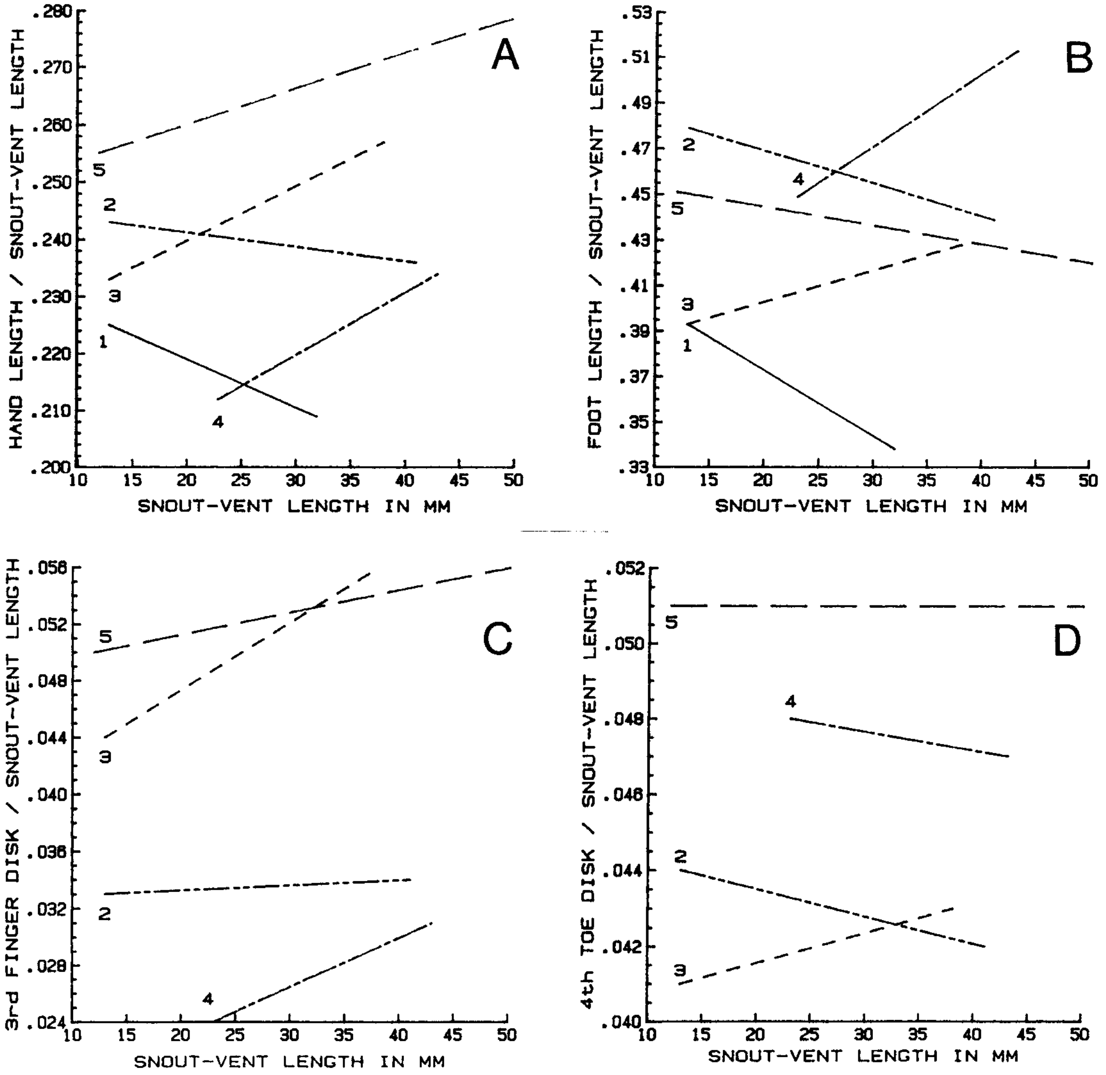

Fig. 62. Changes of proportions relative to body size in five species, key numbers as in fig. 61. (*Oxydactyla stenodactyla* lacks digital discs.)

variable: in one specimen (fig. 65P) there is merely an angle in the anterior arm; another has a short, broad- based, pointed arm; and a third has a longer narrow arm. Wandolleck (1911: fig. 6) illustrated a moderately long branch. Similarly, my specimen of *Liophryne schlaginhaufeni* lacks a prenasal branch, but Wandolleck (1911: fig. 15) shows the vomer with such a branch.

The vomers figured range from relatively massive to rather spindly, and they vary greatly in detail. That of *Sphenophryne cornuta* (fig. 65P) stands out for its broad prenasal arm. The medial plate is large and the lateral arm relatively thick in *L. rhododactyla*, *L. dentata*, and *L. schlaginhaufeni* (fig. 65F–H). Jagged toothlike structures are present on *L. allisoni* (fig. 65E) and *S. cornuta* (fig. 65P), and *A. palmipes* bears a single or double downward- directed spike (fig. 65O). Some of these and other similarities may derive from closeness of relationship, but given the paucity of information on individual variation (see remarks above on *S. cornuta* and

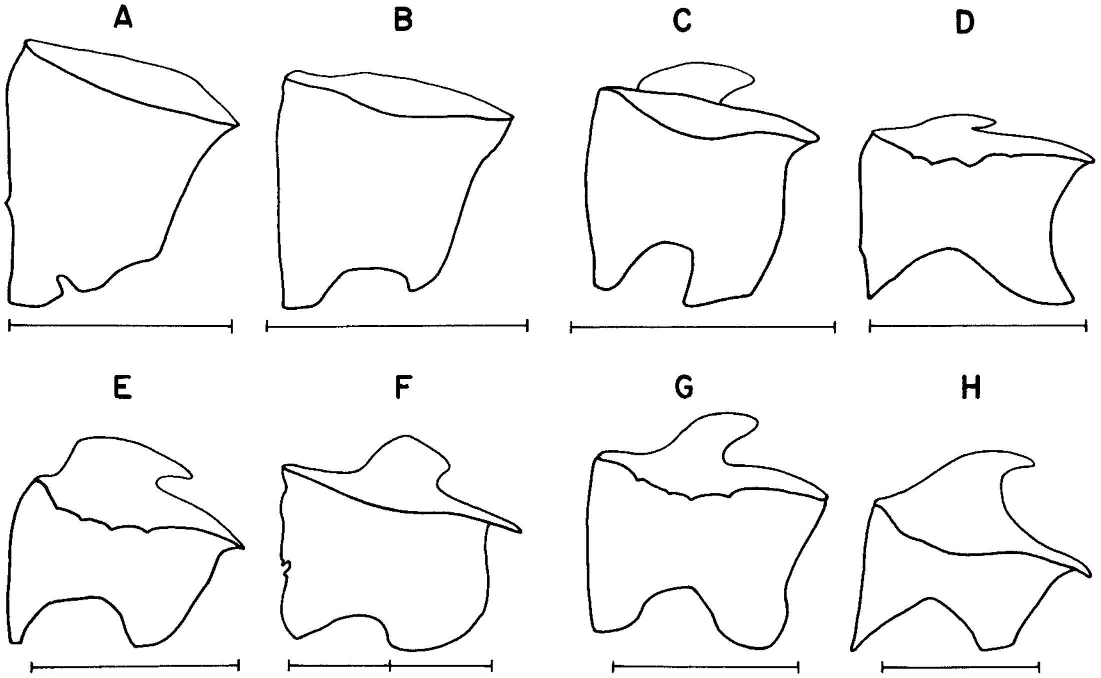

Fig. 63. Left premaxillae of *Oxydactyla*, *Austrochaperina*, and *Liophryne* in ventral view. Scale lines represent 1 mm unless otherwise indicated. **A.** *O. stenodactyla*, AMNH A92800. **B.** *O. alpestris*, AMNH A65299. **C.** *O. coggeri*, AMNH A140874. **D.** *A. brevipes*, AMNH A130527. **E.** *L. allisoni*, BPBM 9631. **F.** *L. rhododactyla*, BPBM 9793 (scale 2 mm). **G.** *S. dentata*, UPNG 2641. **H.** *L. schlaginhaufeni*, AMNH A78183.

L. schlaginhaufeni), such similarities should not be given too much emphasis. However, note that variation among species and genera in degree of lateral expansion is greater than Burton (1986: 425) had recognized in the Genyophryninae.

SQUAMOSAL: The zygomatic ramus of the squamosal varies relatively little in length, being longest in *Oxydactyla alpestris* and *O. stenodactyla* and somewhat shorter in most other species, especially *Sphenophryne cornuta* (figs. 66–68). The extent of the otic ramus is more variable. It may be so short as to be scarcely evident, or an elongate arm extending medially almost as far as the medial end of the columella, or some stage in between. Two small species, *Austrochaperina gracilipes* (Zweifel, 1985b: fig. 45) and *A. novaebritanniae*, show minimal development, whereas maximum elongation occurs in both a relatively small species (*A. brevipes*, fig. 67C) and several larger ones: *A. palmipes*, *L. dentata*, *L. rhododactyla* (fig. 68B), and *L. schlaginhaufeni*. The remaining species for which material is available show intermediate stages not readily quantified: *A. basipalmata*, *A. blumi*, *A. derongo*, *A. fryi*, *A. pluvialis*, *A. rivularis* (fig. 68A), *A. robusta* (short, Zweifel, 1985b: fig. 45), *L. allisoni* (relatively long, fig. 68C), *O. alpestris* (rather short), *O. coggeri* (fig. 67B), *O. stenodactyla* (short, fig. 67A), and *S. cornuta* (fig. 66).

HYOID APPARATUS: If the variation seen in hyoids of the species studied has any systematic significance, elucidation of this must await availability of a suite of specimens that will make both individual and specific variation better known. However, there may be implications on a higher systematic level.

None of the specimens examined has a parahyoid bone, which, so far as is known, is unique in the Microhylidae to the monotypic South American genus *Adelastes* (Zweifel, 1986: fig. 4). Some mineralization of the cartilaginous hyoid plate is present in

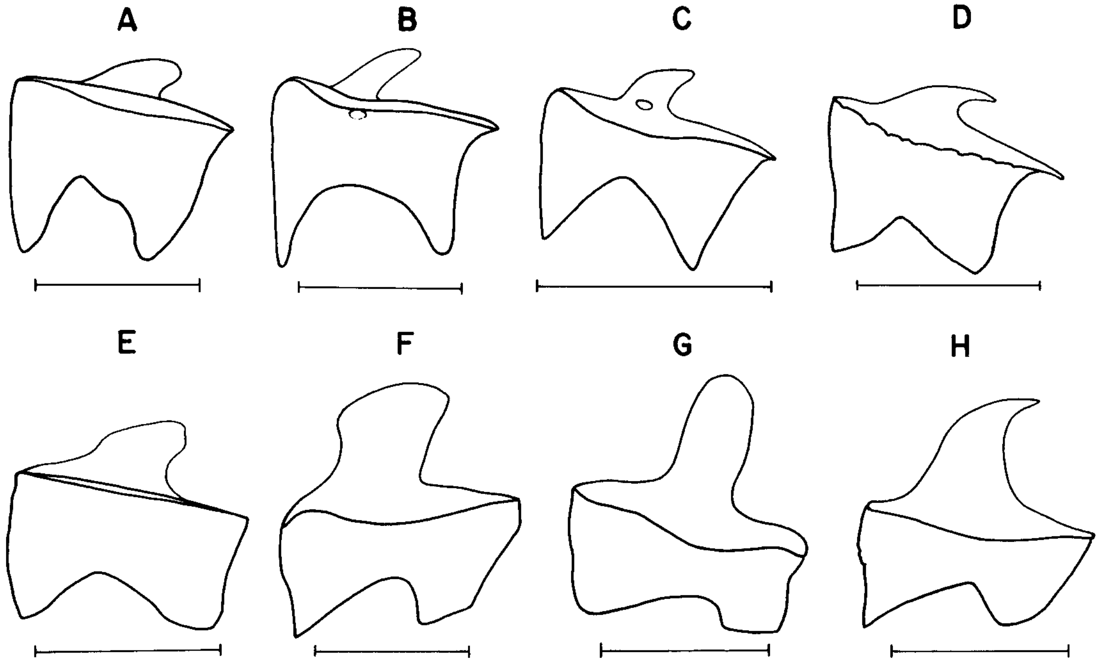

Fig. 64. Left premaxillae of *Austrochaperina* and *Sphenophryne* in ventral view. Scale lines indicate 1 mm unless otherwise stated. **A.** *A. gracilipes,* AMNH A90407 (scale 0.5 mm). **B.** *A. novaebritanniae,* AMNH A88569 (scale 0.5 mm). **C.** *A. blumi,* UPNG 9559. **D.** *S. cornuta,* AMNH A92804. **E.** *A. basipalmata,* AMNH A129495. **F.** *A. rivularis,* AMNH A88445. **G.** *A. palmipes,* AMNH A92807. **H.** *A. derongo,* AMNH A145507.

most species examined here, but the degree is variable. To some extent this variation may be specific: six specimens of *Austrochaperina derongo* all show mineralization, whereas among four *Oxydactyla stenodactyla* that can be scored, three lack mineralization and one has slight mineralization.

There is conspicuous variation in the anterolateral and posterolateral processes of the hyoid plate. The former may be absent (fig. 69C) to very well developed (Zweifel, 1985b: fig. 50E) or some intermediate form (figs. 69A, B; Zweifel, 1985:, figs. 50A–D). The posterolateral processes are less variable (see figures cited).

I direct attention to an anatomical feature of the microhylid hyoid that has been largely ignored in the literature. Trewavas (1933: 519) described ‘‘a median ventral thickening of the cartilage between the origins of the postero-medial processes, and often a mid-ventral ridge in front of this’’ in species of Dyscophinae, Genyophryninae, Microhylinae, and Scaphiophryninae. She referred to those species possessing this morphology as the ‘‘*Gastrophryne*-group’’ and stated that in this and some other respects they ‘‘contrast sharply with other firmisternal families.’’ The feature was found lacking in *Breviceps* and *Hemisus*. These last two genera have been variously considered as microhylids or *Hemisus* has been referred to its own family. Most recently, Blommers-Schlösser (1993) has removed the Brevicipitinae from the Microhylidae and placed it with the Hemisotinae in the Hemisotidae.

One worker to take notice of this feature was Roux (1944, fig. 9), who described and illustrated a ‘‘ventro-median anteriorly directed process . . . . between the origins of the thyroid processes [bony posteromedial processes of Duellman and Trueb, 1986]’’ of *Gastrophryne carolinensis*. De Sá and Trueb (1991: 316, fig. 2) illustrated the hyoid of a South American microhyline, *Hamptophryne boliviana*, and described this structure as a ‘‘small bony projection.’’ What appears to be the same process is shown in an illustration

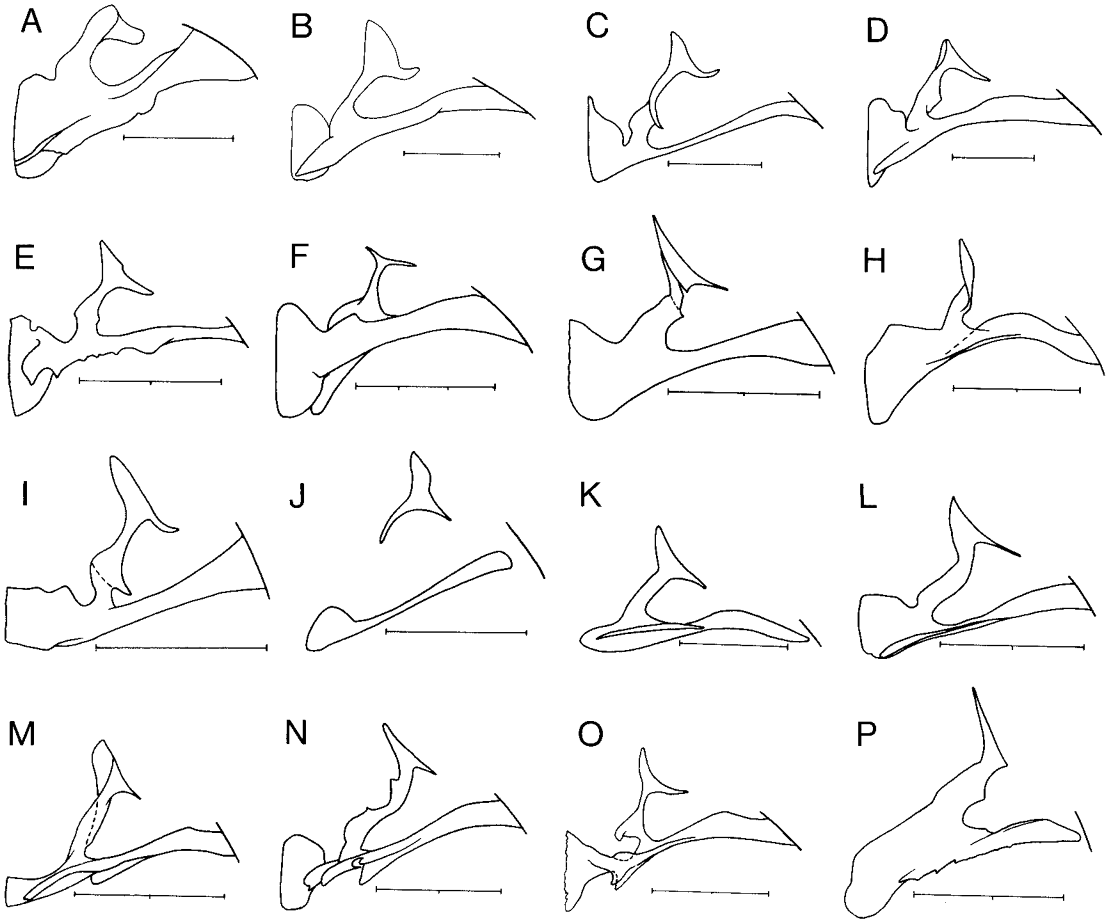

Fig. 65. Outline drawings of left vomers of *Oxydactyla*, *Liophryne*, *Austrochaperina*, and *Sphenophryne* in ventral aspect; scale lines marked in mm. Curved line at right of each figure marks the lingual border of the maxillary shelf. **A.** *O. stenodactyla*, AMNH A92800. **B.** *O. alpestris*, AMNH A65299. **C.** *O. coggeri*, AMS R22822. **D.** *A. brevipes*, AMNH A130527. **E.** *L. allisoni*, BPBM 9631. **F.** *L. rhododactyla*, BPBM 9793. **G.** *L. dentata*, UPNG 2641. **H.** *L. schlaginhaufeni*, AMNH A78183. **I.** *A. gracilipes*, AMNH A90407. **J.** *A. novaebritanniae*, AMNH A88569. **K.** *A. blumi*, UPNG 9559. **L.** *A. derongo*, AMNH A145507. **M.** *A. basipalmata*, AMNH A129495. **N.** *A. rivularis*, AMNH A84445. **O.** *A. palmipes*, AMNH A92805. **P.** *S. cornuta*, AMNH A92803.

of a New Guinean species, *Aphantophryne sabini*, and hinted at (by denser stippling) in another, *Cophixalus verecundus*, but was not discussed (Zweifel and Parker, 1989: fig. 5). In his study of the Microhylidae, Parker (1934) did not deal with the hyoid, but only referred to Trewavas' monograph, which was in press at the time of his writing.

A coathooklike process is present in all the species I examined for this study, although it earlier eluded me (not shown in Zweifel, 1985b: figs. 50A–D). It nestles in the space between the proximal ends of the posteromedial processes, whose ends appear to have slight socketlike concavities. In most specimens it is clear and takes up little cartilage stain so that stained cartilage dorsal to it shows through and commonly has been illustrated as a flat plane of cartilage. In specimens stained only for bone, the process is even more easily overlooked. However, occasionally it is heavily mineralized, and then it is conspicuous in alizarin-stained specimens. This is especially true of my specimen

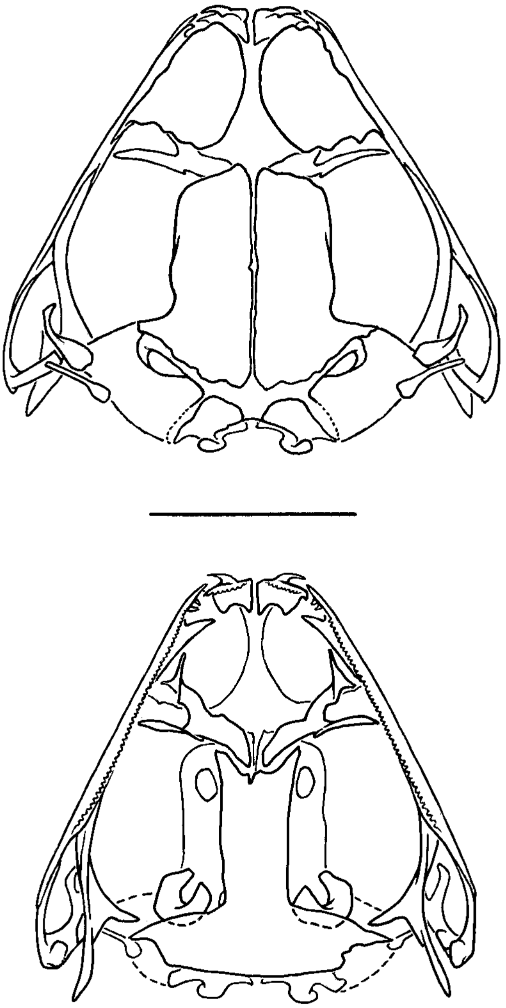

Fig. 66. Dorsal (upper) and ventral views of skull of *Sphenophryne cornuta*, AMNH A92804; scale bar measures 5 mm.

of *Liophryne allisoni* (fig. 70). Although ventromedial thickening of the hyoid and the protruding process evidently are not pertinent at the level of specific and generic inquiry here, this morphology may prove to be an apomorphic state for the Microhylidae.

Appendages

Terminal Phalanges: The tips of the bones may bear T-shaped expansions whose span is more than twice the width of the base of the bone, or at the other extreme the tip may be bluntly rounded with only a slight subterminal constriction, its width less than that of the base. The relative breadths of the fleshy terminal disc and that of the phalangeal "T" are closely correlated. The terminal discs are discussed further under Body Form and Proportions. The terminal phalanx of the third finger, which generally shows the greatest expansion of any of the hand's digits, illustrates the range of variation (fig. 71). Among specimens of 20 species (one examined by dissection), the span of the tip relative to the length of the phalanx or to the width of its base falls into one of three discrete groups: (1) tip span/length of 0.24 and 0.32 in *Oxydactyla alpestris* and *O. stenodactyla* (species with narrow, discless fingers); (2) of 0.54–0.82 in 13 species known or suspected to be litter-dwelling or surface active species; and (3) of 1.09–1.36 in five species of scansorial (*Sphenophryne cornuta*), riparian (*Austrochaperina palmipes, A. rivularis, A. derongo,* and *A. basipalmata*) habits.

Axial Skeleton

Presacral Vertebrae: There are invariably eight nonimbricate presacrals, as described for the Australian species (Zweifel, 1985b: 355). Variations in the transverse processes include relative lengths and angular orientation among vertebrae. For example, I find relatively long processes on vertebrae 2–4 and a strong anterior orientation to those on vertebrae 7 and 8 in *Austrochaperina derongo, A. rivularis, A. pluvialis,* and *A. palmipes,* whereas in *Oxydactyla stenodactyla* the processes are more similar in length and more nearly at a right angle to the column. Morphologies of the other species do not indicate that a classification of discrete types is possible.

Sacral Vertebrae: The sacral vertebrae are slightly to moderately expanded in most species discussed here, more so in one or two (figs. 72, 73). As an index of expansion I use the ratio of broadest diapophyseal measurement (anterior–posterior) to the span between ends of left and right diapophyses, excluding terminal cartilaginous extensions; a larger number implies broader diapophyses. Among 37 specimens of 19 species, including three Australian endemics, this ratio

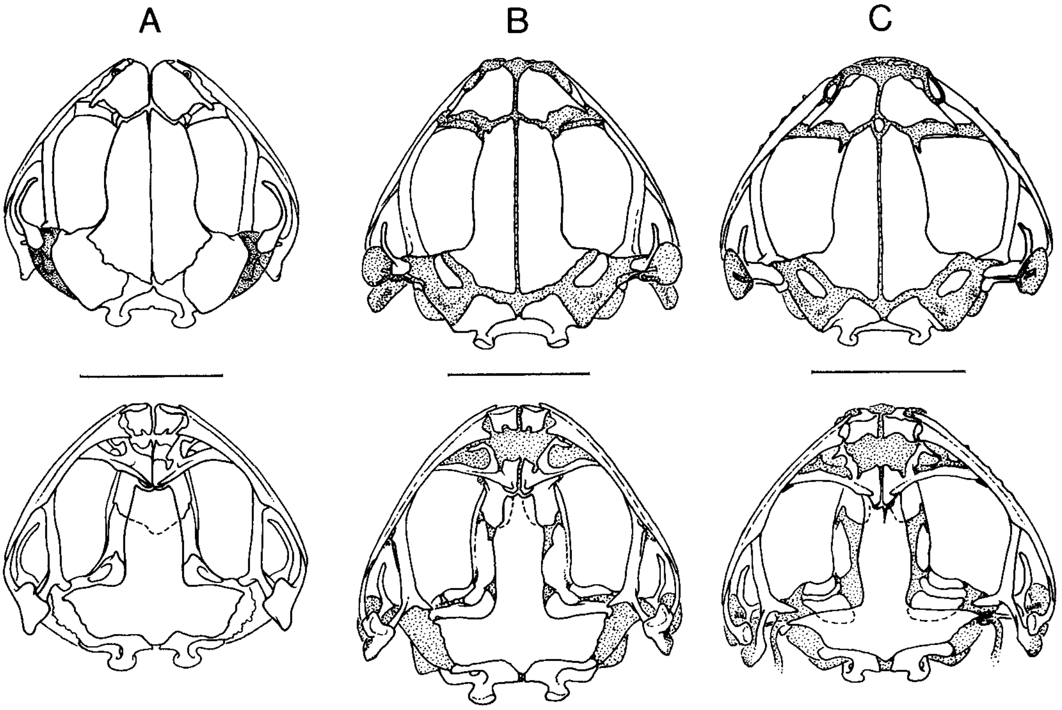

Fig. 67. Dorsal (upper) and ventral views of skulls of *Oxydactyla* and *Austrochaperina*. **A.** *O. stenodactyla,* AMNH A92802. **B.** *O. coggeri,* AMNH A140874. **C.** *A. brevipes,* AMNH A130527. Scale bars measure 4 mm.

ranges from 0.293 to 0.500 (table 14). In 15 species the ratio is <0.400, two single-specimen samples slightly exceed this figure at 0.412 and 0.425, and one sample (N = 6) averages 0.410 (range 0.382–0.448). Two other samples of five and six specimens each have similar variation but much lower means.

Within the assemblage, *Sphenophryne cornuta* stands out with more greatly expanded diapophyses. Its mean (0.467) and range (0.446–0.500, N = 3) are markedly displaced from those of other species. Only *Austrochaperina derongo* (mean 0.410, range 0.382–0.448, N = 6) approaches *cornuta.*

COCCYX: The coccyx articulates freely on paired sacral condyles in all specimens. In none of the specimens are there well-developed diapophyses (figs. 72, 73). The two largest single-species samples, *Austrochaperina derongo* and *Oxydactyla stenodactyla* (N = 6) each include individuals with no trace of diapophyses and others with one short pair, which is the maximum extent seen in any specimen. Therefore, I find nothing in the morphology of the coccyx of systematic utility.

PECTORAL GIRDLE: Evolutionary modifications of the microhylid pectoral girdle involve the reduction or deletion of ventral elements, any of which of the complete firmisternal primitive set of ventral elements (exemplified by *Rana*) except the coracoids may be involved. The girdles of the species studied here, examined by dissection in species for which cleared-and-stained specimens were not available, are among the more primitive in the family. They have in common the most complete set of elements of any Australopapuan microhylid (Genyophryninae and Asterophryinae) in that they possess bony coracoids and elongate clavicles, cartilaginous procoracoids, and a cartilaginous sternal plate (see Zweifel, 1985b: fig. 51, for two typical examples). A number of genera of Madagascar and Asia are more

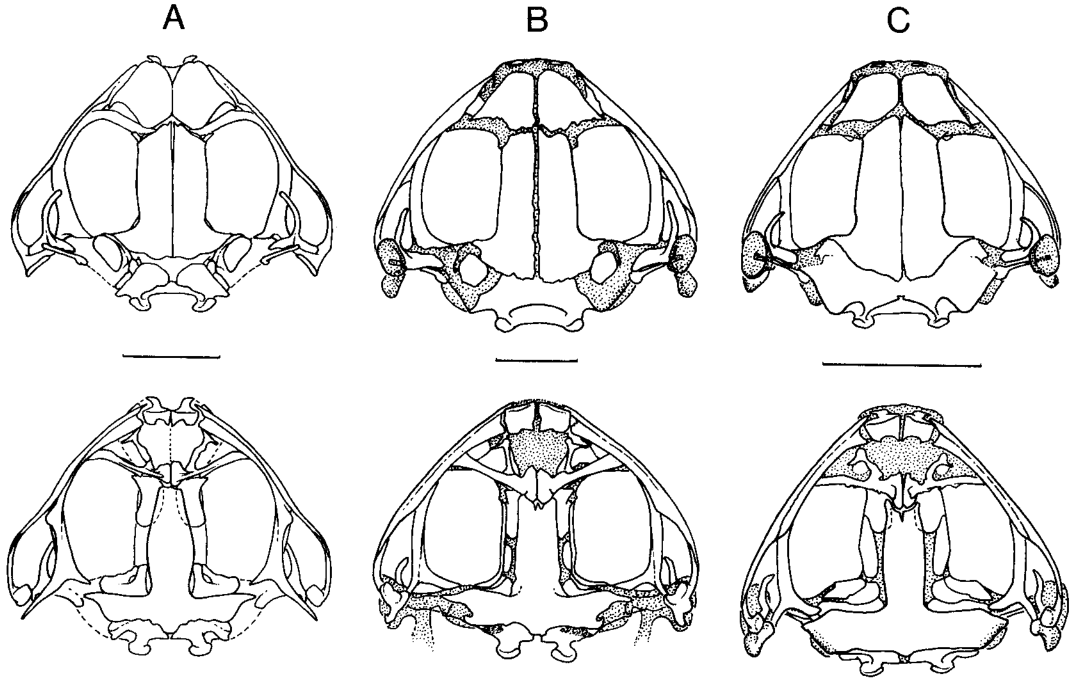

Fig. 68. Dorsal (upper) and ventral views of skulls of *Austrochaperina* and *Liophryne*. **A.** *A. rivularis,* AMNH A84445. **B.** *L. rhododactyla,* BPBM 9793. **C.** *L. allisoni,* BPBM 9631. Scale bars measure 5 mm.

primitive in that they possess, in addition to the elements mentioned above, a cartilaginous omosternum. According to Parker (1934), only one microhylid genus, *Dyscophus* of Madagascar, has a bony style to the omosternum, and none has a bony sternum.

The sternum shows some degree of mineralization in almost all the species studied, although it is slight in one of two *Austrochaperina basipalmata* and one of three *Sphenophryne cornuta* and is very slight in an *Oxydactyla coggeri.* The exception is *O.*

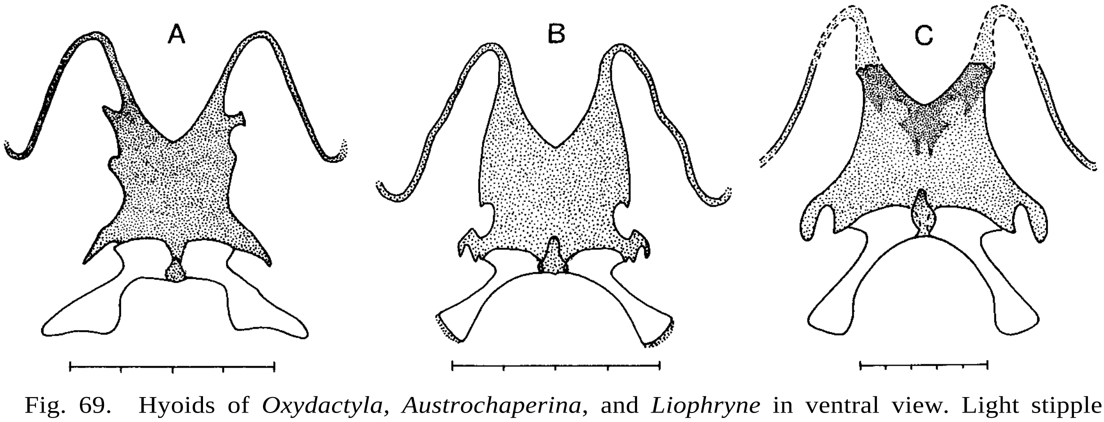

Fig. 69. Hyoids of *Oxydactyla, Austrochaperina,* and *Liophryne* in ventral view. Light stipple indicates cartilage, denser stipple mineralization. Proportions of bony posteromedial processes, which pass into the plane of the drawing, are distorted by foreshortening. **A.** *O. stenodactyla,* AMNH A66049. **B.** *A. brevipes,* AMNH A130527. C. *L. rhododactyla,* BPBM 9793. Scale lines marked in millimeters.

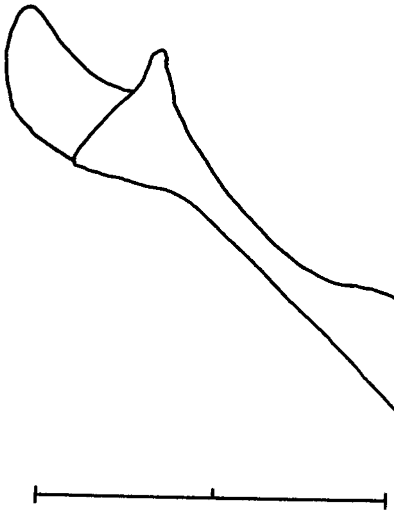

Fig. 70. Lateral view of left posteromedial process of the hyoid of *Liophryne allisoni*, BPBM 9631, with the ventromedian process projecting from its anterior end. The right (posterior) end of the posteromedial process angles toward the viewer. Scale line marked in millimeters.

stenodactyla, where four of six specimens show no mineral deposits and two others show only slight amounts. Dense staining of cartilage may mask mineral deposits in my specimen of *A. robusta*, and the sternum is damaged in specimens of *L. allisoni* and *O. alpestris*.

MYOLOGY

I offer here only a few comments on myology, as this topic was not within the intended scope of the work. This is not to deny the potential importance of further myological study, the value of which in microhylid systematics has been amply demonstrated (e.g., Burton, 1984, 1986).

JAW MUSCULATURE: Burton (1986) noted that in almost all genyophrynines the M. depressor mandibulae arises largely from the dorsal fascia, as illustrated for ‘‘*Sphenophryne schlaginhaufeni*’’ (probably *L. rubra*) by Burton (1986: fig. 11D). *L. rhododactyla* and *O. stenodactyla* (fig. 74) also have this common condition. The exceptions, assigned to the genus *Albericus*, have the origin of this muscle largely restricted to the otic ramus of the squamosal and the prootic region (Burton and Zweifel, 1995, fig. 3).

SUPERFICIAL MANDIBULAR MUSCULATURE: The Asterophryinae exhibit variation in the number and placement of supplementary slips of the M. interhyoidius, whereas the Genyophryninae show only a single slip, presumably a primitive condition (Burton, 1986). Burton (1984) called attention to differences in the supplementary slip that distinguish *Sphenophryne* (in the earlier, broad sense) from *Cophixalus*: ‘‘Supplementary slip . . . narrow, arising from either a posterior tendon or from dentary, and oriented parallel to the mandible’’ (*Cophixalus*), or ‘‘broad, arising from ventral fascia of angulosplenial, and oriented medially and only slightly anteriorly’’ (*Sphenophryne*). Zweifel (1985b) confirmed these observations for additional Australian species of the two genera.

Typical conformation of the supplementary slip for two Australian *Austrochaperina* is illustrated for *A. fryi* (as *Sphenophryne,* sp. nov.) in Burton (1984: fig. 1B) and *A. robusta* (as *S. robusta*) in Zweifel (1985b: fig. 55B). Six New Guinean species, *A. palmipes, Liophryne dentata, L. rhododactyla, L. schlaginhaufeni* (fig. 75C), *Oxydactyla crassa,* and *O. stenodactyla* (fig. 75A), resemble these closely, but *Sphenophryne cornuta* (fig. 75B) differs in that the muscle bundle is abruptly tapered posteriorly and has its fiber orientation more nearly parallel to that of the mandible. While awaiting confirmation of the situation in additional species, a tentative conclusion is that the condition in *cornuta* is derived relative to that common to other species.

KARYOLOGY

Information is available for just nine species of *Austrochaperina* and *Liophryne,* four of them Australian endemics (Kuramoto and Allison, 1989; Mahony et al., 1992; James Menzies (personal commun.). *Sphenophryne* and *Oxydactyla* have not been karyotyped.

Seven species have the presumably primitive diploid number 2N = 26 (see discussion in the papers cited above and in Bogart and Nelson, 1976) consisting of five large and

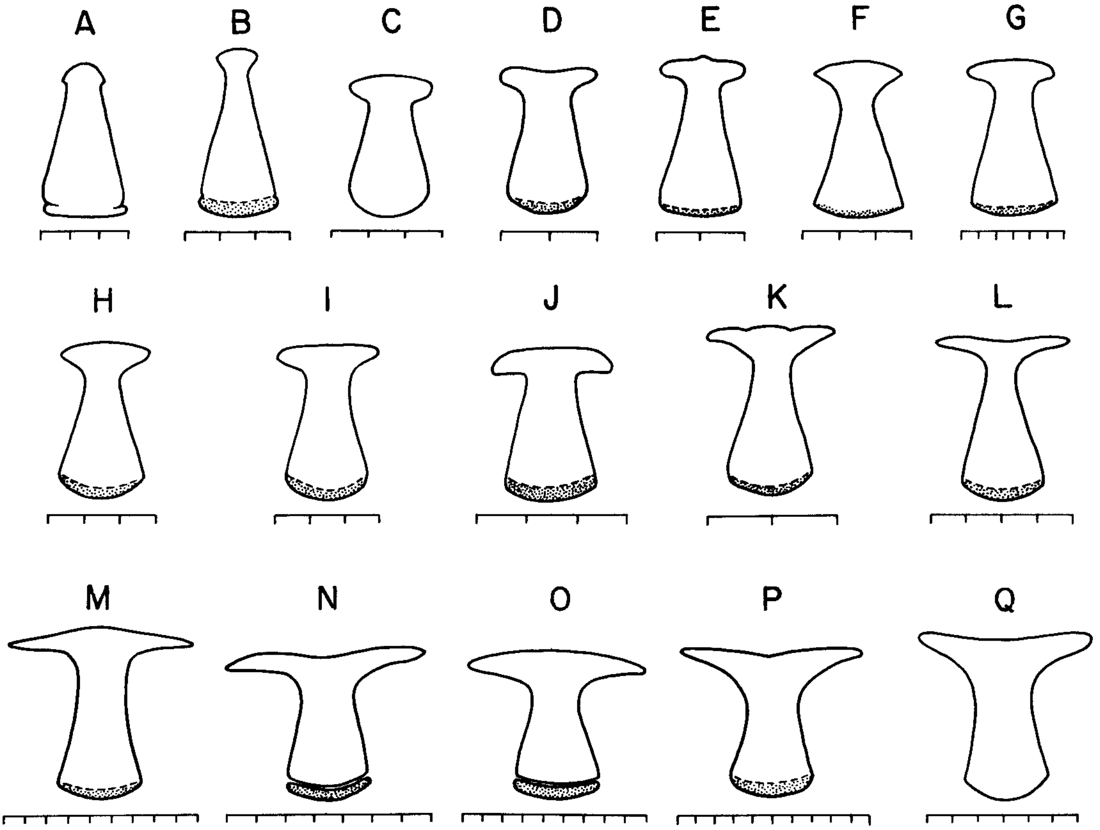

Fig. 71. Terminal phalanges of third fingers of *Austrochaperina*, *Liophryne*, *Oxydactyla* and *Sphenophryne*; scale lines marked in 0.1-mm intervals. **A.** *O. stenodactyla*, AMNH A92801. **B.** *O. alpestris*, AMNH A65299. **C.** *O. brevicrus*, AMNH A43761. **D.** *O. coggeri*, AMNH A140874. **E.** *A. brevipes*, AMNH A130527. **F.** *L. allisoni*, BPBM 9631. **G.** *L. rhododactyla*, BPBM 9793. **H.** *L. dentata*, UPNG 2641. **I.** *L. schlaginhaufeni*, AMNH A78183. **J.** *A. gracilipes*, AMNH A90407. **K.** *A. novaebritanniae*, AMNH A88569. **L.** *A. blumi*, UPNG 9559. **M.** *S. cornuta*, AMNH A92804. **N.** *A. basipalmata*, AMNH A129495. **O.** *A. rivularis*, AMNH A88445. **P.** *A. palmipes*, AMNH A92807. **Q.** *A. derongo*, AMNH A145507.

eight small chromosome pairs: *Austrochaperina adelphi, A. fryi, A. gracilipes* (J. Menzies, personal commun.), *A. pluvialis, A. palmipes, A. robusta,* and *Liophryne rhododactyla*. One Papuan species, *Liophryne schlaginhaufeni,* has 2N = 30, and another, "sp. B" of Mahony et al., probably *A. derongo,*[14] has 2N = 24. Mahony et al. (1992) demonstrated that the karyotype of *schlaginhaufeni* could be derived from a 2N = 26 karyotype by fission, although the recovered karyotype does not precisely match any of those available for comparison. These authors were "unable to suggest a simple mechanism for the diploid number reduction" to 2N = 24 in "sp. B."

The fact of variation in diploid numbers in this small sample gives hope that data from additional species may be of use in estimating relationships, but for the present we have little more than isolated facts.

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[14] I have not examined the two specimens cited, AMS R130754 and R116927 (the latter reported as "R116297," which is a snake, whereas 116927 is an *Austrochaperina* from the locality given), but they were collected along with a series of *A. derongo,* and the only other species of *Austrochaperina* in that collection was the distinctive *A. palmipes,* which has 2N = 26.

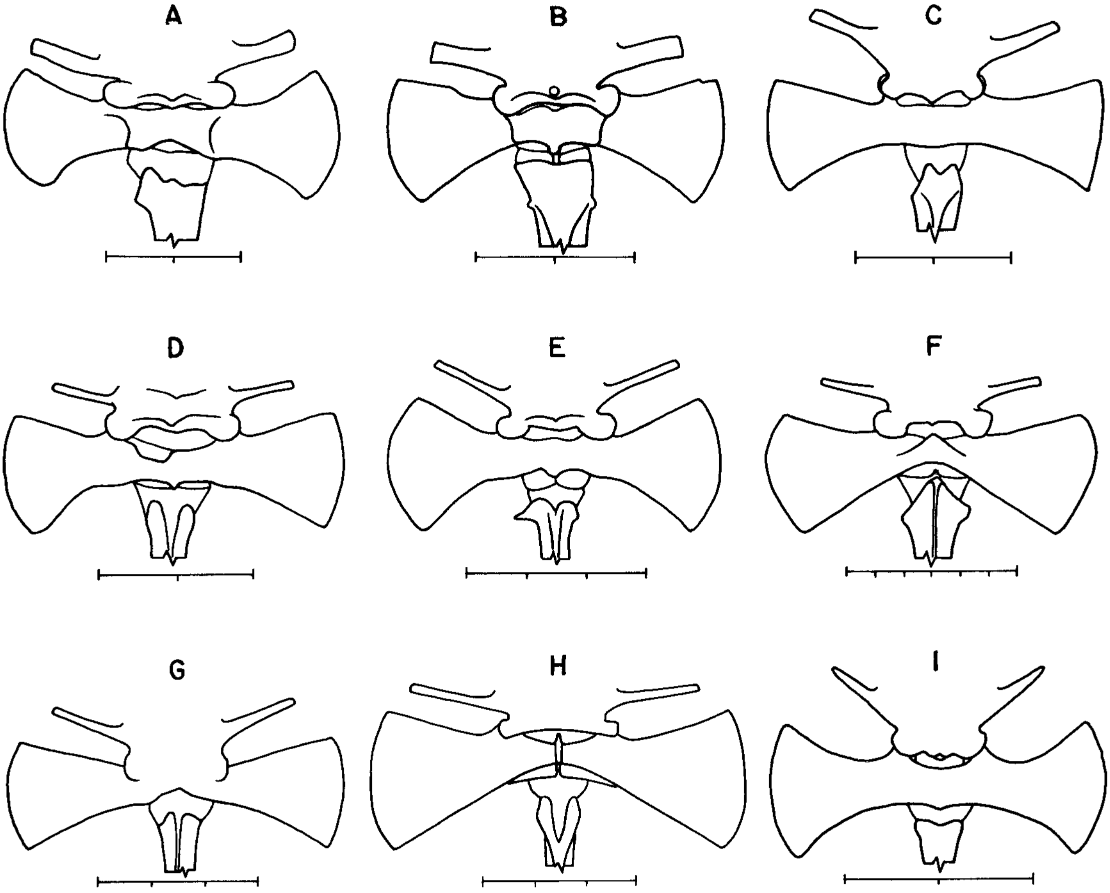

Fig. 72. Outline drawings of sacral regions of *Oxydactyla*, *Austrochaperina*, and *Liophryne* in dorsal view; scale lines marked in millimeters. **A.** *O. stenodactyla*, AMNH A92799. **B.** *O. alpestris*, AMNH A65299. **C.** *O. coggeri*, AMNH A140874. **D.** *A. brevipes*, AMNH A130527. **E.** *L. allisoni*, BPBM 9631. **F.** *L. rhododactyla*, BPBM 9793. **G.** *L. dentata*, UPNG 2641. **H.** *L. schlaginhaufeni*, AMNH A78183. **I.** *A. gracilipes*, AMNH A90407.

VOCALIZATIONS

Data on advertisement calls unfortunately are sparse. I have recordings of just 14 New Guinean species in addition to the four Australian endemics: *Austrochaperina adelphe* (Australian), *A. brevipes*, *A. derongo*, *A. fryi* (Australian), *A. gracilipes*, *A. guttata*, *A. macrorhyncha*, *A. pluvialis* (Australian), *A. rivularis*, *A. robusta* (Australian), *Liophryne allisoni*, *L. dentata*, *L. similis*, *L. rhododactyla*, *L. schlaginhaufeni*, *Oxydactyla coggeri*, *O. crassa*, and *Sphenophryne cornuta*. In addition, there are casual verbal descriptions of two others: *A. palmipes*, and *O. stenodactyla*. This leaves the calls of 16 named New Guinean species unknown. Descriptions and statistics of the calls are given in the species accounts and associated tables (but see below). My purpose here is to examine the possible use of the calls in assessing relationships. The first requirement is to characterize and classify the advertisement calls produced by the species studied. An apparent territorial call is described in the account of *S. cornuta* but is not considered here.

First, I provide some definitions. A *note* is a discrete, continuous utterance, separated from following or preceding utterances by a quiet period. *Pulsing* is repeated amplitude

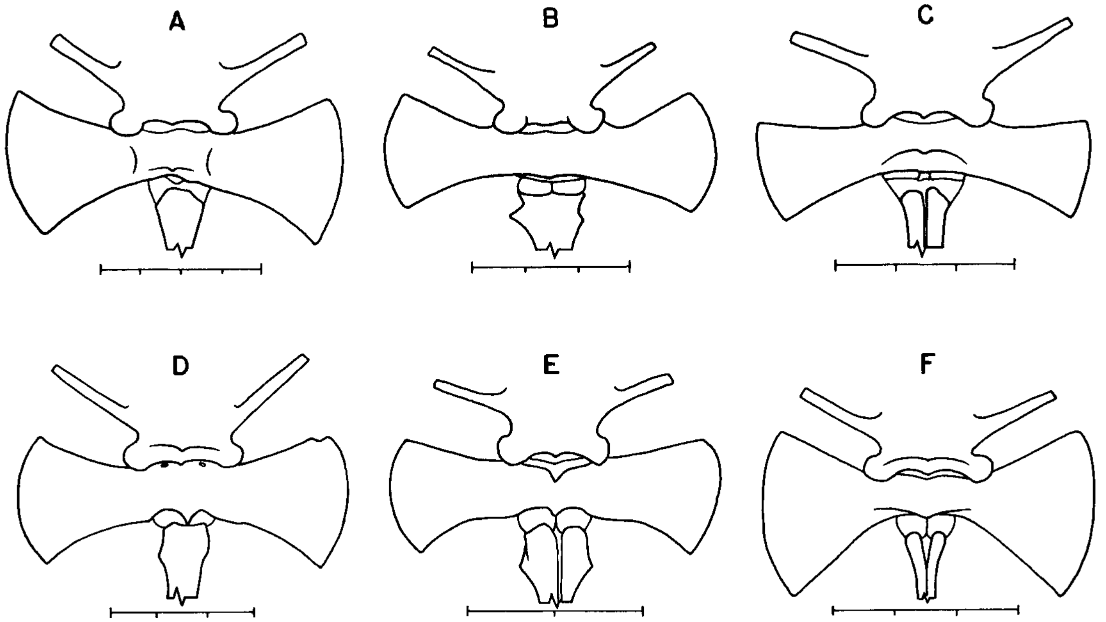

Fig. 73. Outline drawings of sacral regions of *Austrochaperina* and *Sphenophryne* in dorsal view; scale bars marked in millimeters. **A.** *A. rivularis,* AMNH A88445. **B.** *A. basipalmata,* AMNH A129495. **C.** *A. palmipes,* AMNH A92805. **D.** *A. derongo,* AMNH A92794. **E.** *A. blumi,* UPNG 9959. **F.** *S. cornuta,* AMNH A92803.

modulation within a note. A *call* is a unit of vocalization that may consist of a single note (when the period between notes is long with respect to the note duration and often is irregular) or may comprise notes rapidly repeated. Multinote calls may occur as short bursts of sound or may continue for long periods, sometimes seemingly indefinitely.

Subjectivity in classifying notes and pulses occurs when the amplitude variation of pulses (as seen in an expanded waveform) approaches or attains 100% but with little quiet space intervening. For descriptive purposes, it generally is best to let the ear dictate the classification in such cases.

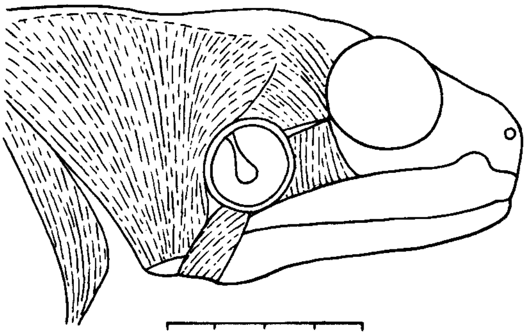

Fig. 74. Right lateral view of jaw musculature of *Oxydactyla stenodactyla.* Scale bar marked in millimeters.

A conspicuous dichotomy in the calls lies between those in which the notes are pure, unpulsed tones, and those whose notes are pulsed, giving a harsher sound sometimes characterized as a chirp. Calls with notes (or pulses) too rapidly repeated to be resolved by the human ear are heard as a buzz; none of the species discussed here has this type of call. The other major variable involves the organization of notes into calls. I identify three levels of increasing complexity: (1) calls consisting of a single note, which is repeated at intervals wide with respect to the duration of the note and is generally irregular; (2) calls including a train of similar notes repeated relatively rapidly and extending over long periods; (3) calls in which rather standardized groups of notes are uttered as units separated by silent periods of variable

TABLE 14
Expansion of Sacral Diapophyses in Species of *Austrochaperina*, *Liophryne*, *Oxydactyla*, and *Sphenophryne*[a]

Species	Mean ratio	Range	N
A. basipalmata	0.354	—	1
A. blumi	0.368	—	1
A. brevipes	0.333	—	1
A. derongo	0.410	0.382–0.448	6
A. fryi[b]	0.389	—	1
A. gracilipes	0.425	—	1
A. novaebritanniae	0.385	—	1
A. palmipes	0.326	0.293–0.368	5
A. pluvialis[b]	0.390	—	1
A. rivularis	0.412	—	1
A. robusta[b]	0.320	—	1
L. allisoni	0.399	—	1
L. dentata	0.333	—	1
L. rhododactyla	0.356	—	1
L. schlaginhaufeni	0.369	0.364–0.375	2
O. alpestris	0.364	—	1
O. coggeri	0.326	—	1
O. stenodactyla	0.362	0.314–0.392	6
S. cornuta	0.467	0.446–0.500	3

[a] The ratio is greatest breadth (anterior–posterior) of a sacral diapophysis/span between the distal ends of the right and left diapophyses, cartilage not included.

[b] Australian endemic species.

length, but usually greatly exceeding the length of the individual multinote call.

Among the species studied, only *O. crassa* and *L. rhododactyla* give unpulsed single-note calls, and there is none with a pulsed single-note call. Prolonged trains of similar pulsed notes occur in the calls of *A. derongo, A. guttata, A. macrorhyncha, A. rivularis,* and *L. dentata.* No unpulsed call falls into this category.

The third category—notes organized into discrete groups—includes most of the species. All four Australian endemic species of *Austrochaperina* and *A. gracilipes* (shared by Australia and New Guinea) have unpulsed calls and are included here, as are the New Guinean *Liophryne allisoni, L. similis,* and *Oxydactyla coggeri.* Three New Guinean species, *A. brevipes, L. schlaginhaufeni,* and *Sphenophryne cornuta,* have pulsed calls of this sort. The call of *A. palmipes,* if indeed it has one, is not well enough known to be characterized (see species account).

In treating the Australian species (Zweifel, 1985b: 378), I suggested that the "similarity of the five calls is consistent with a hypothesis of derivation from a common source (a monophyletic origin for the five species), but aside from the distinctive couplet uttering of

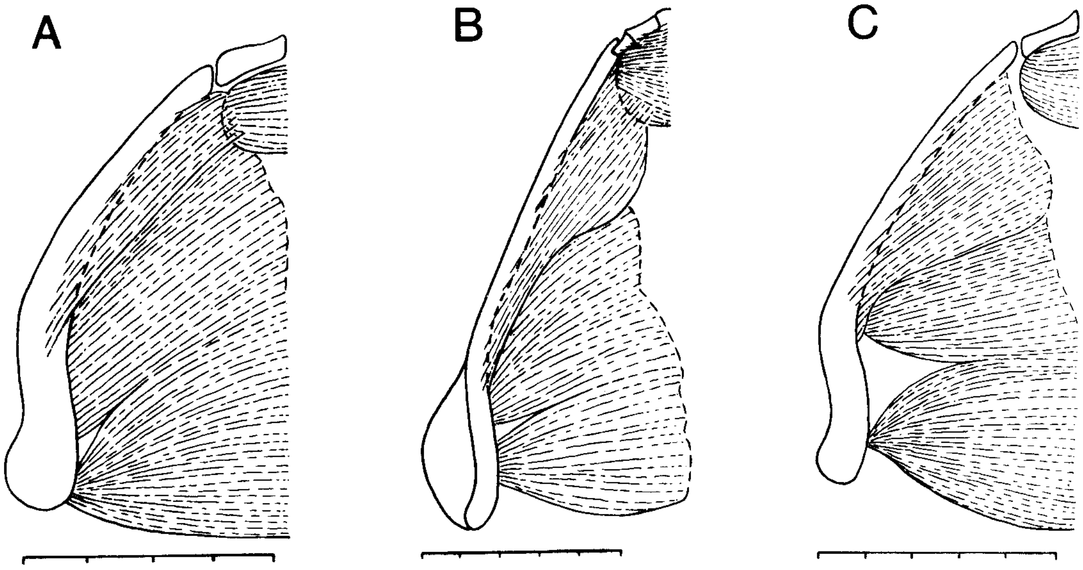

Fig. 75. Superficial mandibular musculature (right side). **A.** *Oxydactyla stenodactyla.* **B.** *Sphenophryne cornuta.* **C.** *Liophryne schlaginhaufeni.* Scale bars marked in millimeters.

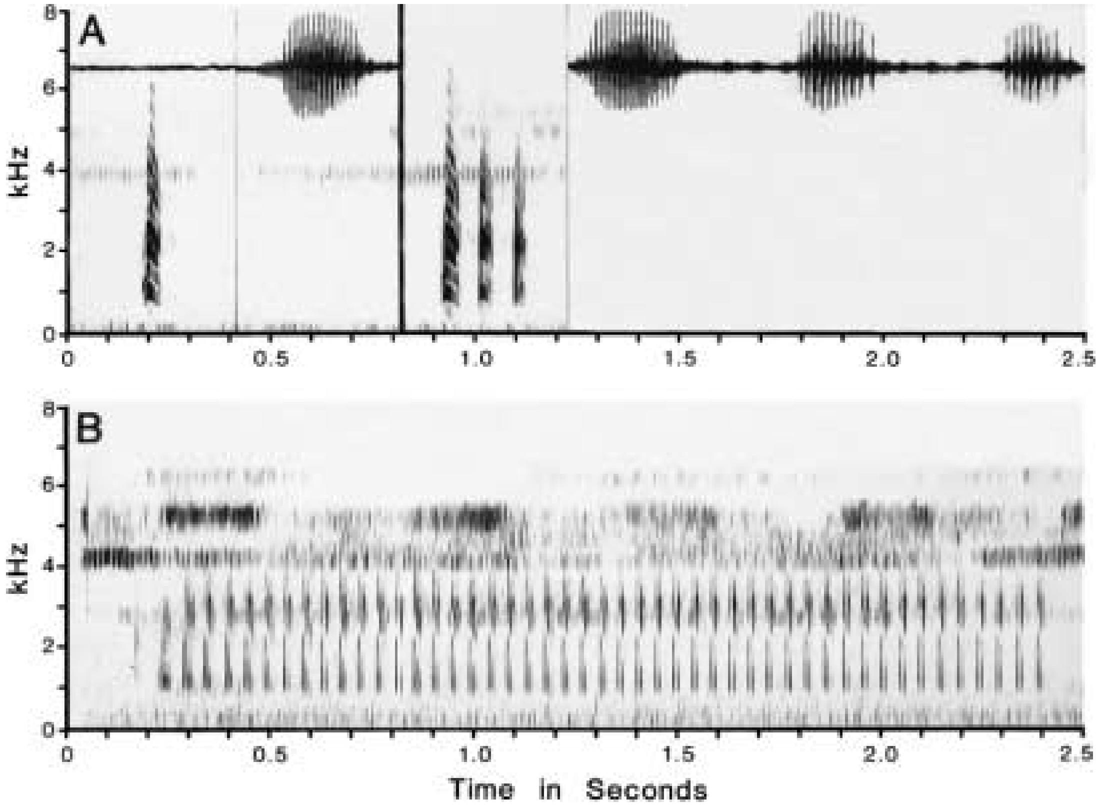

Fig. 76. Audiospectrograms of calls of *Sphenophryne cornuta* recorded in Western Province, Papua New Guinea. **A.** Possible territorial calls recorded at Finalbin, July 27, 1987 (see text); 300-Hz filter, time scale of wave forms 6× that of spectrogram, air 20.3°C, voucher specimen AMNH A130549, AMNH Herpetology tape reel no. 252. **B.** One complete advertisement call recorded by Ian Redmond at the junction of the Strickland and Rentoul rivers, Nov. 14, 1979; 300-Hz filter, no temperature, voucher specimen BMNH 1980.673, British Library of Wildlife Sounds No. 12274.

S. robusta, possibly a derived condition, I see no objective way of arranging the calls on a primitive to derived axis.'' With the New Guinean species added to the sample, one could bolster the argument for increasing complexity as a derived condition. Thus, single-note, unpulsed calls could be considered primitive compared to multinote unpulsed calls, and pulsed multinote calls would be the most derived.

Although the arrangement of calls I present above is useful for descriptive purposes, it would be naive to apply it uncritically in assessing relationships. Slightly more than half of the species (10 of 18) have unpulsed calls, and these (excepting two single-note species) differ mainly in note repetition rate and dominant frequency, with the latter being probably largely a reflection of body size. Given extant knowledge, I see no way of refuting the argument that unpulsed calls are essentially primitive and, in that respect, not phylogenetically informative. With more information available it might be possible to establish a primitive-derived sequence within the unpulsed calls in the third category. The examination of species pairs makes me doubtful, however. One of the two single-note species, *L. rhododactyla*, is morphologically identical to a multinote species, *L. similis*. How often might the change from single to multinotes (or the reverse) have evolved independently in different evolutionary lines?

The pulsed calls of the morphologically similar species *L. dentata* (category 2) and

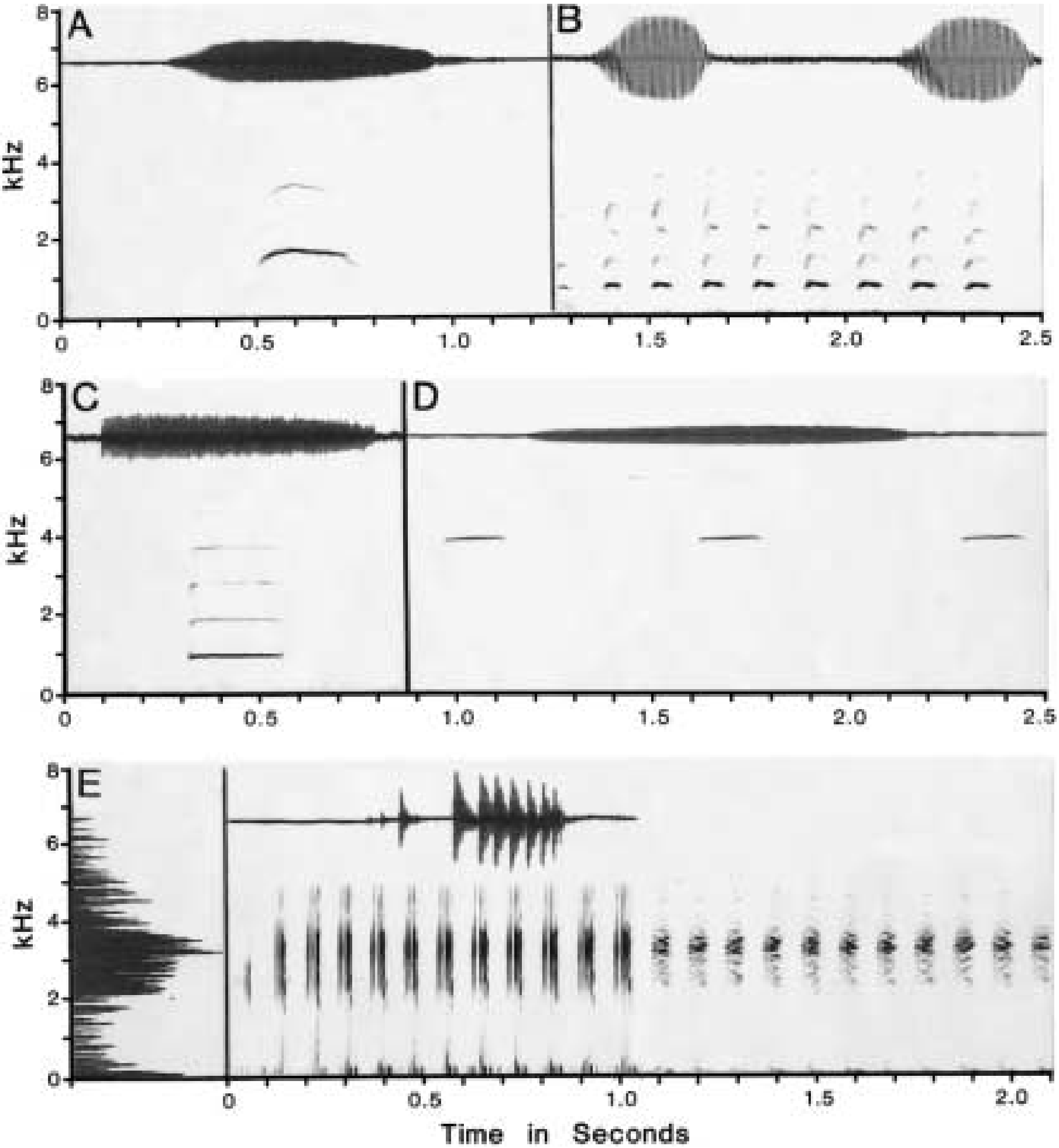

Fig. 77. Audiospectrograms of calls of five species of *Austrochaperina*, *Liophryne*, and *Oxydactyla* recorded in Papua New Guinea. **A.** *L. rhododactyla*, recorded by Allen Allison on Bulldog Road, Morobe Prov., April 30, 1982; 45-Hz filter, waveform in 3× time expansion, no voucher specimen or temperature, copy on AMNH Herpetology tape reel 244. **B.** *L. similis*, recorded at Myola Guest House, Northern Prov., Aug. 10, 1987; 45-Hz filter, waveform in 6× time expansion, air 12.8°C, voucher specimen AMNH A130570, AMNH Herpetology tape reel no. 253. **C.** *O. crassa*, recorded by James Menzies at Betamin, Mt. Dayman, Milne Bay Prov., July 1984; 45-Hz filter, waveform in 3× time expansion, no voucher specimen or temperature, copy on AMNH Herpetology tape reel no. 253. **D.** *A. gracilipes*, recorded at Wipim, Western Prov., Aug. 15, 1969; partial call, 45-Hz filter, wave form in 6× time expansion, air 24.0°C, voucher specimen AMNH A83070, AMNH Herpetology tape reel no. 189. **E.** *A. brevipes*, recorded at Myola Guest House, Northern Prov., Aug. 11, 1987; one complete call, initial notes graphed with 300-Hz filter, terminal notes with 45-Hz, waveform in 12× time expansion, air 12.9°C, no voucher specimen, AMNH Herpetology tape reel no. 253.

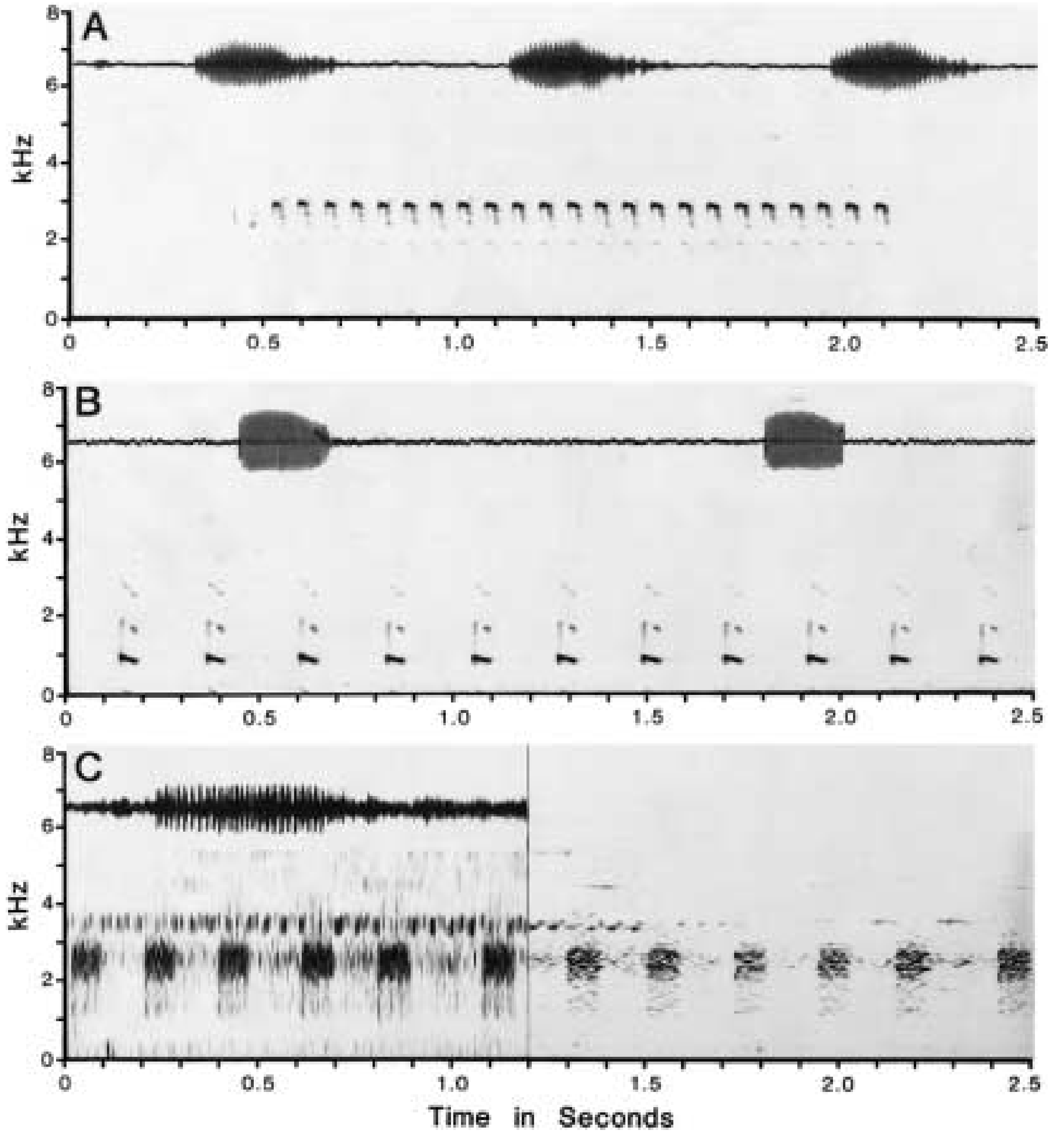

Fig. 78. Audiospectrograms of calls of *Liophryne* and *Oxydactyla* recorded in Papua New Guinea. **A.** *L. allisoni*, recorded by Allen Allison on Mt. Missim, Morobe Prov., Feb. 4, 1982; complete call, 45-Hz filter, waveform in 12× time expansion, air 16.4°C, voucher specimen BPBM 9361, copy on AMNH Herpetology tape reel no. 244. **B.** *O. coggeri*, recorded by James Menzies at Kaironk, Schrader Range, Madang Prov. on Aug. 30, 1968; one complete call, 45-Hz filter, wave form in 6× time expansion, no temperature, voucher specimen UPNG 837, copy on AMNH Herpetology tape reel no. 253. **C.** *L. dentata*, recorded by James Menzies near Alotau, Milne Bay Prov., Oct. 8, 1969; partial call, successive parts graphed with 300-Hz and 45-Hz filters, waveform in 6× time expansion, temperature not noted, voucher specimen UPNG 1727, copy on AMNH Herpetology tape reel no. 253.

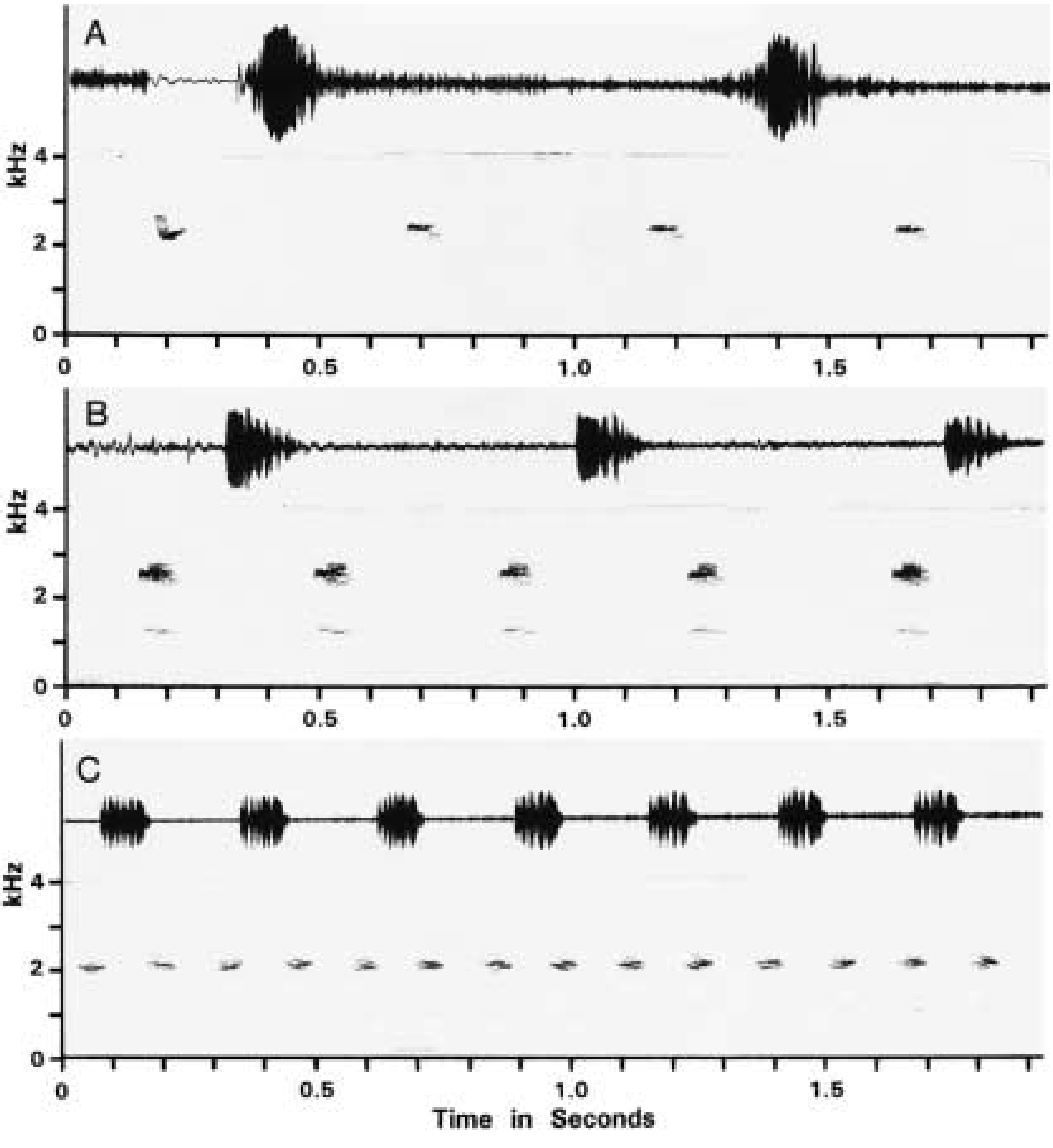

Fig. 79. Audiospectrograms of calls of *Liophryne* and *Austrochaperina*. **A.** *L. schlaginhaufeni*, recorded near Mabimap Village, Adelbert Mountains, Madang Prov., Papua New Guinea, by James Menzies, voucher specimen UPNG 7246 (see table 9), copy of recording on AMNH Herpetology tape reel 286. **B.** *A. rivularis*, recorded by Stephen Richards on Mt. Stolle, 1600 m, West Sepik (Sanduan) Prov., Papua New Guinea, on July 4, 1993, temperature not recorded, voucher specimen QM J67247. **C.** *A. guttata*, recorded by S. Richards at Ivimka Field Station, 5.5 km S, 5.6 km W of Tekadu Airstrip, Gulf Prov., Papua New Guinea, on Nov. 19, 1996; voucher specimen QM J67256, air temperature 26.3°C. In all figures the audiospectrograms were made with a 59-Hz filter and the waveforms, representing notes 1–N, are in 2× expansion. Copies of S. Richards recordings are on AMNH Herpetology tape reel no. 284.

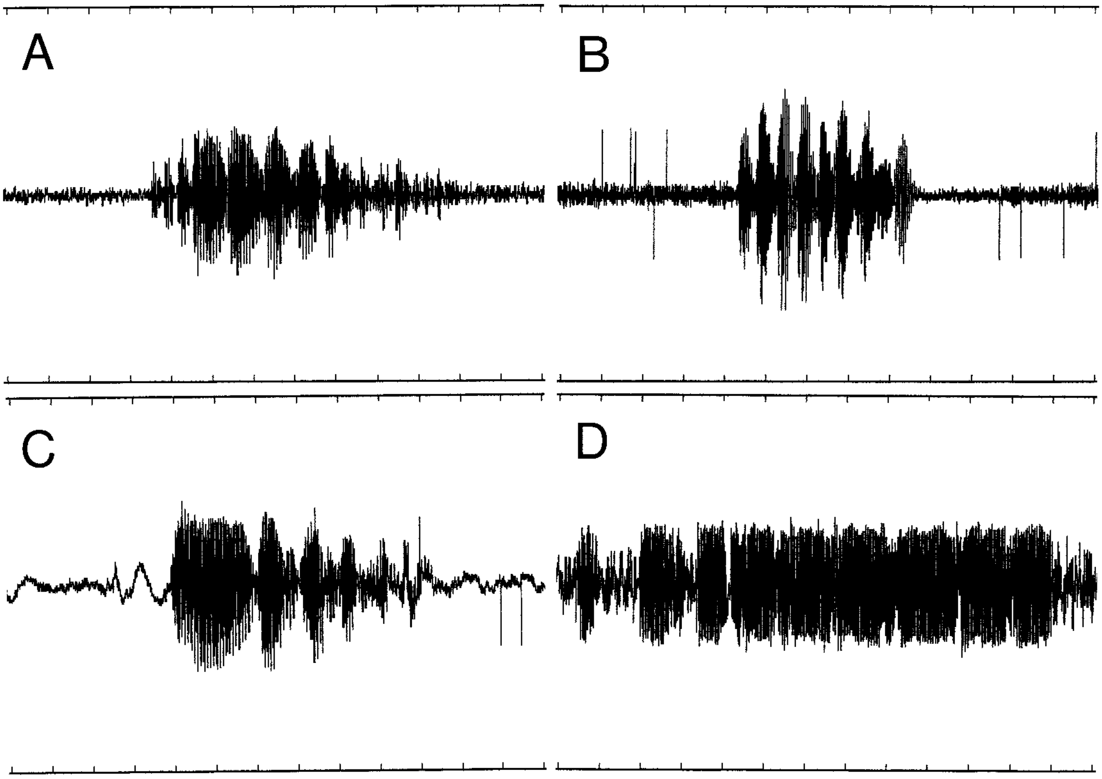

Fig. 80. Waveforms of call notes of four species of *Austrochaperina*. **A.** *A. derongo*. **B.** *A. guttata*. **C.** *A. rivularis*. **D.** *A. macrorhyncha*. Scale markings are in 0.01-sec intervals.

L. schlaginhaufeni (category 3) are comparable except that in the former, note utterance continues for minutes and varies in rate, whereas the latter species calls in discrete, individual units. The other category 2 species, *A. derongo*, *A. macrorhyncha*, *A. rivularis*, and *A. guttata*, certainly have no close relationship to *L. dentata*, nor do the other pulsed-note species in category 3, *A. brevipes* and *S. cornuta*, to each other or to *L. schlaginhaufeni*.

Advertisement calls of these microhylids are invaluable for distinguishing among species and may yet yield useful information on interspecific relationships, but I remain dubious about utility at higher taxonomic levels.

STRUCTURE OF PULSED NOTES: FOUR SIMILAR CALLS COMPARED

Four species of *Austrochaperina—derongo, guttata, macrorhyncha,* and *rivularis*—have calls of common structure: prolonged series of short, harsh, pulsed notes that are superficially similar, at least to the human ear. Table 5 summarizes pertinent characteristics of their calls (but bear in mind that this is based on only one call from each of three individuals and two of another). *A. derongo* is distinguished by the relative brevity of its call and by the high number of pulses per call. *A. guttata* has the shortest note duration and the highest note repetition rate. *A. macrorhyncha* has a slow repetition rate of the longest notes, whereas *rivularis*, with a similar repetition rate, has notes little more than half as long. Thus, the calls differ in at least two quantities each. Whether the range of dominant frequencies (ca. 2100–2800 Hz) is significant is uncertain.

Examination of the internal structure of the notes reveals other differences in addition to number of pulses (fig. 80). Two calls of what evidently was the same individual of *A.*

guttata recorded about an hour apart have notes with somewhat different structure. In one, 30 notes have pulses of essentially uniform length (fig. 80B). Among 30 notes of the second call, 16 have the terminal pulse abruptly longer (fig. 79C), 3 resemble notes in the first call, and 11 show a more gradual increase in pulse length.

One call of *A. rivularis* has two sorts of pulse structure: 27 of 40 notes have the initial pulse much the longest (figs. 79B, 80C), whereas in 13 notes the pulses are more nearly equal in length. In a single call of *A. derongo* the notes (14 of 16) start with short pulses, then change to distinctly longer ones (fig. 80A); in only two notes are the pulses about equal in length. The notes of *A. macrorhyncha* begin with a short pulse and, after a brief pause, continue with longer, tightly spaced pulses. Variation in pulsation in these and other species deserves attention when more recordings are available.

INTERGENERIC AND INTRAGENERIC RELATIONSHIPS

Burton (1986) put forth a solid argument for monophyly of the Asterophryinae, but (p. 443) stated that ‘‘The monophyly of the Genyophryninae has not been demonstrated. Nor has its paraphyly.’’ Phylogenetic analysis of the subfamilies of Microhylidae that might affirm the status of the Genyophryninae has not been accomplished. However, the close relationship of the Genyophryninae and Asterophryinae is strongly supported by a shared derived character—direct embryonic development. This reproductive mode is indicated in all species of the two subfamilies for which adult female specimens are available. Not only is the presence of large, unpigmented, heavily yolked ova in specimens sufficient evidence, but no tadpole of the characteristic microhylid sort has been found in New Guinea. Some compression of the life-cycle is seen occasionally in other subfamilies of Microhylidae (e.g., nonfeeding tadpoles), but direct development is uncommon elsewhere in the Microhylidae. I am aware of only one example, the South American microhyline *Myersiella microps* (Izecksohn and Jim, 1971). In view of the independent attainment of direct development in several other families of Anura and the lack of any other apparent apomorphies linking this South American form with the Australopapuan genera, I consider the similarity an instance of homoplasy.

Whereas the Genyophryninae and Asterophryinae may be considered as closest relatives, with the Asterophryinae the more derived, I have no evidence to indicate where the nearest relationship between the Genyophryninae and non-asterophryine microhylids may lie.

Direct development in the genera *Austrochaperina*, *Liophryne*, *Oxydactyla*, and *Sphenophryne* (as well as in the Asterophryinae) is a derived character with respect to the situation in the vast majority of microhylids, but the four genera are more primitive in other respects. This is most evident in the pectoral girdle, which in all has a nearly complete complement of ventral elements, lacking only the omosternum. A complete girdle, including the omosternum (cartilaginous in all but *Dyscophus* of Madagascar, small or vestigial in some), is present in several genera, mostly of Madagascar, but with southern India (*Melanobatrachus*), Africa (*Parhoplophryne*), and South America (*Otophryne*) also represented. A girdle with the single apomorphy of loss of the omosternum is also geographically widespread, including (in addition to the Australopapuan genera treated here) southeast Asia (*Chaperina*), North and Central America (*Hypopachus*), and South America (*Dermatonotus* and *Stereocyclops*).

Most of the Madagascar microhylids possess well-developed maxillary and vomerine teeth, certainly a primitive character. Vestigial(?) teeth or toothlike structures occur sporadically in the four Australopapuan genera, but not regularly enough to establish any one genus as more primitive.

As an aside, I note that the dentition, pectoral girdle structure, and lack of pharyngeal folds in many microhylids of Madagascar marks this fauna as the most primitive of the Microhylidae.

The monotypic *Sphenophryne* is the most derived form in the four genera, with its reduced first finger, enlarged digital discs, broad sacral diapophyses, and short braincase. None of the more advanced genyophrynine genera is likely to be directly related to *Sphenophryne*.

Liophryne too does not appear to relate well to other genyophrynines. The long legs, large eyes, and subarticular elevations of these mostly surface-active species are not found in other genyophrynines, although the less typical *L. allisoni* could be a link with *Austrochaperina*.

Oxydactyla, adapted for living cryptically in leaf litter or grass tussocks, could be derived by way of terrestrial *Austrochaperina*, with *A. brevipes* being perhaps closest morphologically to *Oxydactyla*.

Given the specializations of the other three genera, *Austrochaperina*, apart from those species with adaptations for semiaquatic life, is the most generalized and perhaps the most primitive of the genyophrynine genera. I find, however, no satisfactory way of relating *Austrochaperina* to microhylids outside of the Australopapuan region. Such an investigation is well beyond the scope of this work. Note, however, similarities between certain *Austrochaperina* and another genyophrynine genus, *Copiula* (see following).

RELATIONSHIPS WITHIN *AUSTROCHAPERINA*

The 23 species of *Austrochaperina* may be arranged by body size in two groups. One, composed of relatively small frogs (maximum adult size range 21–35 mm SVL), includes the New Guinean species *adamantina, aquilonia, blumi, brevipes, gracilipes, kosarek, mehelyi, novaebritanniae, parkeri, polysticta*, and *yelaensis*, as well as the four Australian endemics, two of which are the largest species in the group. The eight species of the other group are larger (38–52 mm)—*archboldi, basipalmata, derongo, guttata, hooglandi, macrorhyncha, palmipes*, and *rivularis*. I shall refer informally to the first group as the Small group, and to the others as the Large group.

Three of the five Australian members of the Small group dwell in rainforest leaf litter. The sibling species *A. adelphe* (Australian) and *A. gracilipes* (common to Australia and New Guinea) are apparent exceptions, living in seasonally dry environments and sometimes calling from sites slightly above the substratum. Only two of the New Guinean species, *brevipes* and *novaebritanniae*, are confirmed as leaf-litter inhabitants, but the morphology of the others suggests that habit.

An attempt to infer relationships within the Small group is frustrated by paucity of material—four of the New Guinean species are known from only one specimen each, another from two, and the unique specimen of another was destroyed. Second, the leaf-litter habitat preference evokes no distinctive adaptations such as the long hind legs, large eyes, and subarticular elevations of surface-active *Liophryne*, the enlarged finger discs of scansorial *Sphenophryne*, the short hind legs and pointed toe-tips of burrowing *Oxydactyla*, or the large digital discs and toe-webbing of riparian *Austrochaperina*.

The Small group is essentially what remains when the slightly better characterized Large group is removed. The Australian species (including *gracilipes*) have some claim to monophyletic distinction within the Small group. They are the only *Austrochaperina* with unpulsed, multinote advertisement calls (Zweifel, 1985b, but the calls of many New Guinean species of both groups are yet unknown), and Mahony et al. (1992) cited karyological evidence for monophyly. No New Guinean endemics of the Small group have been karyotyped, while all five Australian species have the presumably primitive 2N = 26. Two of the Australian species, at maximum sizes of 33 and 35 mm SVL, are the largest species of the Small group; the largest New Guinean species attains 31 mm.

Five of the eight Large group species are riparian along small watercourses, a habitat preference unknown among other Australopapuan microhylids. *A. palmipes* and *A. basipalmata* have toe webbing (slight in the latter). These, together with *A. macrorhyncha* and *A. rivularis*, have relatively large finger and toe discs; in *palmipes* the finger discs may be broader than those of the toes, a condition not seen elsewhere in *Austrochaperina* (table 3). I consider this disc development as an adaptation to wet, slippery, rocky riparian conditions. *A. derongo*, with relatively smaller discs, is also riparian, but the habits of *archboldi* and *hooglandi* are unknown. The only information on *A. guttata* is that it calls from sheltered leaf-litter sites not closely associated with water.

The advertisement calls of four species of the Large group are prolonged bouts of short, pulsed notes: *derongo*, *guttata*, *macrorhyncha*, and *rivularis*. If, as I suspect, this is a derived call, the similarity may indicate a close relationship; calls of this sort are unknown elsewhere in *Austrochaperina*. I anticipate that such calls will characterize three of the other four species of the Large group as well. The fourth species, *A. palmipes*, may utter soft, clicking sounds (see species account). The difference in vocalization, if confirmed, may be a derived character of this species, along with lack of vocal slits, concealed tympanum, vomerine spikes, and webbed toes.

Austrochaperina palmipes is morphologically the most derived species of the Large group, but its primitive 2N = 26 karyotype contrasts with the 2N = 24 of *A. derongo*. A peculiar feature uniting *A. rivularis* and *A. palmipes* is a mosaic appearance to the dorsal skin; this shows well in figure 31E and F. The possession of slight toe webbing would seem to place *A. basipalmata* in a phylogenetic position between *palmipes* and the more primitive species lacking webbing. However, the unusual character of the skin suggests that *palmipes* and *rivularis* are closest relatives.

An anatomical peculiarity, presumably a derived condition, unites some species of the Large group. In these frogs the snout is rather elongate, projecting conspicuously past the lower jaw (fig. 21). Adult males tend to be more extreme in this respect, and the snout tip usually is pale, often quite white. Juveniles of both sexes generally have dark snout tips, and females only occasionally show some lightening. Parker (1940) was the first to call attention to this sexual dimorphism in *A. basipalmata* (as *Sphenophryne macrorhyncha*). The pale condition is well developed in *A. palmipes* and present in *A. rivularis*. Adult males of three morphologically similar species—*archboldi*, *derongo*, and *hooglandi*—generally show this condition. In contrast to other species of the Large group, *guttata* and *macrorhyncha* have a more rounded, less projecting snout and they do not appear to develop a pale tip.

Menzies and Tyler (1977: 434) cited as one of the diagnostic characteristics of the genus *Copiula*, ‘‘a hypertrophied serous dermal gland whose location is distinguished externally by a translucent white, and sometimes uptilted, tip to the snout.’’ Apparently the condition in *Copiula* is not sexually dimorphic. The histology of the pale snout tip in *Austrochaperina* has not been investigated, so there is no assurance that the conditions are homologous. If they are, this would suggest a possible derivation of *Copiula* (a leaf-litter genus with a more derived pectoral girdle) from within the clade of large *Austrochaperina*. *A. derongo* and *Copiula fistulans* share the derived chromosome number, 2N = 24 (Mahony et al., 1992), which may be another indication of relationship.

RELATIONSHIPS WITHIN *LIOPHRYNE*

Liophryne similis and *L. rhododactyla* are an allopatric sibling pair distinguished only by different advertisement calls and by the absence of vocal slits in one. Three other species, *L. rubra*, *L. dentata*, and *L. schlaginhaufeni*, are morphologically distinct but more similar to one another than either is to any other species, whereas *L. allisoni* stands somewhat apart. The latter species is much the smallest *Liophryne* and has a considerably less well-defined external ear than do the other species.

The relatively large size of *similis* and *rhododactyla* is unusual within the Genyophryninae and may be considered as a derived state. The absence of teeth or toothlike structures in these species may also be a derived condition, considering that *allisoni*, *dentata*, *rubra*, and *schlaginhaufeni* all have teeth (albeit vestigial ones) or toothlike structures (see Morphology, Dentition). In karyology, however, *rhododactyla* has the presumably plesiomorphic chromosome number 2N = 26, whereas *schlaginhaufeni* is 2N = 30 (see Morphology, Karyology). Within the context of *Liophryne*, the small size and indistinct tympanum of *allisoni* may be primitive characters.

RELATIONSHIPS WITHIN *OXYDACTYLA*

Frogs of this genus are adapted to a cryptic existence, dwelling in such habitats as grass tussocks, saturated moss, and deep leaf litter. Morphological features that appear to relate to habits include absence or reduction of digital expansion, short hind legs, and small eyes. Considering principally these features, the five species may be arranged in an essentially linear sequence from least to most derived. *O. crassa* and *O. coggeri* are at the bottom of the scale, *O. brevicrus* is intermediate, with *O. alpestris* and *O. stenodactyla* occupying the most derived position.

In *alpestris* and *stenodactyla* the toetips and fingertips are rounded, showing no flattening, expansion, or terminal grooving. These species have the shortest hind legs in the genus, and *stenodactyla* has the smallest eyes, with those of *alpestris* slightly larger but matched by one other species. These two species also share the presumably derived character of a robust premaxillary bone (see Morphology, Osteology).

O. brevicrus has fingertips like those of *alpestris* and *stenodactyla*, but the toe tips, Although not expanded and lacking terminal grooves, are somewhat flattened. The legs are slightly longer and eyes slightly larger than in *alpestris* and *stenodactyla*.

Fingertips of *coggeri* and *crassa* are rounded to slightly flattened, but not clearly disclike, and may show a weak terminal groove. The toe tips of both are disclike with terminal grooves but are scarcely if at all broader than the penultimate phalanges. The legs are slightly longer than and the eye size within the range of the other species.

Whereas *alpestris* and *stenodactyla* are unquestionably each other's closest relative, the relationship at the other end of the sequence is less certain. The features associating *coggeri* and *crassa*, while derived with respect to other genera, are plesiomorphic within *Oxydactyla*. The geography of the situation also raises questions. *O. crassa* is isolated at moderately high elevations on the southeastern tail of New Guinea, more than 600 km from the closest *Oxydactyla* populations in the Eastern Highlands. The intervening region has not been fully explored, but forms similar in habitat preference to *crassa* and other *Oxydactyla* have been found in the genera *Aphantophryne* and *Austrochaperina*. The possibility that including *crassa* within *Oxydactyla* renders that genus paraphyletic deserves further study if adequate material becomes available.

ZOOGEOGRAPHY

The zoogeographic relationships of the New Guinean microhylid subfamilies Genyophryninae and Asterophryinae are obscure and will remain so until a satisfying cladistic analysis of the microhylid subfamilies can be achieved. Conflicting hypotheses—perhaps better called scenarios—of Savage (1973) on the one hand and of Zweifel and Tyler (1982) and Zweifel (1985b) on the other have the Australopapuan microhylids derived from Gondwana by way of Australia or from Southeast Asia across Wallace's Line. Either is compatible with the likely Gondwanan origin of microhylids, although the latter requires a more circuitous route by way of a drifting Indian subcontinent.

Whatever their origin, microhylids dominate the New Guinea frog fauna in number of species, constituting more than half of the total of more than 200 species. *Austrochaperina* has the widest distribution of the four genera treated in this monograph, with species throughout most of mainland New Guinea and on some adjacent islands as well as one species on New Britain (where only one other microhylid is known, an *Oreophryne*) and a disjunct center of diversity in northern Australia. Four of the Australian species are endemic, and the fifth, *A. gracilipes*, inhabits seasonally dry country and may have dispersed to New Guinea when lowered sea level in the Pleistocene afforded a land connection.

Liophryne and *Sphenophryne* are widely distributed in New Guinea but have no known insular populations and are absent from Australia. Species of *Oxydactyla* are likewise restricted to New Guinea and are found in disjunct populations at high elevations.

Too little is known of the details of geographic distribution of species within New Guinea to support speculation about distribution patterns and areas of endemism. On a broader scale, however, the diversity of microhylids very likely relates to their reproductive mode that divorces them from the need to lay their eggs in water. New Guinea is an extremely mountainous island with high rainfall. Under such conditions, upland standing water habitats are not abundant, and streams tend to be torrential, but moist terrestrial and arboreal habitats are everywhere and are utilized by microhylids from sea level to the highest mountains. A parallel situation is in the Admiralty and Solomon islands, where a diversity of platymantine ranid frogs, all with direct embryonic development, dominate the faunas.

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