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ABSTRACT

Study of abundant new material leads to the recognition of 16 species in the Australian microhylid fauna, all but one endemic, in contrast to 8 previously known. One of 5 *Sphenophryne* and 6 of 11 *Cophixalus* are described as new species. Differences between advertisement calls are crucial to distinguishing between members of two pairs of sibling species and are important in diagnosing other species. One species of *Sphenophryne* inhabiting northern Cape York Peninsula and southern New Guinea is the only microhylid common to both areas. It and its sibling in the Northern Territory inhabit regions with prolonged dry seasons, in contrast to the three remaining species of *Sphenophryne* which are confined to rainforest in tropical northeast Queensland. One species of *Cophixalus* occurs in a boulder-jumble area a few kilometers outside the rainforest boundary, whereas the other ten apparently live only in rainforest. Most species of *Cophixalus* are known only from one or two localities but one—*C. ornatus*—has an extensive range, more than 300 km from north to south. The species of *Sphenophryne* inhabit leaf litter. Only one *Cophixalus* is principally a ground dweller, the remaining species being more or less scansorial. Like other genyophrynine microhylids, the Australian species presumably all lay large eggs in sheltered, terrestrial situations. An adult frog, male in the few verified instances, accompanies the eggs, which undergo direct development, producing fully formed froglets.

The five species of *Sphenophryne* include two sibling pairs, with all five species being so similar morphologically that they were taxonomically confused in the earlier literature. The Australian species share no characters clearly apomorphic for the genus, and little can be said as to relationships with the more diverse New Guinean *Sphenophryne*. Similar mating call structure among the Australian *Sphenophryne* suggests that they form a monophyletic group, but the possibility remains that the calls are primitive and not indicative of close relationship.

Australian *Cophixalus* are morphologically much more diverse than *Sphenophryne*, though similarly tied together by communality of elements in the advertisement calls (quite different from those of *Sphenophryne*) that implies monophyly. Interspecific comparisons of body proportions by use of regression lines reveal many similarities and differences among species, but placement of particular characters on a primitive-derived axis is far from satisfactory. Furthermore, parallel development of presumably apomorphic traits seems to have been common. As a result, the relationships diagrammed are even more subjective than usual.

Previous assessments of the Australian microhylids as a slightly differentiated group derived by dispersal from New Guinea are rejected. Paleoclimatic evidence that tropical rainforest habitat suitable for microhylids has been present in northern Australia since well before the Pleistocene, the accessibility of Australia–New Guinea to Southeast Asia since the Miocene collision of plates, and the high degree of endemicity in Australia argue for a long history in situ. Whether the Australian microhylids derive directly from a Gondwanan source, originate from Gondwana indirectly by way of Indian continental drift and subsequent dispersal through Southeast Asia to Australia, or are not of Gondwanan origin at all remains unresolved.

INTRODUCTION

Frogs of the family Microhylidae occupy only the far northern periphery of the Australian continent (figs. 1, 2) and constitute less than five percent of the anuran fauna of 174 species recently catalogued by Cogger, Cameron, and Cogger (1983). Many Australian species of frogs have been described in recent years, and the list may be expected to grow as increased exploration and intensive study reveal more of the fauna of the tropical northern areas. Microhylid frogs had been poorly represented in museum collections. However, faunal surveys conducted by the Australian Museum, the Queensland Museum, and units of the Queensland National Parks and Wildlife Service, as well as fieldwork by individual collectors, have greatly altered the situation. For my first review of the Australian microhylids (Zweifel, 1962) I had only slightly more than 100 specimens at hand, but I have examined more than 1600 in this study. Of no less importance, I have been able

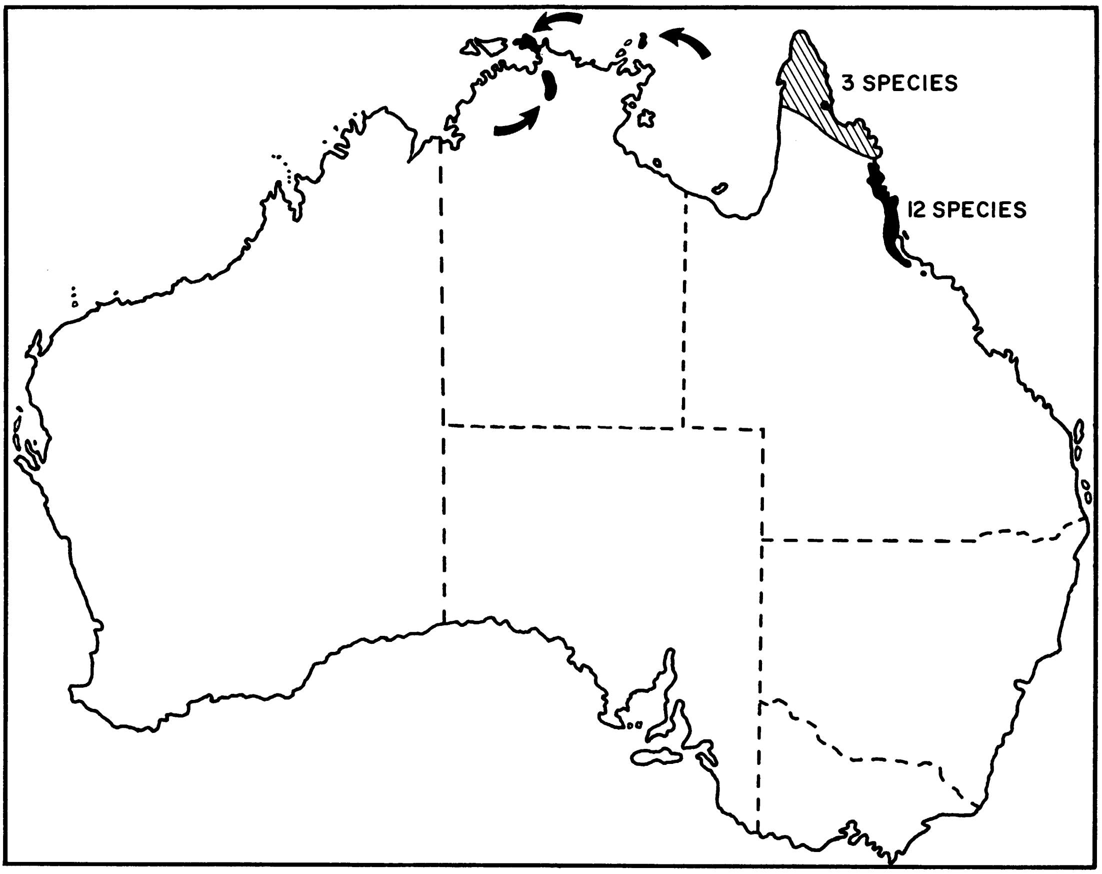

FIG. 1. Distribution of microhylid frogs in Australia. A single species occupies the areas indicated by arrows; one species occurs throughout the shaded area of Cape York Peninsula with two others confined to the area marked by a black spot; 12 species occupy various parts of the blackened area of rainforest on the northeastern edge of Queensland (see fig. 2).

to work with the frogs in the field, seeing in life more than half of the species I now recognize, observing their habits and habitats, and tape recording their calls.

The principal objectives of this study were to improve the systematics of the Australian microhylids and to assemble and present information on their distribution and ecology. I have investigated and discussed certain aspects of anatomy, especially as these pertain to inferring relationships, and have reviewed work on the biogeography of Australian microhylids. I now recognize 16 species, 7 of them described herein. This doubles the number previously listed, but it is likely that other species remain undiscovered, especially in rainforest pockets between Cape York and Cooktown.

The present work adds considerably to our knowledge of Australian microhylids, but it will be evident that much remains to be done. In some species accounts I call attention to particular problems, but any reader familiar with the biology of frogs will see many more opportunities for field and laboratory studies. For example: the calls of three species have yet to be recorded and analyzed; there is scarcely any information on social and breeding behavior; information of interest to population biologists such as numbers, survival, growth, and movements is lacking; details of distribution remain sketchy except for the commonest species. As access to remote rainforest areas improves, the opportunity for research and discovery increases. (These animals are best sought in the wettest season, when travel is most difficult.) Concurrently, however, delicate rainforest ecosystems are being destroyed at an increasing rate, making the need for increased research effort all the more pressing.

PREVIOUS STUDIES ON AUSTRALIAN MICROHYLIDAE

Discovery and study of Australian microhylids lagged well behind that of much of the fauna, largely a result of the remoteness of their range from the more populated fringe of the continent. The earliest collection of an Australian microhylid of which I am aware—the holotype of *Cophixalus ornatus* in 1888—preceded by 24 years the first published notice of an Australian microhylid by Fry (1912). Fry had only time to publish one more paper (1915) dealing with Australian microhylids before his death in the First World War. Based on the promise shown in his published papers, it is perhaps no exaggeration to say that Fry's loss set Australian herpetology back a generation.

Nothing of much consequence happened in the systematics of Australian microhylids until the publication of Parker's (1934) monograph of the family. Though this was a great and important study on a worldwide scale, its effect on knowledge of the Australian microhylids was negative in part. Parker examined only three specimens of Australian microhylids. He recognized three of Fry's four species as valid but considered the fourth synonymous with a New Guinean form, and also thought (incorrectly, it turns out) that one of the three valid species occurred also in New Guinea. This contributed to the long-held impression that the Australian microhylids are but a tiny faunal fragment recently derived from New Guinea, whereas they actually are a group almost wholly endemic to Australia on the species level.

While Parker's monograph was being published, Loveridge (1935) studied a much larger and more diverse collection of microhylids (42 specimens) but came to even more conservative conclusions, recognizing only three species and, like Parker, considering one of them synonymous with a species named earlier from New Guinea. Both Parker's and Loveridge's confusion are understandable (Loveridge included six species of two genera under the name of a New Guinean species that does not occur in Australia); because of the morphological similarity among several species, some systematic problems could not be resolved until recordings of the frogs' calls became available.

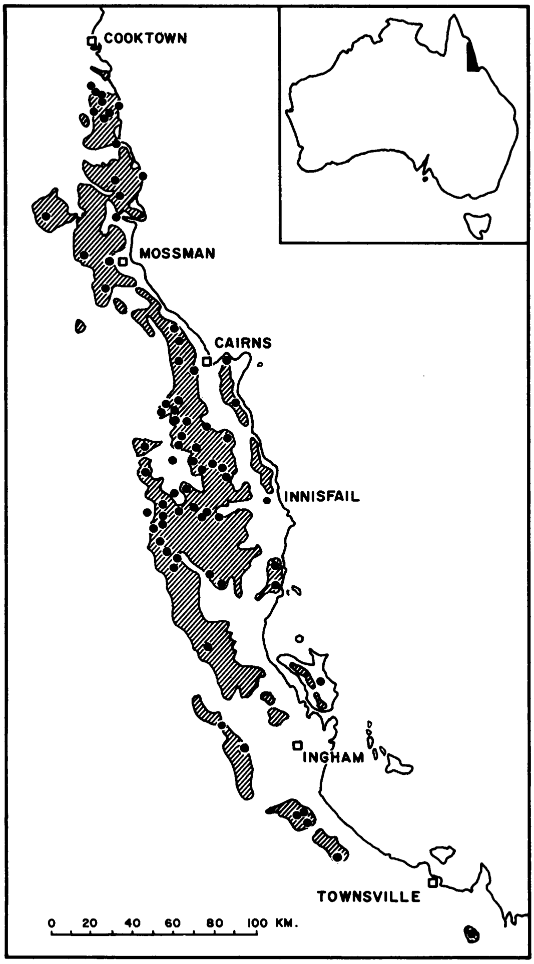

FIG. 2. Distribution of microhylid frogs in the major areas of rainforest in northeast Queensland. Shaded areas indicate rainforest; spots mark collecting localities for one or more species of microhylid.

Following the publications of Parker and

Loveridge, study of Australian microhylids again stagnated for decades. As an adjunct to my studies of New Guinean microhylids, I reviewed the Australian species (Zweifel, 1962), working with the Museum of Comparative Zoology specimens studied earlier by Loveridge and with specimens more recently collected by William Hosmer and deposited in the American Museum of Natural History and the Field Museum of Natural History. This study and a subsequent one (Zweifel, 1965) straightened out some of the confusion inherited from Parker and Loveridge, but both studies contained murky elements that could not be cleared up until the animals could be studied in the field. Descriptions of new species by Tyler (1979b) and by Zweifel and Parker (1969, 1977)—the latter based on Parker's fieldwork—hinted at the diversity of the Australian microhylids that is more fully explored herein.

ACKNOWLEDGMENTS

My primary debt is to the Australian Museum, its Director Dr. D. J. G. Griffin, and Deputy Director Dr. H. G. Cogger, for the award of a Visiting Fellowship that enabled me to spend six months in Australia (October 1980—March 1981). This provided the opportunity for research in the field and in the museums. Most of my time was spent at the Australian Museum where the staff of the Herpetology Department—Dr. Cogger, Dr. Allen Greer, Ms. Elizabeth Cameron, and Mr. Ross Sadlier—were unfailingly cheerfully helpful. Dr. Cogger's critical comments on the manuscript were very helpful.

Other workers unselfishly shared their experience, time, and specimens with me. Mr. Keith McDonald of the Queensland National Parks and Wildlife Service devoted three weeks of his vacation to traveling with me and my wife in the rainforests of northeast Queensland, leading us to choice localities and joining in the collecting activities. In addition, he made the collections of microhylids held by the Queensland National Parks and Wildlife Service available for my study and allowed use of his valuable tape recordings. Mr. William Hosmer served as our host in Cairns, accompanied us on field trips, and freely gave the use of his tape recordings and large collection of microhylids. Mr. Glen Ingram of the Queensland Museum facilitated my study of the large number of microhylids in that museum and provided copies of his tape recordings. Dr. David Liem donated important specimens.

I reserve a special note of thanks for my wife, Frances W. Zweifel, for her assistance in the laboratory and in the field, and for contributing her artistic talents to many of the illustrations in this work.

As listed below, persons responsible for several institutional and one private collection generously made Australian microhylids available for study.

COLLECTION ABBREVIATIONS USED IN THE TEXT

AM, Australian Museum, Sydney; H. Cogger and A. Greer
AMNH, American Museum of Natural History, New York
DU, Duke University Department of Zoology, Durham; J. Bailey
FMNH, Field Museum of Natural History, Chicago; H. Marx
LACM, Museum of Natural History of Los Angeles County, Los Angeles; J. Wright
MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; E. Williams
MSNG, Museo Civico di Storia Naturale, Genoa; E. Tortonese and L. Capocaccia
MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; H. Greene
NMV, Museum of Victoria, previously National Museum of Victoria, Melbourne; J. McNally
QM, Queensland Museum, Fortitude Valley; G. Ingram
QNPWS, Queensland National Parks and Wildlife Service, Townsville; K. McDonald
SAMA, South Australian Museum, Adelaide; T. Schwaner and M. Tyler
UMMZ, University of Michigan Museum of Zoology, Ann Arbor; A. Kluge
WH, private collection of W. Hosmer, Cairns

COLLECTING PERMIT: My collections of microhylid frogs made in National Parks in Queensland were authorized by permit number 392 issued by the Queensland National Parks and Wildlife Service. In accord with provisions of that permit, specimens initially cataloged in the American Museum of Natural History but later designated as holotypes have been transferred to the Queensland Museum and catalogued there.

METHODS

Anatomy: Examination of most specimens entailed a suite of measurements made with dial calipers read to the closest 0.1 mm or, if appropriate, made with an ocular micrometer and read to the closest 0.05 mm. I made all measurements myself, in an effort to minimize variation in technique. Except for male frogs found calling, sex was determined by dissection, as these frogs lack external sexual dimorphism. Skeletal morphology is important in the systematics of microhylid frogs. Most of the species studied are small, even tiny, and their osteology was investigated by means of specimens cleared and stained for bone and cartilage rather than by the use of dried skeletons. X-ray photographs were of supplemental use. Color descriptions derive from notes taken in the field and from my photographs.

In many instances the availability of large numbers of frogs over a range of sizes made it possible to define ontogenetic trends in body proportions by regression analysis. I also calculated ratios of several body parts, since these ratios often are useful in comparing and diagnosing species or populations. Samples for ratios were restricted to adults in order to decrease the influence of allometric growth.

Measurement Abbreviations: The following abbreviations are used in the text:

EAR, greatest diameter of tympanum, including tympanic ring, measured horizontally.

EN, distance between anterior edge of eye opening and center of external naris.

EYE, eye or orbit length between anterior and posterior edges or corners of eye opening.

FOOT, distance between proximal edge of inner metatarsal elevation and tip of fourth toe (fig. 3); comments made under HAND also apply here.

HAND, distance between proximal edge of inner metacarpal elevation and tip of finger (fig. 3); the sometimes featureless nature of the frogs' hands may make it difficult to standardize on the first of these points.

HW, head width at widest point, generally at the level of the tympanum or jaw angle.

IN, distance between centers of external nares.

SV, length from snout to vent—from tip of snout to cloacal opening.

TL, tibia length, between heel and outer surface of flexed knee.

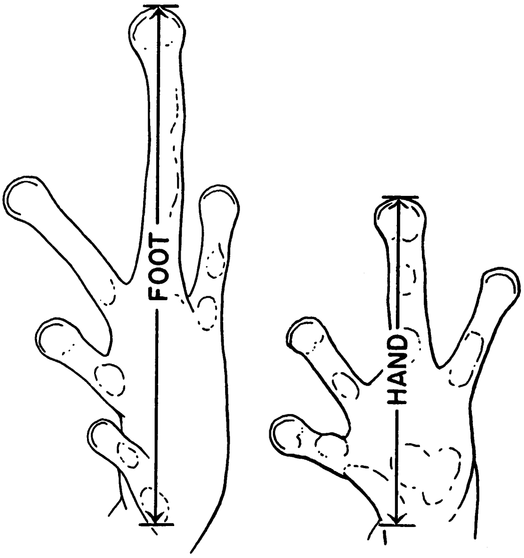

Fig. 3. Points for measurement of FOOT and HAND.

Widths of digital discs were measured at a right angle to the digital axis with the disc flattened against a glass plate. Relative lengths of fingers and toes were determined by placing them parallel to the third finger or fourth toe.

Locality Records: Collectors may describe the same locality in different ways—i.e., by referring to different towns or physical features of the landscape, by road or airline distances, by map coordinates—and with varying degrees of accuracy. Using maps of the 1:100,000 National Topographic Map Series, I have attempted to settle on one designation for a single locality. Hence, curators may find some localities for specimens in their collections cited differently than in the museum catalogues. In addition, I have converted distances cited in miles to kilometers, and elevations in feet to meters. Localities in the lists of locality records and specimens examined are arranged, with minor deviations, from north to south and west to east.

Vocalization: I made recordings on a Sony TC-150 cassette recorder modified to permit manual gain control and I used a TEAC ME-120 electret condenser microphone. Under typical rainforest conditions it often was necessary to enclose both the recorder and the microphone in plastic bags but, apart from the sound of raindrops on the bag, this had no obvious effect on the quality of the recordings. At least once on each cassette I recorded a series of tones from a TEAC TO-122A test tone oscillator (later calibrated against a Hewlett Packard frequency counter). Timing beeps (one per second) recorded from a shortwave radio broadcast furnished an accurate time base and, together with the recordings of test tones, provided adequate frequency and time calibration for spectrographic analysis. My own recordings were thus reasonably well controlled, but I also used recordings made and copied by other workers. It is therefore possible that some of the variation noted among the calls analyzed may be spurious, but if so the effects are not sufficient to confuse the essential differences among species.

I took the temperature at each recording site with a Schultheiss quick-registering mercury thermometer graduated to 0.2°C and read to 0.1°C. The frogs studied are, for the most part, too small to permit direct recording of body temperatures even with this small thermometer, but under typically saturated rainforest conditions it is unlikely that the body temperatures differed significantly from the substratum or air temperature that (as appropriate) I measured. The frogs are wholly nonaquatic; therefore difference between air and water temperatures is not a factor.

Audiospectrographic analyses were done with a Kay Electric Company Sona-Graph model 6061A, using as many calls of each individual frog as were available up to a maximum of ten. My original recordings and copies of all others used are filed and catalogued in the Department of Herpetology, AMNH; original recordings other than my own are privately held and not yet committed to institutional archives. Data for most species are summarized in individual tables and for the remainder are in the appropriate text.

In characterizing vocalizations I have followed certain definitions. A *call* is a discrete unit of vocalization composed of one or more separate bursts of sound and temporally distinct from units similarly uttered. A *note* is heard as a single unit of sound. A call may thus consist of a single note, or of a number of notes grouped into one call. *Pulses* are discrete units of sound energy resolvable on the Sona-Graph as commonly employed (300 Hz filter, 2.4 sec analysis period). Some calls are composed of brief notes that appear on the Sonagram as single pulses; these are referred to onomatopoetically as clicks. More often, however, a note is composed of pulses too closely spaced in time to be heard as separate units. (It is appropriate to recognize the generally pulsatile nature of frog calls, even where this is not evident aurally or upon gross audiospectrographic analysis—Watkins, 1967.) *Modulation* is a change in dominant frequency over the course of a note or call. *Tuning* refers to the distribution of energy with respect to frequency: a finely tuned note has the energy largely confined to one or more discrete frequency levels and is more musical sounding than a harsh, poorly tuned note which has less emphasis at particular levels and more "noise" between emphasized frequencies.

Generally, a call that is distinctly pulsed on a spectrogram but has pulses too closely spaced to be separately resolved by the human ear is heard as a buzz. Finely tuned notes are called peeps, whistles, or chirps, with the first sometimes implying a note with little frequency modulation and the last a somewhat harsher but not obviously pulsed sound. I have avoided the term "trill," commonly used for a series of rapidly repeated notes. As used in music, the word may imply alternation of notes one or one-half scale step apart, or a similarly modulated continuous sound, whereas the "trills" of frogs are trains of discontinuous notes which may or may not be modulated either individually or over the course of the call, but whose modulations do not alternate.

Given enough calls of different species of frogs, one could establish a continuum of kinds of sounds that would defy rational subdivision. Even the calls of a single individual, uttered at different temperatures, could straddle the boundary between calls composed of a series of rapidly repeated clicks (low temperature) and pulsed, buzzing calls. Hence, verbal characterization of calls is to some extent an arbitrary convenience.

TABLE 1
Status of Trivial Names Applied to Australian Microhylid Frogs

Original Combination	Author, Date	Proposed Status
1. *adelphe, Sphenophryne*	—	New species
2. *bombiens, Cophixalus*	—	New species
3. *brevipes, Austrochaperina*	Fry, 1915	*Sphenophryne fryi*
4. *concinnus, Cophixalus*	Tyler, 1979b	Same combination
5. *crepitans, Cophixalus*	—	New species
6. *exiguus, Cophixalus*	Zweifel and Parker, 1969	Same combination
7. *fryi, Sphenophryne*	Zweifel, 1962	Same combination
8. *gracilipes, Austrochaperina*	Fry, 1912	*Sphenophryne gracilipes*
9. *hosmeri, Cophixalus*	—	New species
10. *infacetus, Cophixalus*	—	New species
11. *mcdonaldi, Cophixalus*	—	New species
12. *neglectus, Cophixalus*	Zweifel, 1962	Same combination
13. *ornata, Austrochaperina*	Fry, 1912	*Cophixalus ornatus*
14. *peninsularis, Cophixalus*	—	New species
15. *pluvialis, Sphenophryne*	Zweifel, 1965	Same combination
16. *reginae, Phrynixalus*	Andersson, 1916	*Cophixalus ornatus*
17. *robusta, Austrochaperina*	Fry, 1912	*Sphenophryne robusta*
18. *saxatilis, Cophixalus*	Zweifel and Parker, 1977	Same combination

SYSTEMATICS

The Australian microhylid frogs belong to the Genyophryninae, one of a sister group pair of subfamilies restricted largely to the Australo-Papuan region. The sister group, the Asterophryinae, ranges throughout the Papuan region from the Moluccas to New Guinea (Zweifel, 1972). The Genyophryninae is most diverse in the Papuan region, but occupies New Britain and northern Australia and crosses Wallace's Line to the southern Philippines, Sulawesi, and Bali. The Genyophryninae has been called Sphenophryninae, following Noble (1931) and Parker (1934), but a revision that added the genus *Genyophryne* to the group (Zweifel, 1971) necessitates adoption of a subfamily name based on the earlier Genyophrynidae of Boulenger (1890); see Dubois (1983).

The Australian microhylids are referred to two genera—*Cophixalus* and *Sphenophryne*. Species names based on microhylids originating in Australia are listed in table 1.

The status of *Pachybatrachus petersii*: Keferstein (1868) described this new genus and species based on a single specimen said to be from "Neu-Süd Wales."[1] Subsequent authors treated *Pachybatrachus petersii* as a synonym of a microhylid of India and Sri Lanka, *Uperodon systoma,* implying that the type specimen had incorrect locality data. However, Bohme and Bischoff (1984), reporting on type specimens in the Museums Alexander Koenig, have revived the question of the identity of *Pachybatrachus*. These authors state that Parker's (1934) synonymization of *Pachybatrachus* (done without examination of the type specimen) was wrong, that the type locality is "scarcely to be doubted," and that rediscovery of the species in New South Wales may be anticipated.

The implication that Parker was the first to synonymize *Pachybatrachus petersii* should be disposed of. At least as early as 1882,

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[1] Keferstein also described "*Pachybatrachus Petersii* gen. et sp. nov." in another publication of 1868: Nachr. K. Gesell. Wiss., 1868, no. 15, pp. 326–332. This might have appeared earlier than the one referred to in the Literature Cited, but for present purposes this is irrelevant.

Pachybatrachus was considered a synonym of *Cacopus* (= *Uperodon*), and *petersii* a probable synonym of *systoma* (Boulenger, 1882, p. 174). Nieden (1926, p. 19) also included the species in the synonymy of *Cacopus systoma.*

Reading Keferstein's description and viewing his illustrations leaves no doubt as to why Boulenger and later authors, even without examining the type specimen, concluded that *Pachybatrachus* was *Cacopus-Uperodon,* probably the species *systoma.* The size, pigmentation, habitus, and skeletal features described and illustrated all are consonant with that determination. No known Australo-Papuan microhylid closely resembles *Pachybatrachus.* I attach particular significance to the presence in *Pachybatrachus* of enlarged metatarsal tubercles, a characteristic of *Uperodon systoma* but found in none of more than 100 species of Asterophryinae and Genyophryninae.

Because *Pachybatrachus* was associated with numerous specimens unquestionably of Australian origin, Bohme and Bischoff (1984) assumed that the somewhat indefinite type locality was correct, evidently discounting any possibility of error either before or after the specimens reached Göttingen. Continuing discoveries of new and sometimes striking species of frogs in Australia, even in regions thought well collected, inspire caution in rejecting published locality data as probably erroneous. However, the northern boundary of New South Wales is almost 1000 km south of the southernmost known outpost of microhylids in Australia in a patch of rainforest isolated on a mountaintop near Townsville. The Sydney area, where Schutte's specimens with specific locality data originated, is almost 1700 km from Townsville. Considerations of both morphology and geography lead me to reject the supposition of Bohme and Bischoff that *Pachybatrachus* is a microhylid awaiting rediscovery in New South Wales.

IDENTIFICATION OF GENERA AND SPECIES

The key that follows may serve as much to emphasize the morphological similarity of the frogs as to assist in identification. It is intended for use with well-preserved specimens of adult size measured as described in the foregoing section on methods, but even with the best specimens and technique, morphology alone may in some instances be inadequate for assessing taxonomic status. The key will serve best as a guide to further reading in the species accounts.

Generic Identification: The traditional means for distinguishing between *Cophixalus* and *Sphenophryne* utilizes the presence of a bony clavicle and cartilagenous procoracoid in the latter and their absence in *Cophixalus* (fig. 51). With sufficient experience, the distinction can be made by dissection of adults of even the smallest species, but the use of cleared and stained skeletal preparations resolves any lingering doubts.

Recently Burton (1984) added a character distinguishing the two genera that involves only superficial dissection of throat musculature. *Cophixalus* has the supplementary slip of the intermandibularis muscle oriented parallel to the jawbone, whereas in *Sphenophryne* this muscle is oriented more medially (fig. 55). Again, determining the state of this character requires some experience and an adequate microscope.

There are no characters of external morphology that allow all *Sphenophryne* to be distinguished from all *Cophixalus.* The first finger is long in *Sphenophryne,* about half the length of the second, and these frogs have only weakly developed finger discs (fig. 4). Thus, an Australian microhylid with a reduced, discless first finger, or with well-developed finger discs (especially if they equal or exceed the toe discs in width) is a *Cophixalus* (figs. 5, 6). Not all *Cophixalus* can be separated from *Sphenophryne* by these criteria, however.

Specific Identification: Where proportions are cited, they are intended to characterize a large percent of the specimens but are not necessarily absolutes. In using characters of the digital discs it is particularly important to have well-preserved specimens. Several species have restricted ranges, so far as known at present, allopatric to those of species with which they might most readily be confused. Including ranges in the key is merely a convenience for the reader, and does not imply that I regard geography (apart from sympatry) as a criterion for recognizing species.

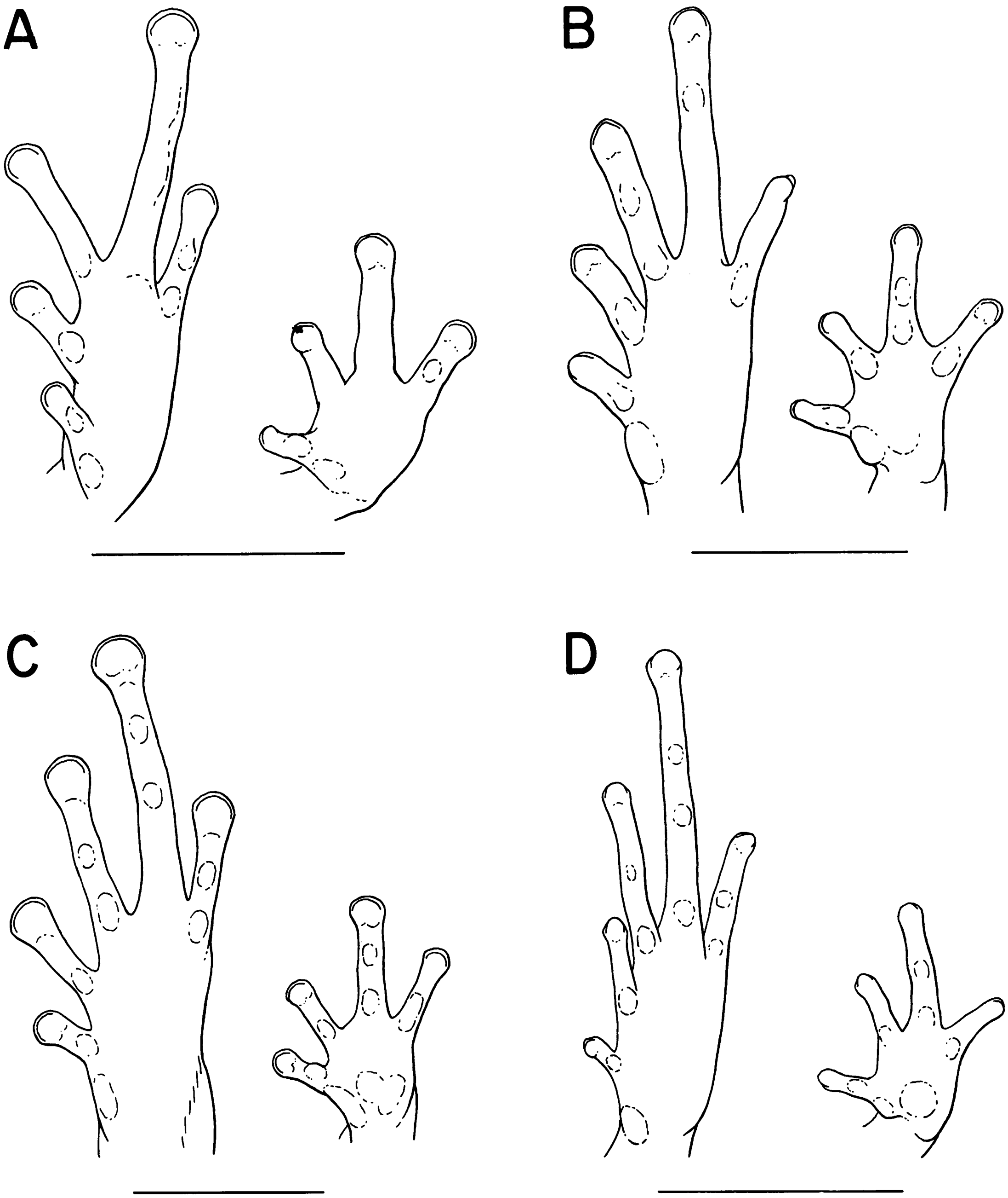

FIG. 4. Undersides of feet and hands of *Sphenophryne*. **A**, *S. robusta*, AMNH 111473; **B**, *S. fryi*, AM R56444; **C**, *S. pluvialis*, AM R87856; **D**, *S. gracilipes*, AM R62053. Scale lines represent 5 mm.

KEY TO AUSTRALIAN MICROHYLID FROGS

1. Clavicle and procoracoid present (fig. 51C, D), supplementary slip of M. intermandibularis oriented medially (fig. 55B) .... *Sphenophryne*, 2

Clavicle and procoracoid absent (fig. 51A, B), supplementary slip of M. intermandibularis

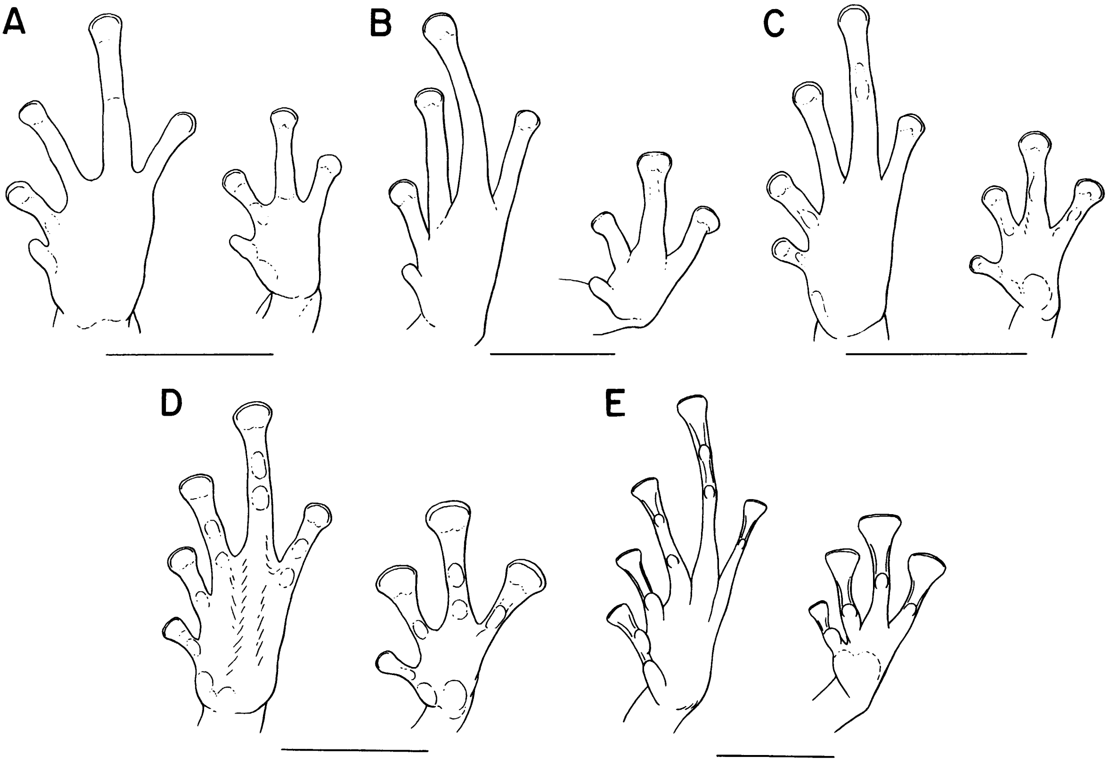

FIG. 5. Undersides of feet and hands of larger species of *Cophixalus*. **A,** *C. neglectus,* QM J35668; **B,** *C. mcdonaldi,* QM J42064 (holotype); **C,** *C. concinnus,* AM R56592; **D,** *C. ornatus,* AM R29514; **E,** *C. saxatilis,* MCZ 90205 (holotype). Scale lines represent 5 mm.

oriented parallel to mandible (fig. 55A) .. .. *Cophixalus,* 6

2. Maximum size less than 23 mm SV, TL/SV 0.43 or greater 3
   Maximum size up to 35 mm SV, maturing at or greater than 20 mm, TL/SV less than 0.43 4
3. Call a series of peeps uttered at a rate of more than 200 per minute; Northern Territory (not distinguished morphologically from the following species) .... *adelphe*
   Call a series of peeps uttered at a rate of 100 per minute or less; Cape York Peninsula . ... *gracilipes*
4. Iris red in life; a distinct pale canthal stripe continued along edge of upper eyelid (fig. 15); melanic pigment of throat and chest of preserved specimens gives way rather abruptly to paler abdominal pattern (fig. 8C) .... *pluvialis*
   Iris with little or no red; pale canthal stripe indistinct or lacking; throat pattern grades gradually into abdominal pattern without abrupt shift in intensity of melanin (fig. 8B) 5
5. Call a series of evenly spaced, short, whistle-like notes; northern edge of Atherton Tableland northward to mountains south of Cooktown (most individuals not distinguishable morphologically from the following species) .... *fryi*
   Call a series of peeps or chirps uttered in couplets; northern edge of Atherton Tableland southward to mountains northwest of Townsville .... *robusta*
6. Disc of third finger broader than that of fourth toe, more nearly truncate than rounded (fig. 5D, E) 7
   Disc of third finger equal to or narrower than that on fourth toe, or if slightly broader then clearly more rounded than truncate (figs. 5A–C, 6A–F) 8
7. Size large, females to 46 mm SV, males to 35 mm; Black Trevethan Range south of Cooktown .... *saxatilis*
   Smaller, maximum 30 mm SV but rarely at-

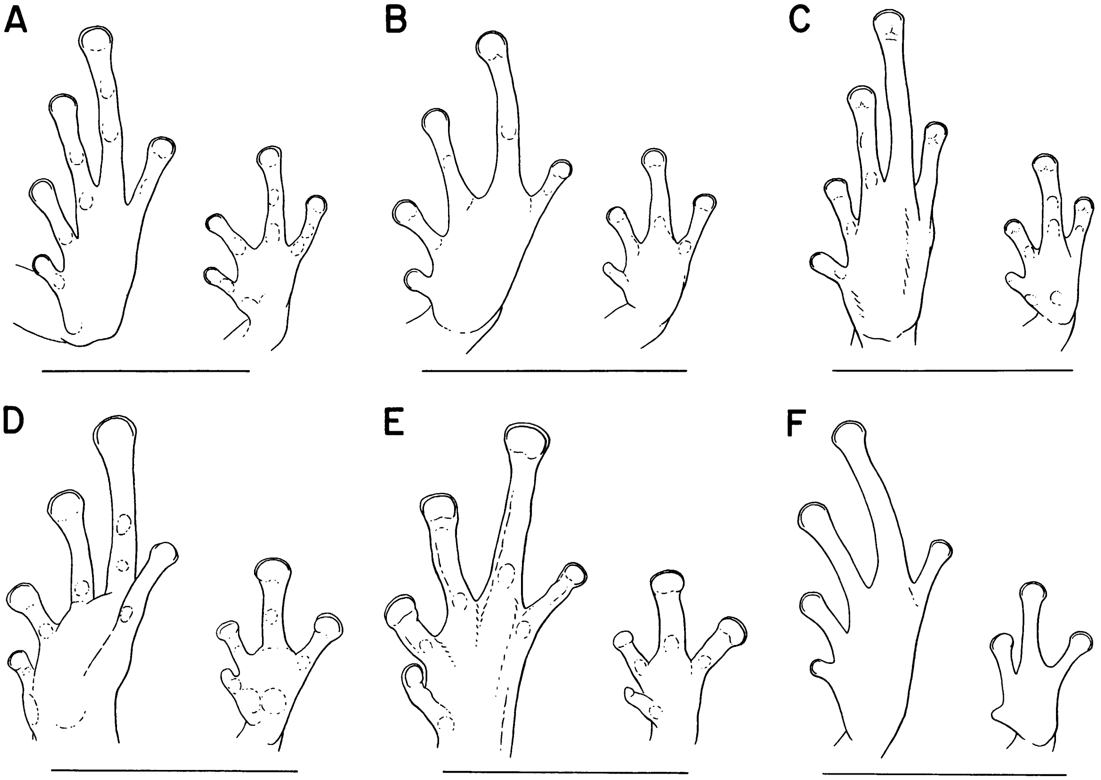

FIG. 6. Undersides of feet and hands of smaller species of *Cophixalus*. **A,** *C. exiguus,* AMNH 81308; **B,** *C. hosmeri,* AMNH 111441; **C,** *C. bombiens,* AM R62560; **D,** *C. infacetus,* QM J42059 (holotype); **E,** *C. peninsularis,* QM J42062; **F,** *C. crepitans,* QM J28817 (holotype). Scale lines represent 5 mm.

taining 27 mm; widespread from Mt. Spurgeon southward to mountains northwest of Townsville .... *ornatus*

8. SV length 20 mm or greater 9
SV length less than 20 mm 11

9. First finger with a grooved, slightly broadened disc (fig. 5C) .... *concinnus*
First finger short with rounded tip, not disclike, ungrooved (fig. 5A, B) 10

10. TL/SV 0.40 or greater, EN/IN 0.78 or greater; Mt. Elliot .... *mcdonaldi*
TL/SV less than 0.40, EN/IN less than 0.78; Bellenden Ker Range .... *neglectus*

11. EN/IN less than 0.70, SV 17–18 mm (two male specimens only) .... *peninsularis*
EN/IN greater than 0.70, or if equal to 0.70, maximum size of males 15 mm SV .. 12

12. First finger short, one-third length of second or less; tip rounded, neither grooved nor disclike 14
First finger longer, about one-half length of second; tip slightly flattened and disclike with at least a weak terminal groove .. 13

13. Size larger, adult males 15 mm SV or larger, females 18 mm or larger ...... *concinnus*
Size smaller, maximum for males 16 mm SV, females 19 mm .... *exiguus*

14. First finger short, a mere nubbin (fig. 6F); call a rattle lasting about 2 seconds; McIlwraith Ranges .... *crepitans*
First finger short, but clearly digitlike; call a buzz or series of clicks averaging 1 second or less in length; localities south of Cooktown 15

15. Legs short, TL/SV less than 0.43; call a series of about 15 soft clicks in about 1 second; Mt. Lewis and Mt. Spurgeon ... *hosmeri*
Legs longer, TL/SV 0.43 or greater; call a brief buzz or a series of closely spaced clicks lasting about 1 second 16

16. Finger and toe discs smaller (fig. 6C); call a buzz about ½ second long; Mt. Windsor Tableland .... *bombiens*
Finger and toe discs larger (fig. 6D); call a series of closely spaced clicks lasting about 2 seconds; Palmerston National Park area north to Cairns .... *infacetus*

GENUS *SPHENOPHRYNE* PETERS AND DORIA

DIAGNOSIS: Genyophrynine microhylid frogs (*sensu* Zweifel, 1971, for Sphenophryninae—see preceding section on systematics) possessing both clavicles and procoracoid cartilages, with the clavicle a long, slightly curved bone reaching from the scapula almost to the midline of the pectoral girdle. No other genyophrynine microhylid possesses this combination of characters.

COMMENTS: The Australian species of *Sphenophryne* are rather generalized microhylids, all similar to one another and lacking any unusual adaptations or aspects of life-history except for direct embryonic development (skipping the free-living tadpole stage), a feature presumably shared with all other Australo-Papuan microhylids. The most recent list (Zweifel, 1985) recognizes 17 species of *Sphenophryne* to which one is added in the present work. Four species are found only in Australia, one is shared between Australia and New Guinea, one problematic species is recorded only from the Aru Islands, and 12 occur only in New Guinea. Several undescribed species, including one in New Britain, are included in an ongoing investigation. In contrast to the Australian species, the New Guinean ones exhibit more diversity in body form and habits.

SPECIES-LEVEL SYNONYMY: The specific names of Australian *Sphenophryne* have been so confused that it is desirable to present a historical account to complement the brief entries in the species synonymies.

Fry (1912), in the initial report of microhylid frogs from Australia, described a new genus and two new species—*Austrochaperina robusta* and *A. gracilipes*—that are referable to *Sphenophryne*. In the first of these he recognized two sorts—"Variety A" comprising nine specimens from Russell River, and "Variety B" for one specimen from Bloomfield River. Subsequently (Fry, 1915), he designated the specimen of Variety B as the type of a new species, *A. brevipes*.

Nothing of importance happened in the synonymies of these species (Nieden, 1926, synonymized *Austrochaperina* in *Sphenophryne*) until the publication of Parker's monograph (1934). Parker was hampered by a scarcity of material, having examined only three specimens of Australian microhylids, one of them a *Sphenophryne*. He recognized *gracilipes* and *robusta* as species, but considered *brevipes* to be a junior synonym of *S. polysticta* (Méhelÿ), a species described from the Huon Peninsula of New Guinea.

While Parker's work was in press, Loveridge (1935) completed a report on Australian frogs in which he recognized only two Australian *Sphenophryne*: he assigned three specimens (correctly, based on my current assessment) to *S. gracilipes* and 26 to *S. polysticta*, under which name he included Fry's two species *robusta* and *brevipes*. Loveridge's use of *polysticta* for the Australian species evidently was independent of Parker's. The specimens Loveridge cited as *S. polysticta* include three species of *Sphenophryne* (none of them *polysticta*) and three of *Cophixalus*. In part the situation reflects the external morphological similarity of the frogs, but Loveridge's disinclination to investigate internal anatomy also contributed to the confusion.

More than two decades passed before these frogs again received systematic scrutiny. Utilizing Loveridge's MCZ material as well as newer specimens in the AMNH and CNHM collections (but without access to type material), I (Zweifel, 1962) reviewed the Australian microhylids and recognized Fry's three species as valid, though it was necessary to provide a new name (*fryi*) for *brevipes* which was preoccupied in *Sphenophryne* by a Boulengerian name for a Papuan species. I based my concept of *fryi* (*brevipes*) and *robusta* on one of Fry's principal distinguishing criteria—leg length. Aside from *gracilipes* of northern Cape York Peninsula and New Guinea, the Australian *Sphenophryne* fell readily into two groups distinguished by leg length and differing in other proportions as well; I referred the shorter legged form to *fryi* and the longer legged to *robusta*.

Shortly thereafter I was able to examine Fry's type material and introduced both clarification and confusion (Zweifel, 1965). It was apparent that the sample I had referred to *robusta* in my 1962 paper did not agree with the type series of *robusta* and was unnamed, so I described it as *pluvialis*. Thus, this species achieved proper recognition for the first time

TABLE 2

Body Proportions in Thirteen Samples of the Genus *Sphenophryne*

Sample	TL/SV			HW/SV			HAND/SV			FOOT/SV		
	Mean ± σ_m	Range	n	Mean ± σ_m	Range	n	Mean ± σ_m	Range	n	Mean ± σ_m	Range	n
S. adelphe	0.458 ± 0.005	(0.43–0.49)	19	0.348 ± 0.002	(0.33–0.38)	19	0.217 ± 0.008	(0.20–0.23)	3	0.451 ± 0.001	(0.43–0.47)	3
S. gracilipes[a]	0.459 ± 0.003	(0.43–0.49)	24	0.357 ± 0.003	(0.32–0.39)	24	— —	—	—	— —	—	—
S. gracilipes[b]	0.464 ± 0.006	(0.41–0.51)	27	0.332 ± 0.003	(0.29–0.37)	38	0.221 ± 0.003	(0.19–0.26)	27	0.469 ± 0.005	(0.42–0.51)	27
S. fryi[c]	0.398 ± 0.003	(0.36–0.46)	28	0.381 ± 0.003	(0.35–0.42)	28	— —	—	—	— —	—	—
S. fryi[d]	0.398 ± 0.004	(0.37–0.43)	21	0.395 ± 0.004	(0.37–0.45)	21	— —	—	—	— —	—	—
S. fryi[e]	0.390 ± 0.003	(0.34–0.43)	31	0.394 ± 0.002	(0.35–0.43)	31	— —	—	—	— —	—	—
S. fryi[f]	0.389 ± 0.006	(0.36–0.42)	13	0.387 ± 0.004	(0.37–0.41)	13	— —	—	—	— —	—	—
S. fryi[g]	—	—	—	—	—	—	0.205 ± 0.004	(0.18–0.22)	10	0.392 ± 0.006	(0.35–0.44)	17
S. robusta[h]	0.407 ± 0.004	(0.36–0.44)	29	0.401 ± 0.003	(0.37–0.45)	29	0.206 ± 0.003	(0.17–0.23)	16	0.405 ± 0.004	(0.35–0.45)	25
S. robusta[i]	0.400 ± 0.003	(0.36–0.44)	45	0.374 ± 0.003	(0.36–0.41)	18	0.210 ± 0.003	(0.18–0.23)	26	0.411 ± 0.003	(0.38–0.45)	37
S. robusta[j]	0.404 ± 0.003	(0.38–0.44)	24	0.394 ± 0.001	(0.38–0.41)	24	— —	—	—	0.419 ± 0.004	(0.39–0.45)	24
S. pluvialis[d]	0.464 ± 0.004	(0.43–0.49)	20	0.387 ± 0.002	(0.37–0.40)	20	— —	—	—	— —	—	—
S. pluvialis[k]	0.440 ± 0.004	(0.40–0.48)	29	0.391 ± 0.004	(0.34–0.43)	29	0.213 ± 0.003	(0.20–0.23)	12	0.443 ± 0.008	(0.39–0.39)	12

[a] Queensland.
[b] Papua New Guinea.
[c] Region north of Thornton Peak.
[d] Thornton Peak and vicinity.
[e] Mt. Lewis.
[f] Mt. Windsor Tableland.
[g] Combined sample.
[h] Mt. Spec vicinity.
[i] Boonjee and vicinity.
[j] Majors Mountain.
[k] Kuranda and vicinity.

TABLE 3
Body Proportions in Twelve Samples of the Genus *Sphenophryne*

Sample	Eye/SV			EN/IN		
	Mean ± σ_m	Range	n	Mean ± σ_m	Range	n
S. adelphe	0.109 ± 0.001	(0.100–0.117)	19	0.750 ± 0.011	(0.66–0.82)	19
S. gracilipes[a]	0.106 ± 0.001	(0.098–0.123)	23	0.710 ± 0.007	(0.62–0.77)	23
S. gracilipes[b]	0.103 ± 0.001	(0.092–0.113)	38	0.750 ± 0.008	(0.65–0.85)	38
S. fryi[c]	0.109 ± 0.001	(0.097–0.128)	28	0.746 ± 0.008	(0.64–0.86)	28
S. fryi[d]	0.104 ± 0.001	(0.094–0.116)	21	0.733 ± 0.007	(0.67–0.80)	21
S. fryi[e]	0.107 ± 0.001	(0.089–0.116)	31	0.708 ± 0.007	(0.61–0.79)	31
S. fryi[f]	0.111 ± 0.001	(0.107–0.121)	13	0.754 ± 0.010	(0.69–0.83)	13
S. robusta[g]	0.113 ± 0.001	(0.104–0.126)	29	0.663 ± 0.004	(0.61–0.72)	29
S. robusta[h]	0.113 ± 0.001	(0.104–0.124)	45	0.664 ± 0.004	(0.60–0.73)	51
S. robusta[i]	0.114 ± 0.001	(0.107–0.120)	24	0.656 ± 0.005	(0.57–0.72)	40
S. pluvialis[d]	0.123 ± 0.001	(0.113–0.132)	20	0.702 ± 0.010	(0.64–0.79)	20
S. pluvialis[j]	0.118 ± 0.001	(0.105–0.131)	29	0.720 ± 0.007	(0.65–0.81)	29

[a] Queensland.
[b] Papua New Guinea.
[c] Region north of Thornton Peak.
[d] Thornton Peak and vicinity.
[e] Mt. Lewis.
[f] Mt. Windsor Tableland.
[g] Mt. Spec vicinity.
[h] Boonjee and vicinity.
[i] Majors Mountain.
[j] Kuranda and vicinity.

since the initial specimen was misidentified by Barbour (1914) as *Uperoleia marmorata.* Unfortunately, I also concluded that *gracilipes* and *robusta* were conspecific—that the type series of *robusta* appeared to be composed of larger individuals of the form I had earlier called *gracilipes.* Following my erroneous identification, Cogger and Lindner (1974) reported as *robusta* the first *Sphenophryne* from Northern Territory.

The arrangement of *Sphenophryne* given in the present work differs from earlier ones in that all four described Australian taxa are considered to be valid species (one with a substitute name, *fryi*), and one more is described. Information on mating calls was essential to this resolution. It should be apparent that descriptions of microhylid species without information on calls, though sometimes necessary, must be considered incomplete. At a higher level, identification to genus without information on pertinent characteristics of internal anatomy is a dubious undertaking.

Sphenophryne adelphe, new species

Figure 7

Sphenophryne robusta: Cogger and Lindner, 1974, p. 72, fig. 20. Cogger, 1975, figs. 339–340. Barker and Grigg, 1977, p. 205 (fig.).

HOLOTYPE: SAMA R17344, collected at Back Jungle, Croker Island, Northern Territory, Australia, on January 23, 1979, by Ian Morris.

PARATYPES: SAMA R17345, R17346 (same data as holotype); AM R30240, R30334, R30335, R32686–32690, Caiman Creek, Port Essington; AM R30236, Knocker Bay, Port Essington; AM R30237, R30238, Victoria, Port Essington; AM R30241, R32685, Port Essington; AMNH 118820–118822, Cobourg Peninsula, 11°16′S, 131°54′E, 1st perennial creek running S of Saddle Hill, collected by Harold Cogger, Sept. 8, 1968; AM R41388–41403, Marchinbar Island, Wessel Islands, collected by D. A. Lindner, January 30, 1974; AM R41418–41421, Rocky Creek near Koongarra Camp, collected by H. Cogger and D. A. Lindner; AM R39774, R39775, R64208, R64209, Deaf Adder Gorge. All localities are in the Northern Territory.

ETYMOLOGY: The Greek *adelphe,* meaning "sister" and used as a noun in apposition, indicates the inferred relationship of this species to its sibling *Sphenophryne gracilipes.*

DIAGNOSIS: *Sphenophryne adelphe* is a small species with a maximum known length of less than 22 mm SV. Other Australian species except *S. gracilipes* are larger, attain-

TABLE 3
Continued

EN/SV			IN/SV		
Mean ± σ_m	Range	n	Mean ± σ_m	Range	n
0.076 ± 0.001	(0.070–0.082)	19	0.101 ± 0.001	(0.096–0.108)	19
0.072 ± 0.001	(0.063–0.078)	23	0.101 ± 0.001	(0.096–0.108)	23
0.073 ± 0.001	(0.061–0.082)	38	0.097 ± 0.001	(0.085–0.106)	38
0.073 ± 0.001	(0.059–0.081)	28	0.097 ± 0.001	(0.089–0.104)	28
0.071 ± 0.001	(0.066–0.078)	21	0.097 ± 0.001	(0.091–0.104)	21
0.069 ± 0.001	(0.062–0.079)	31	0.098 ± 0.001	(0.082–0.106)	31
0.070 ± 0.001	(0.066–0.075)	13	0.092 ± 0.001	(0.087–0.100)	13
0.070 ± 0.001	(0.064–0.076)	29	0.105 ± 0.001	(0.095–0.116)	29
0.070 ± 0.001	(0.066–0.076)	51	0.106 ± 0.001	(0.096–0.116)	51
0.071 ± 0.001	(0.064–0.077)	39	0.109 ± 0.001	(0.100–0.118)	39
0.079 ± 0.001	(0.073–0.084)	20	0.113 ± 0.001	(0.103–0.118)	20
0.080 ± 0.001	(0.073–0.088)	29	0.110 ± 0.001	(0.094–0.122)	29

ing maturity only at or above the maximum size of *adelphe.* The melanic pigment of the chin of *adelphe* (mottled, or a more or less solid background for pale spots) becomes gradually less intense posteriorly, whereas in *S. pluvialis* there is a relatively abrupt change from dark to light between chest and abdomen, most evident in preserved specimens. Ventral pigmentation of *S. fryi* and *S. robusta* is similar to that of *adelphe,* but the two larger species typically have a TL/SV ratio of less than 0.43, whereas it is at least that high in *adelphe.*

I cannot distinguish the sibling species *S. gracilipes* and *S. adelphe* on morphological grounds. The call of *adelphe,* a series of high-pitched peeps uttered at a rate of more than 200 per minute, differs markedly from that of *gracilipes,* a series of longer peeps produced at an average of about 88 per minute. The difference is of a degree seen in sympatric congeneric species, and I consider this sufficient grounds for treating these two allopatric populations as different species, their apparent morphological identity notwithstanding.

DESCRIPTION OF HOLOTYPE: Male, adult (calling when captured), with the following measurements and proportions: SV 15.0, TL 6.8, HW 5.8, EYE 1.75, EN 1.05, IN 1.5, disc of third finger 0.4 (penultimate phalange 0.3), disc of fourth toe 0.65 (0.35), HAND 3.5, FOOT 7.0; TL/SV 0.453, HW/SV 0.387, EYE/SV 0.117, EN/SV 0.070, IN/SV 0.100, EN/IN 0.700, third finger disc/SV 0.027, fourth toe disc/SV 0.043, HAND/SV 0.233, FOOT/SV 0.467.

TABLE 4
Digital Disc Proportions in Seven Samples of the Genus *Sphenophryne*

	Third Finger Disc/SV			Fourth Toe Disc/SV		
Sample	Mean ± σ_m	Range	n	Mean ± σ_m	Range	n
S. adelphe	0.025 ± 0.001	(0.021–0.029)	11	0.034 ± 0.001	(0.027–0.043)	11
S. gracilipes[a]	0.026 ± 0.001	(0.021–0.033)	12	0.036 ± 0.001	(0.032–0.039)	11
S. gracilipes[b]	0.025 ± 0.001	(0.022–0.028)	18	0.036 ± 0.001	(0.031–0.040)	18
S. fryi	0.026 ± 0.001	(0.023–0.029)	16	0.038 ± 0.001	(0.032–0.041)	16
S. robusta	0.027 ± 0.001	(0.023–0.031)	29	0.040 ± 0.001	(0.034–0.044)	28
S. pluvialis[c]	0.029 ± 0.001	(0.026–0.034)	11	0.045 ± 0.001	(0.041–0.050)	11
S. pluvialis[d]	0.029 ± 0.001	(0.021–0.035)	21	0.043 ± 0.001	(0.032–0.049)	21

[a] Queensland.
[b] Papua New Guinea.
[c] Thornton Peak and vicinity.
[d] Kuranda and vicinity.

FIG. 7. *Sphenophryne adelphe* from Port Essington, Northern Territory. Photograph by Harold Cogger.

Head notably narrower than the chunky body, which tapers from the abdominal region to the bluntly pointed snout. Snout rounded in profile, protruding beyond lower jaw; canthus rounded, loreal region sloping, almost flat; nostrils lateral, just visible from above; internarial distance greater than eye-naris distance; nostrils about equidistant from tip of snout and eye, but appearing much closer to tip in lateral perspective. Eyes lateral, corneal outline broadly visible from beneath; eyelid narrower than interocular distance. Skin over tympanum not differentiated, only part of tympanic ring barely visible. Relative lengths of fingers 4>3>2>1, first about one-half length of second; tips of fingers 2–4 disclike with faint terminal grooves, but only third slightly broader than penultimate phalange; subarticular tubercles rounded, slightly prominent; low, rounded inner and middle metacarpal tubercles present. Relative lengths of toes 4>3>5>2>1, tips of toes 2–5 disclike, 2–4 with faint terminal grooves, disc of fourth only much flattened and expanded; subarticular tubercles rounded, moderately prominent; a low, rounded inner metatarsal tubercle present but no outer. Skin of body and limbs smooth dorsally and ventrally.

The color in preservative is three shades of brown, with the dorsal pattern arranged as follows: a dark loreal streak passing posteriorly through the tympanic region, becoming somewhat ragged edged and curving downward into the groin; a somewhat paler middorsal area, separated from the lateral streaks by still paler ground color with scattered dark spots. The upper surfaces of the legs are the same pale ground color with darker spots, and the posterior surfaces of the thighs are slightly darker with obscure small light spots. The lips, sides of the body below the dark streaks, groin, and anterior surfaces of the thighs are mottled, more boldly posteriorly. The undersurfaces have a fairly coarse melanin network, tighter on the chin and becoming more open posteriorly on the abdomen and hind legs.

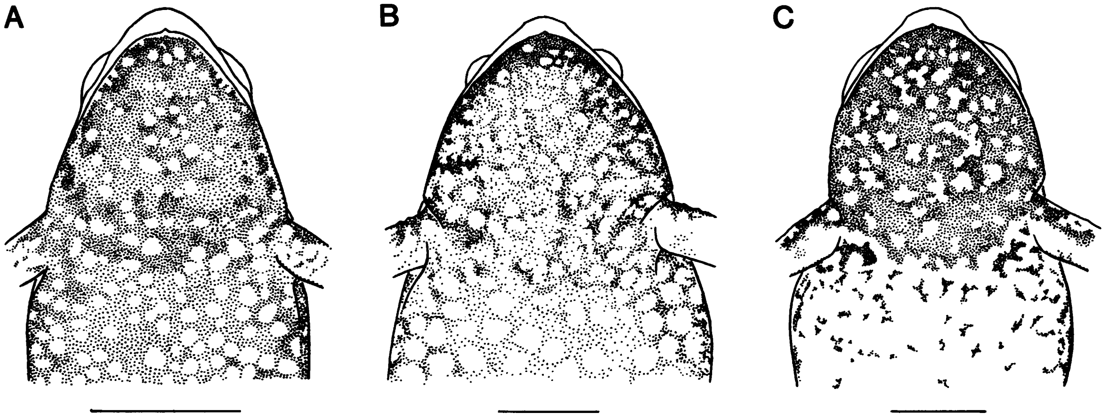

FIG. 8. Throat and chest patterns in three species of *Sphenophryne*. **A,** *S. adelphe,* AM R41393, Marchinbar Island; **B,** *S. fryi,* AM R56443, Thornton Peak; **C,** *S. pluvialis,* AM R87856, Danbulla State Forest. Scale lines span 5 mm.

VARIATION IN TYPE SERIES: See tables 2–4 for ranges and means of selected proportions. The largest specimen among 33 measured is a female from Marchinbar Island, 21.9 mm SV; males attain at least 19.1 mm.

I have not seen living examples of this species, but a color photo in Barker and Grigg (1977, p. 205) shows a brown frog not much different in color from the preserved specimens. There is little variation among preserved specimens. Some individuals have a pale vertebral hairline (fig. 7; Cogger and Lindner, 1974, fig. 20) that may only be evident posteriorly. Cogger (1975, figs. 339–340) illustrates a frog from Mt. Brockman with more contrast in the ventral pattern than in many preserved specimens (light spots on a more uniformly dark ground color), but a similar pattern appears in a specimen from Marchinbar Island (fig. 8A), and metachrosis may be at least partly responsible. It would be of interest to know if *S. adelphe* has the orange groin and axillary color noted for Australian *gracilipes.*

COMPARISONS WITH OTHER SPECIES

Sphenophryne adelphe is not known to be sympatric with any other microhylid. See the account of *S. gracilipes* for comparisons with that species and others. Comments on *gracilipes* in the account of *S. pluvialis* apply to *adelphe* as well.

HABITAT AND HABITS

Cogger and Lindner (1974, p. 72) provided information on the habitat and habits of this species, based on observations made in September in the vicinity of Port Essington, Cobourg Peninsula: "This species was found in the same habitat as *Litoria dorsalis,* viz. in moist leaf-litter or root-masses on the floors of paperbark swamps at Knocker Bay and at the head of Caiman Creek. Several specimens were also taken from litter in a small pool in monsoon forest inland from Victoria. All specimens were found only when the leaf-litter was disturbed, and are apparently nocturnal." These authors remark that the "dry season on Cobourg Peninsula extends from about April to October, and is characterized by . . . an almost total lack of precipitation." The wet season of heavy, monsoonal rains usually extends only through January and February, but is highly variable in extent.

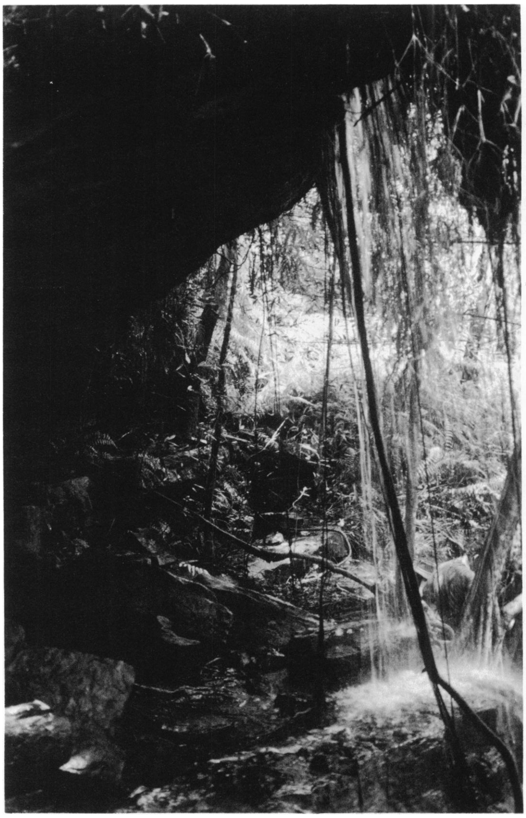

FIG. 9. Beneath sandstone escarpment near Jabiru, Northern Territory, late in wet season. *Sphenophryne adelphe* was found here in the dry season. Other frogs found at this locality were *Megistolotus lignarius* in sandstone crevices and *Litoria coplandi* and *L. meiriana* in the stream.

In the vicinity of Jabiru, Ian Morris (*in litt.*) has found *Sphenophryne* "rather numerous, not just in pockets of monsoon forest, but way up on the sandstone plateau beneath tussocks of spinifex (*Triodia iritans*). They only seem to call after rains, but at any time of day or night." In mid-March, Ross Sadlier guided me to a site near Jabiru where he had on an earlier occasion collected *Sphenophryne adelphe.* The spot was part way up the steep escarpment of a sandstone outlier, disjunct from the main body of the Arnhem Land plateau. This was late in the rainy season only a few days after a cyclone had brought extensive flooding to the adjacent lowlands

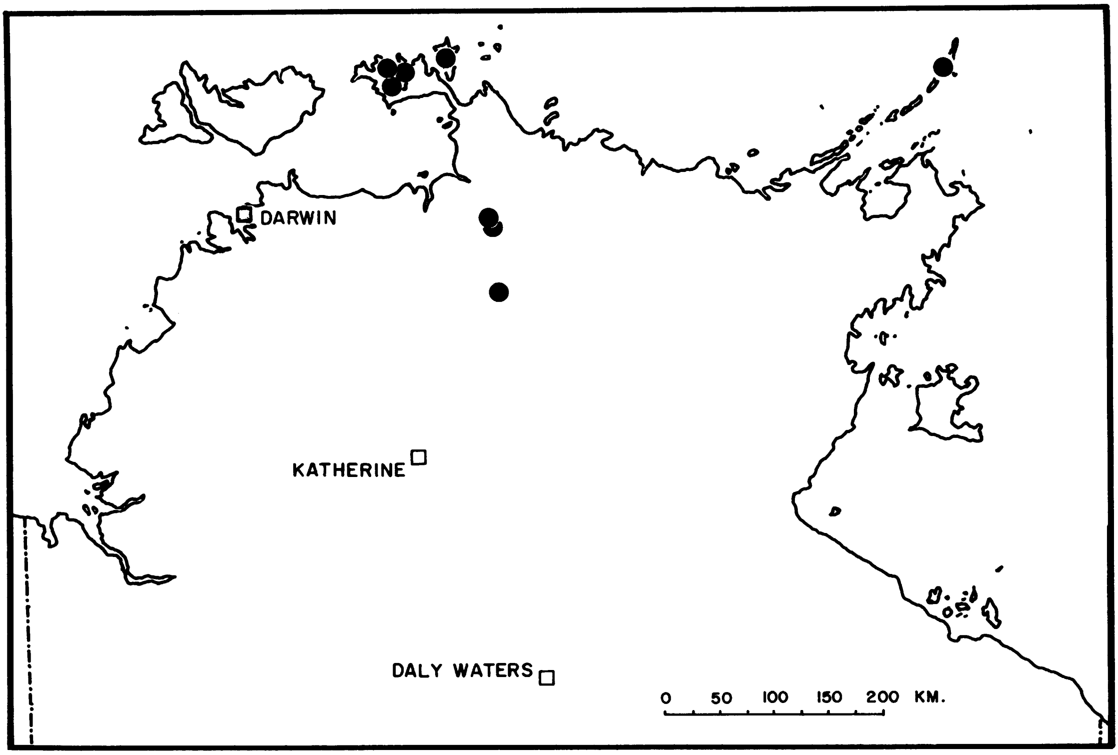

FIG. 10. Locality records for *Sphenophryne adelphe* in northern part of Northern Territory.

that we crossed by boat to get to the site. Water falling over the edge of the escarpment saturated the rock rubble where Sadlier had found the frogs in the dry season (fig. 9). We collected here both by day and night but neither saw nor heard *Sphenophryne*. Other frogs present at this specific site were *Megistolotis lignarius, Litoria coplandi,* and *L. meiriana.*

Frogs tape recorded at the type locality were "calling from beneath damp leaf litter on the floor of the spring-fed monsoon forest. The individuals were well spaced out and particularly difficult to pinpoint" (Ian Morris, *in litt.*). These observations suggest a possible difference from *S. gracilipes*; both Keith McDonald in Australia and I in Papua New Guinea found *gracilipes* calling from slightly elevated positions.

CALL

Recordings of only two individuals of this species are at hand: one recording includes only one incomplete call, and neither (recorded at the same time) has temperature data. The recordings, made at the type locality by Ian Morris on January 23, 1979, were sent to me through the courtesy of Michael Tyler (copies on AMNH Herpetology tape no. 219).

The call is a moderately rapidly repeated series of high-pitched peeps, each note about 0.12 seconds long and with a midpoint frequency of about 4600 Hz (fig. 63C). Fourteen calls have a mean duration of 3.56 seconds (range 1.9–4.8 sec), mean of 14.6 notes per call (7–20), and a mean rate of 4.08 notes per second (3.6–4.3). The single, incomplete call from a second individual differs in its greater duration (>7 sec) and concomitant greater number of notes (>31), but the rate of 4.4 notes per second is similar.

REMARKS

There is need to verify, by means of recordings of the calls, that the widely scattered populations referred to this species are properly allocated. In view of the morphological identity of the two forms, there is no assurance that *S. gracilipes* does not enter the supposed range of *S. adelphe* from the east.

Sphenophryne adelphe is of special interest in being the only microhylid frog known to occur in Australia outside of the Cape York Peninsula. More data on its habitat requirements and distribution are badly needed.

A remotely possible taxonomic complication for this species or *S. gracilipes* involves *Sphenophryne pusillus* (Roux), described from the Aru Islands, Indonesia, on the basis of a juvenile specimen only seven millimeters in length and now in badly damaged condition (Tyler, 1978). No other specimens referable to the species are known and it cannot adequately be diagnosed. The possibility that *pusillus* is a senior synonym of *adelphe* or *gracilipes* must be kept in mind until better material becomes available to settle the question.

DISTRIBUTION

All known localities for this species are in the extreme northern part of Northern Territory, northeast to east-southeast of Darwin (fig. 10). Three areas are represented: Croker Island and the nearby Port Essington region of Cobourg Peninsula; the western edge of Arnhem Land, north and south of Jabiru; Marchinbar Island in the Wessel Islands, far to the east. Specific localities are given in the section above on paratypes.

Sphenophryne fryi Zweifel

Figures 11, 18

Austrochaperina robusta Fry, 1912, p. 89 (part, Variety B).

Austrochaperina brevipes Fry, 1915, p. 61 (type locality, "Bloomfield River, near Cooktown, North-eastern Queensland"; holotype, AM R2285, collected by Geo. Hislop in 1897).

Sphenophryne polysticta: Parker, 1934, p. 157 (*brevipes* synonymized with *polysticta*). Loveridge, 1935, p. 56 (*brevipes* synonymized with *polysticta*).

Sphenophryne fryi Zweifel, 1962, p. 26 (substitute name for *Austrochaperina brevipes,* preoccupied by *Sphenophryne brevipes* [Boulenger] 1897).

DIAGNOSIS: *Sphenophryne fryi* is distinguished from some of its Australian congeners by its combination of relatively large size (adulthood reached at about 23 mm SV, maximum size almost 35 mm), gradual transition of melanic pigmentation from most intense on the throat to less so on the abdomen, absence of a distinct light line on the canthus and edge of the eyelid, and absence or slight amount of red in the iris. The last two characteristics are best seen in living frogs, whereas the ventral melanic pigmentation is more conspicuous in preserved specimens.

FIG. 11. *Sphenophryne fryi,* AMNH 111454, Mt. Windsor Tableland; subadult female, SV 25.6 mm.

Sphenophryne gracilipes and *S. adelphe,* species which are allopatric to *S. fryi,* are much smaller than *fryi,* whose minimum size at attainment of maturity equals the maximum size of the other two. *Sphenophryne pluvialis* is similar in size to *fryi,* but has an abrupt transition from the relatively heavily pigmented throat to the paler abdominal region; *pluvialis* also has a pale canthal streak and, in life, much red in the iris. The remaining Australian species, *S. robusta,* is a sibling of *fryi.* Only one morphological criterion—internarial distance—affords a partial separation of the two species, though calls are distinctive. See the Diagnosis and Comparisons sections of the *robusta* and *pluvialis* accounts for discussion.

The call of *fryi* is a series of whistlelike notes, averaging about 14 notes in each 2-second call. The basically similar call of *pluvialis* has a much faster note repetition rate, and the notes of *robusta* are uttered in couplets.

DESCRIPTION

MORPHOLOGY: The largest of 163 specimens is a female from Mt. Lewis that measures 34.9 mm snout to vent; several other females exceed 30 mm. The largest male, from Mt. Finnigan, is 30.4 mm. Females mature at about 23–25 mm, for this size range includes individuals that apparently are immature, as well as others with enlarged ova. The smallest mature male (calling when captured) measures 23.1 mm.

Head narrower than relatively rotund body. Snout rounded to bluntly pointed seen from above, rounded and only slightly projecting beyond lower jaw in profile; canthus rounded, loreal region sloping and flat; nostrils lateral, just visible from above, closer to snout tip than to eye but appearing much closer to tip in profile, internarial distance greater than eye-naris distance. Eyes lateral, corneal outline visible from beneath, eyelid narrower than interorbital span. Tympanum equal to one-half of orbit or less, quite obscure. Relative lengths of fingers 3>4>2>1, first well developed, one-half length of second; all fingers with rounded, grooved terminal discs, but broadest disc (third finger) scarcely wider than penultimate phalange; subarticular tubercles low, rounded; inner and middle metacarpal elevations similarly obscure (fig. 4B). Toes unwebbed, relative lengths 4>3>5>2>1; all toes with rounded, grooved terminal discs larger than those of fingers, and all but disc of first toe conspicuously broader than penultimate phalange; subarticular tubercles low, rounded; a slightly elongate, low, rounded inner metatarsal tubercle but no outer (fig. 4B). Skin smooth above and below; a weak skin fold passing from posterior corner of eye, curving down behind tympanum.

COLOR AND PATTERN: The ground color in preservative is gray to brown. The loreal region and often the entire side of the face are uniform dark brown, the color extending posteriorly along the skin fold above the tympanum. The dorsal pattern is of small, irregular dark spots, thinly scattered in some individuals and so dense as almost to form a reticulum in others. This pattern is common to the head, body, and limbs, though the sides of the abdomen often have a mottled rather than spotted appearance. The lower lip is usually heavily pigmented, often solid brown with a ragged inner edge. The chin, throat, and chest may be almost clear to variously spotted or mottled, the variation probably due to metachrosis (fig. 8B). The abdomen is usually less heavily pigmented than the chest, but there is no sharp line of demarcation. The groin and anterior and posterior surfaces of the thighs are spotted or mottled in no distinctive fashion. The back of the tarsus and the sole are brown, generally with a few light spots.

My field notes describe living frogs from the Mt. Windsor Tableland as gray brown anteriorly, becoming reddish brown in the sacral region, groin, and posterior surfaces of the thighs, and having a face mask that was almost black. One specimen was peach beneath, another almost colorless. The iris was deep gold, and one frog had a trace of a light line along the canthus. An adult from Mt. Lewis had a pinkish brown ground color anteriorly, lightening to orange brown posteriorly, with dorsal spots and face mask dark brown and peach undersides. The iris was dark brown with a few golden flecks above the red-rimmed pupil. Three juveniles from the same locality had much less red dorsally, and one showed a trace of a canthal light line. The ventral colors varied—pale yellow and unmarked in one, similar but with white flecks in another, and darkly mottled in the third.

VARIATION IN PROPORTIONS: See tables 2–4 for variation in proportions among adults of four geographic population samples. No differences of consequence are evident. Ranges of variation overlap widely, and for the most part means fall within a narrow range. Comparison of growth trends by regression shows the same picture; lines exhibit highly similar slopes and are closely spaced, often with virtually identical placement. These statements refer in particular to the measurements TL, HW, EYE, EN, and IN and to the ratio EN/IN. Samples of disc, hand, and foot sizes are not adequate for interpopulation comparisons.

COMPARISONS WITH OTHER SPECIES

Sphenophryne fryi is broadly sympatric with *S. pluvialis* but barely contacts the range

TABLE 5
Call Statistics for *Sphenophryne fryi*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Notes per Call Mean (Range)	Notes per sec Mean (Range)	Frequency, Hz	Number of Calls
AMNH 111452[a]	229	25.3	20.6	2.16 (1.45–2.45)	12.9 (9–14)	5.7 (5.4–5.8)	3300	7
AMNH 111451[a]	229	23.1	20.8	1.51 (0.60–2.38)	9.4 (4–15)	5.8 (5.5–6.1)	3400	5
No spec.[a]	229	–	20.8	1.94 (1.44–2.38)	11.9 (9–14)	5.8 (5.6–5.9)	3400	7
QNPWS N28772[a]	239	26.0	20.8	2.04 (1.84–2.25)	12.0 (11–13)	5.6 (5.5–5.7)	3200	4
No spec.[b]	241	–	22.0	2.64 (2.46–3.00)	19.0 (18–21)	7.1 (7.1–7.2)	1900	3
AMNH 111459[c]	230	27.0	22.5	2.34 (2.18–2.50)	14.5 (13–16)	5.9 (5.6–6.1)	3200	2
No spec.[d]	229	–	22.6	3.52 (3.46–3.57)	22.0 (21–23)	6.1 (5.9–6.3)	3400	2
No. spec.[b]	248	–	–	2.28 (2.15–2.36)	13.7 (13–14)	5.7 (5.6–5.7)	3000	3

[a] Mt. Windsor Tableland.
[b] Mt. Lewis.
[c] North of Tinaroo Lake.
[d] 7.5 km N, 3 km W Kuranda.

of *S. robusta*. See the accounts of *S. pluvialis* and *S. robusta* for comparisons with *fryi* in addition to those in the several diagnoses. The account of *robusta* includes a discussion of the contact zone between that species and *fryi*.

HABITAT AND HABITS

This species inhabits the floor of the rainforest, where it may be found during the daytime hours beneath logs, sticks, and similar cover lying on or in the leaf litter. At night the males typically call from superficial concealment rather than from deep within the litter. Specimens have been taken in a variety of forest types mapped by Tracey and Webb (1975) and discussed in Tracey (1982): mesophyll vine forest; semideciduous mesophyll vine forest; complex notophyll vine forest; simple microphyll vine-fern forest; simple microphyll vine-fern forest thicket. The range in elevation is from virtually sea level at Pilgrim Sands, Cape Tribulation, to 1100 m on Mt. Finnigan.

There are two records of male frogs evidently attending eggs. AM R55079, 29.5 mm SV, was found under debris on Thornton Peak, November 8, 1975, with a clutch of 12 ova about 5.7 mm in diameter. Well-developed, pigmented embryos were within an inner capsule 5.1 mm in diameter. The preserved ova are without connecting cords. A second male from Thornton Peak (Allen E. Greer no. 4934, SV 27.4 mm), found on July 20, 1976, accompanied seven eggs with well-developed embryos and two hatchling frogs 6.2 mm SV. In this instance four eggs were connected by mucilaginous cords.

Dennis and Trenerry (1984, p. 4) observed *S. fryi* on Mt. Lewis. They report a "female . . . observed for three years under the same rock . . . first found with a clutch of eleven eggs. Disturbance invoked a conspicuous protective response whereby the female straddled the eggs and remained motionless." Unfortunately, these authors do not state how they determined the sex of the frog (*fryi*, like other Australian microhylids, has no external sexual dimorphism) nor how they verified it was the same individual each time.

CALL

The call of *Sphenophryne fryi* (fig. 64B, table 5) is a series of brief, whistlelike notes. Calls last from about 0.6 to 3.6 seconds and include from 4 to 23 notes, with the average being 2.3 seconds and 14.5 notes in the seven individuals recorded. The note repetition rate averages 6.0 per second; the range of temperatures over which the calls were recorded, 20.6–22.6°C, is too narrow to demonstrate an influence of temperature. Individual notes are about 0.05–0.07 seconds long and well tuned, rising about 300–500 Hz through a midpoint frequency of about 3300 Hz (but see below). Calling is irregular, and several minutes may elapse between calls.

The call of an individual recorded by William Hosmer on Mt. Lewis, while conforming to calls of the species recorded elsewhere

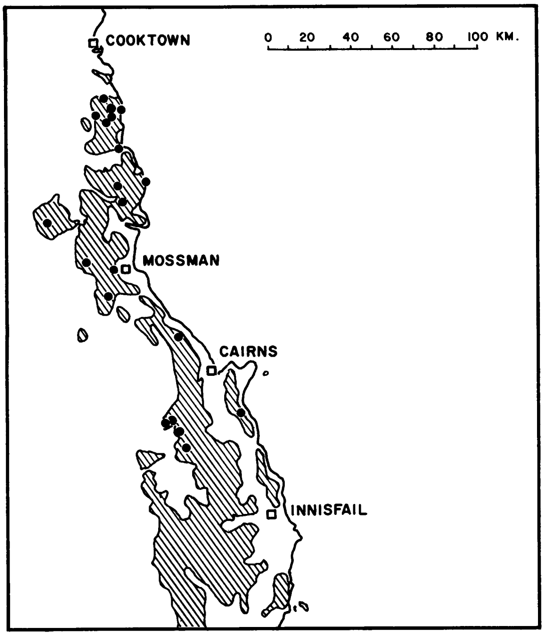

FIG. 12. Distribution of *Sphenophryne fryi*. Range is probably continuous in shaded (rainforest) areas as far as the southernmost spots, where *fryi* is replaced by *S. robusta* (see fig. 21).

in most respects, differs in that the dominant frequency is much lower—about 1900 Hz rather than about 3300 Hz. It appears that in this recording a lower harmonic (the first) is emphasized. Traces of this harmonic are seen in some audiospectrograms of other calls. Another individual recorded at the same locality by G. Ingram has a more normal dominant frequency of about 3000 Hz.

DISTRIBUTION

Sphenophryne fryi ranges from the rainforested areas east of Helendale (about 30 km south of Cooktown) south at least to the northern edge of the Atherton Tableland (fig. 12). It has not yet been found, however, in relatively well-collected areas around Ravenshoe and along the Palmerston Highway. See the account of *S. robusta* for details of the southern range limit. In the northern part of the range, where rainforest reaches the coast, *S. fryi* evidently occurs virtually at sea level, as at Cape Tribulation, whereas in the south it is not known below 400 m. The upper elevational limit has not been established, but the species attains at least 1100 m and possibly 1500 m. (The elevation of 1500 m on Mt. Spurgeon was given as part of a range of elevations over which the collector worked.)

LOCALITY RECORDS AND SPECIMENS EXAMINED: All localities are in Queensland: Big Tableland, 610 m, 30 km S, 3 km E Cooktown (AM R26384, R26385); near The Granites, vicinity of Home Rule (QM J25224); foot of path to The Granites (QM J25331); Granite Creek, Home Rule (QM J25324, J25325); 0.4 km E of The Granites (QM J25275); just west of Obree Point (QM J25225); Mt. Hartley, 610 m, 37 km S, 5 km E Cooktown (AM R26846–26852; QM J24852–24856, J24892–24900; SAM 9729 (3 specimens), 9813 (5 specimens), 9846; Shiptons Flat (QM J17844, J17845, J21345, J21346); Mt. Finnigan, 1040–1100 m (QM J25176, J25177; AMNH 111492–111494); Bloomfield, via Helendale (QM J24798, J24799); Bloomfield River (AM R2285, holotype); Pilgrim Sands, Cape Tribulation (QM J37279); Mt. Sorrow, 300–800 m, Cape Tribulation (QM J39147); McDowall Range, 550 m, 17 km N, 2 km E Daintree (QNPWS N14157, N14158, N14161, N14172–14176); ridge between Thornton Peak and Daintree River (AM R87922, R87923, R87939–87944); Thornton Peak, 1000 m (AM R55079–55081); Thornton Peak (AM R56333, R87919–87921, R87932, R87933); Hilda Creek, south side of Thornton Peak (AM R56443, R56444); Mt. Windsor Tableland, where road crosses Spencer Creek (QNPWS N14364–14366, N14370, N14373, N14374); southwest side of Mt. Windsor Tableland (AM R62629–62632); 31.5 to 34 km northeast of Cooktown Road via Mt. Windsor Tableland Forestry Road (AM R62600–62625); 41 km northeast of Cooktown Road via Mt. Windsor Tableland Forestry Road, 900 m (AMNH 111453–111458; QNPWS N28772); Mt. Spurgeon, 900–1500 m (MCZ 18383, 18387–18389; WH 1816–1819, 1826); Mossman Gorge Park, 5 km W Mossman (DU 10053); Mossman (AM R106971); Mt. Lewis, 900–1000 m, 6 km W, 9 km N Mount Molloy (AMNH 111451, 111452, 111460–111463; AM R61435–61442, R87924, 87925; QM J27369, J29422, J29605, J39146; QNPWS N14358, 14361; WH 1326, 1327, 1521, 1524–1527, 1539–1542, 1585, 1635, 1636, 1638, 1639, 1641, 1865, 2142, 2143, 2147, 2212); Mt. Lewis Road near Julatten (AM R106998); 7.5 km N, 3 km W Kuranda, 440 m (AMNH, tape recording only); 10.4 km north of Kennedy Highway on Black Mountain Road (less than 1 km from previous locality, AM R87929–87931); Kuranda State Forest (QNPWS A776); South Bell Peak, Malbon Thompson Range, 860 m (QNPWS N28741, N28742); Tinaroo Creek Road, 1070 m (MCZ 106113, 106114; SAMA 12576); Upper Tinaroo Creek, 700 m, 2 km N Platypus Creek (WH 1403); Mt. Edith, 3 km N Tinaroo Dam (AMNH 111521); Forestry Road B, 5.1 km north of road around Tinaroo Lake (AM R87927, R87928); 4 km W Kauri Creek Picnic Area, Danbulla State Forest, north side of Tinaroo Lake (AM R87889); 1.4 km W Kauri Creek Picnic Area (AM R87926); 4 km N, 6.5 km E Tinaroo Dam, 720 m (AMNH 111459); 3.9 km E Danbulla State Forest Camp and Office (AM R87896–87898); Lake Barrine (AM R29512, R29513, R73668).

Sphenophryne gracilipes (Fry)
Figure 13

Austrochaperina gracilipes Fry, 1912, p. 93 (type locality, "Somerset, Cape York, North Queensland"; holotype, AM R4536, collected by C. Hedley and A. R. McCulloch in October 1907).

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

Sphenophryne gracilipes: Parker, 1934, p. 155. Zweifel, 1962, p. 31.

Sphenophryne robusta: Zweifel, 1965, p. 2 (part, *gracilipes* considered a synonym). Cogger et al., 1983, p. 54 (part).

DIAGNOSIS: This species is distinguished from most other Australian *Sphenophryne* by its small size, rarely exceeding 20 mm SV. At this size *Sphenophryne fryi, S. pluvialis,* and *S. robusta* are just attaining maturity. The characteristic ventral pigmentation of *S. pluvialis,* showing a relatively abrupt change from densely pigmented chest to sparsely pigmented abdomen, also will distinguish it from *gracilipes,* which has a much more gradual gradation of ventral markings. *Sphenophryne gracilipes* has relatively long legs compared to *S. fryi* and *S. robusta.* A TL/SV ratio of 0.43 or higher serves as a criterion for separating *gracilipes* from most *robusta* and *fryi.*

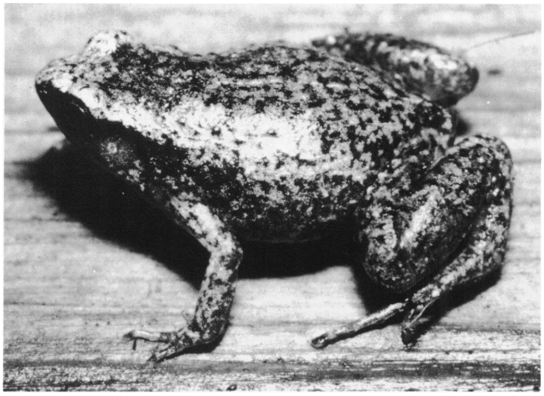

FIG. 13. *Sphenophryne gracilipes,* AMNH 83072, Wipim, Papua New Guinea; adult male, SV 18.0 mm.

The sibling species *gracilipes* and *adelphe* evidently cannot be separated morphologically. The call of *gracilipes,* a drawn-out series of high-pitched peeps uttered at an average rate of about 88 per minute, is much slower than *adelphe* which calls at more than 200 notes per minute.

DESCRIPTION

MORPHOLOGY: The largest of about 100 specimens from Papua New Guinea is a female 22.8 mm SV. All eight frogs measuring 20 mm or more are females, though males attain at least 19.5 mm. Females mature by at least 19.1 mm, and the smallest of three calling males measured only 17.5 mm. The situation is similar in the Australian frogs, where the largest of about 100 specimens are two females measuring 20.1 mm. Males reach at least 19.6 mm; three calling males measured 17.5 to 17.8 mm.

This description applies equally to Australian and New Guinean frogs. 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, 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 tubercles moderately prominent (fig. 4D). 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 phalange; subarticular and inner metatarsal tubercles moderately prominent (fig. 4D). Skin of 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, 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.

I have not examined living specimens of *S. gracilipes* from Australia, but Keith McDonald has kindly furnished his notes on specimens from Lankelly Creek: dorsal surface brownish gray with darker brown markings, or with a tinge of orange with grayish brown and dark brown speckling; snout tends to be more grayish than area posterior to eyes; dark streak from snout breaks up along lateral part at midbody; hidden surfaces of thighs, groin, upper arm, and axilla bright orange; ventral surfaces speckled light and dark; upper half of iris coppery, lower brown.

The colors I noted from living specimens taken at Wipim, Papua New Guinea (fig. 13) are similar: dorsal color grayish to golden brown anteriorly, changing to reddish brown on the posterior part of the back and 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 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; iris golden in the upper half, much darker reddish gold in the lower half. The only clear difference between the Australian and Papuan frogs is the bright orange leg and groin color described for the Australian sample; no such color was present in the Papuan frogs.

VARIATION IN PROPORTIONS: See tables 2–4 for proportions of adult *gracilipes* from Queensland and Papua New Guinea. In ratios expressive of tibia length, eye size, and eye-naris distance, the means of the two samples are closely similar. Somewhat greater differences between means, but still with large overlaps in ranges, occur with the IN/SV, EN/IN, and HW/SV ratios. Regression of TL, EYE, and EN against SV produces curves for each pair that are virtually superimposed. The curves for EN diverge, with larger New Guinea frogs having an average narrower IN distance. The scatter in the data is wide, however, and I doubt that any biological significance should be attributed. The curves for HW are more nearly parallel, diverging from about 0.25 mm apart in juveniles to 0.5 mm in adults, with New Guinea specimens averaging narrower heads. Again, the overlap in ranges is so great compared to the difference in means that I doubt any biological significance exists.

COMPARISONS WITH OTHER SPECIES

Sphenophryne gracilipes is allopatric to other Australian species of the genus with one possible exception. A specimen of *S. pluvialis* is recorded far from the body of its range from Leo Creek, McIlwraith Ranges, where *gracilipes* also occurs. See the accounts of distribution and comparisons of the former species for information.

The morphological identity of *S. gracilipes* and *S. adelphe* is most apparent in body proportions of animals of adult size (tables 2–4). The means for some ratios of interspecific samples are virtually identical, and in some instances *adelphe* and one or the other (Australian or Papuan) samples of *gracilipes* are more alike than are the two geographic samples of *gracilipes.*

In averages of some proportions *gracilipes* and *adelphe* fall within the ranges circumscribed by the three larger species *fryi, robusta,* and *pluvialis.* This is true of tibia length, where the small species fall between the longer legged *pluvialis* (but closest to it) and the shorter legged *fryi* and *robusta.* The regression lines for eye-naris distance also do not distinguish the small species as a group apart from the larger, and the finger discs of *gracilipes* and *adelphe* resemble those of *robusta* and *fryi* in size.

In several respects *gracilipes* and *adelphe* are set apart from the other Australian species. Regression lines for head width, orbit length, and internarial distance all lie below the lines for other species indicating that *gracilipes* and *adelphe* have relatively narrower heads, smaller eyes, and more closely spaced nostrils. I call attention to the apparent differences in the size of fourth toe discs (fig. 61C) only to remark that the sample of *adelphe* is small and the points widely scattered, encompassing the regression lines of *fryi* and *robusta* as well.

HABITAT AND HABITS

Sphenophryne gracilipes differs from most Australian and New Guinean microhylids in not being confined to rainforest habitats (exceptions in Australia are the sibling *S. adelphe* and the boulder-dwelling *Cophixalus saxatilis*). Most localities for the species on Cape York Peninsula fall in areas mapped broadly by Pedley and Isbell (1971) as open forest or low open forest, though *gracilipes* also occupies isolated tracts of rainforest (closed forest of Pedley and Isbell). Where I collected *gracilipes* at Wipim, Papua New Guinea, the vegetation was grassy woodland with denser gallery forest along small streams. Notes accompanying specimens collected in Queensland by Keith McDonald mention open forest and inland riparian forest. A specimen was found "under log in creek bed," and a series of 61 specimens in the Australian Museum came from a 1.5 square meter area of leaf litter. These latter specimens, collected near Weipa in early October, possibly were aggregated at a favorably moist site at the end of the winter dry season. The situation at Weipa, where an average of less than 1 cm of rain falls per month for seven months of the year (Specht et al., 1977, fig. 2), contrasts markedly with more typical microhylid rainforest habitat, where the driest three or four months average at least 2 or 3 cm of rain, usually much more (Tracey, 1982, table 3).

The rainforest species of *Sphenophryne* call from the shelter of leaf litter and differ in this respect from *S. gracilipes,* which adopts a more exposed calling site above ground. Those I observed in Papua New Guinea had climbed up on blades of grass. Keith McDonald (field notes) made similar observations of frogs calling from blades of grass 5–45 cm above ground, and once from a leaf on a shrub about 45 cm up. Nothing is yet known of the breeding habits of *S. gracilipes.*

Tyler (1972) tested the tolerance of *Sphenophryne gracilipes* (*"robusta"*) for seawater, finding an average time to loss of righting reflex of 1 hour 7 minutes, maximum 1 hour 40 minutes.

CALL

I know the call of *Sphenophryne gracilipes* from individuals I recorded in Papua New Guinea and from recordings made by Keith McDonald at two locations on the Cape York Peninsula. The call is a train of relatively high-pitched peeps (ca. 3700–4300 Hz) uttered over a period of about 10–20 seconds, each peep about 0.14–0.17 seconds in length (fig. 63A, B). Over the small temperature span of 23.4–24.8°C at which the recordings were made, the number of notes per minute ranges from 77 to 100 and the number of notes per call from 15 to 33 (table 6). A period of a minute or more may elapse between calls.

No differences of consequence are evident between the calls of two individuals from New Guinea and five from Australia. The call rate (notes/min) is 91.5 and 82.3 in two New Guinea frogs and 93.0, 86.0, and 83.0 in three Australian (the other two Australian frogs

TABLE 6
Call Statistics for *Sphenophryne gracilipes*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Notes per Call Mean (Range)	Notes per min Mean (Range)	Frequency, Hz	Number of Calls
AMNH 83069[a]	189	18.6	22.8	14.2 (13.3–15.0)	22.5 (21–24)	91.7 (90–93)	3900	4
QNPWS N32256[b]	223	17.6	23.4	19.7 (19.2–20.6)	31.3 (30–33)	93.0 (91–95)	3800	3[c]
AMNH 83070[a]	189	17.8	24.0	14.8 (13.9–15.4)	21.0 (20–22)	82.3 (81–83)	3900	3
QNPWS N22879[d]	241	17.5	24.8	16.2	24	86	4400	1
QNPWS N32254[b]	223	17.8	24.0	18.8 (17.8–20.0)	26.8 (26–28)	83.0 (82–85)	3750	4
No spec.	223	—	24.6	14.4 (9.5–16.6)	22.8 (15–26)	90.3 (77–100)	4000	8[e]

[a] Wipim, Papua New Guinea.
[b] Lankelly Creek, Coen, Queensland.
[c] N = 4 for notes per minute.
[d] Weipa, Queensland.
[e] 2 individuals cannot be segregated on this recording.

cannot individually be segregated on the recording). The range in call length in the Australian sample encompasses that of the New Guinea sample.

REMARKS

The southernmost specimens of *Sphenophryne gracilipes* were taken by Glen Ingram at Carrol Creek near the Hope Vale Reserve, about 27 km northwest of Cooktown. The northernmost records for *S. fryi* are about the same distance south of Cooktown at Big Tableland. It would be worthwhile to search appropriate habitats in the area north and south of Cooktown to establish how closely the ranges of the two species approach. Though widespread in drier, more seasonal habitats, *gracilipes* occurs in rainforest pockets farther north, in the McIlwraith and Iron Range regions. Thus, it might overlap ecologically with *fryi*.

DISTRIBUTION

Sphenophryne gracilipes is the only Australian microhylid known also to occur in New Guinea. In Australia, *gracilipes* occupies the northern half of the Cape York Peninsula, from Cape York itself south to the Hope Vale settlement area just north of Cooktown on the east coast, and south at least to the Arukun settlement on the west (fig. 14). In New Guinea, it is known from savanna and woodland areas of the southern part of Western Province, Papua New Guinea, ranging from the south coast (Daru Island) to the northern end of Lake Murray. Discovery of the species to the west in southern Irian Jaya may be anticipated, but rainforest at the head of the Gulf of Papua may limit the eastern edge of the range. No *gracilipes* has been found on the islands in Torres Straits (other than Daru, close on shore), though experienced collectors have worked intensively on some of these islands. Even without the Papuan segment of its range, *gracilipes* occupies a far greater area than any other Australian microhylid.

LOCALITY RECORDS AND SPECIMENS EXAMINED: AUSTRALIA (all localities in Queensland): Somerset (AM R4536 [holotype], R56019, R57134, R56183, R57184); Lockerbie (QM J24621, J24623–24625); 2 km E Lockerbie (QM J25609–25612); 1.6 km S Jardine River crossing (AM R38387, R38388); 22 km E Heathlands on Captain Billy Creek Road (AM R94419); Heathlands (QM J27874); 40 km N Moreton Post Office (AM R38479); 10 km N Moreton Post Office (AM R38385, R38386); Wenlock River at Moreton (AM R38396, R38397); Weipa (AM R62050–62058, R62688–62695); Sunrise Creek, Weipa (AM R62496–62556); Cool Pool Road, Weipa (QNPWS N28879); 29 km NE Pasco River (AM R38400); 24 km NE Iron Range (AM R38389–38395, R38398, R38399); 13 km NW Iron Range (AM R38473); N foot of Tozer Range (AMNH 54263); Iron Range (QM J27873); Line Hill, 2 km N Lockhart River Settlement (QM J28074–28079); King Park, Iron Range (QM J28029–28038); Archer River, Arukun Re-

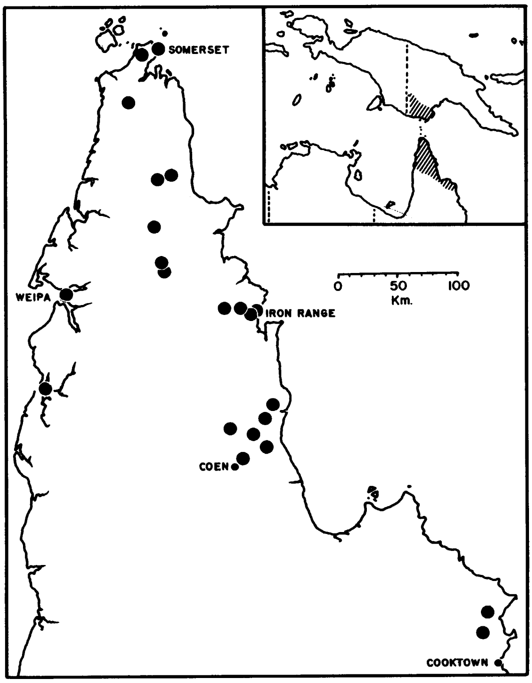

FIG. 14. Locality records for *Sphenophryne gracilipes* in Cape York Peninsula. Inset shows range in Cape York and Papua New Guinea.

serve (QM J34897); Buthen Buthen, Nesbitt River (QM J34457); Leo Creek (QM J32489, J32490); Leo Creek Road, 500 m (QM J28920, J32493, J32494); Peach Creek, 14 km NNW Mt. Croll (QNPWS N15253, N15255); Weather Station Creek, 19 km ENE Mt. Croll (QNPWS N32459–32461); Steen's Hut, 30 km NE Coen (QM J34522–34525); 8 km SW mouth of Rocky River (QNPWS N32105, N32106, N32143, N32144, N32151–32153); Rocky Scrub, McIlwraith Range (MCZ 18375–18377); Lankelly Creek, 10 km NE Coen (QNPWS N32254–32256, N32263, N32264); Coen (QNPWS N32439); 33 km N Carrol Creek, near Hope Vale Reserve (QM J32496); Carrol Creek, near Hope Vale Reserve (QM J32376–32378).

PAPUA NEW GUINEA (all localities in Western Province): Maka (MCZ 80009); Aramia River (MCZ 28390–28394); Emeti (MCZ 82614); Balamuk, Bensbach River (MCZ 82615–82617; AMNH 90402, 90403); Morehead (MCZ 82613, 86391–86407, 86700–86703, 86706, 86707; AM R40745–40747); Mata (MCZ 86222–86272, 86301–86350, 86460–86470; AMNH 90404–90407); Gubam (MCZ 86704, 86705); Wipim (AMNH 83069–83075; MCZ 80014–80016, 80999); Gamaeve (MCZ 80017, 86485–86487); 6 km W Oriomo Station (MCZ 80010, 80011); Kuru (MCZ 82318, 88385); Oriomo Station (MCZ 84875, 84876, 86699); Old Zim, Oriomo River (MCZ 66000, 80012, 80013); Boze (MCZ 80007, 80008); Wuroi, Oriomo River (AMNH 53390–53395, 90408–90410); Daru (AMNH 53389).

FIG. 15. *Sphenophryne pluvialis,* AMNH 111464, Palmerston National Park vicinity; adult male, SV 25.7 mm.

Sphenophryne pluvialis Zweifel
Figure 15

- *Uperolia marmorata:* Barbour, 1914, p. 202 (misidentification of possibly first specimen of species).
- *Sphenophryne polysticta:* Loveridge, 1935, p. 56 (part).
- *Sphenophryne robusta:* Zweifel, 1962, p. 19.
- *Sphenophryne pluvialis* Zweifel, 1965, p. 6 (type locality, "Speewah, elevation 1500 feet, Queensland"; holotype, AMNH 54195, collected by the Archbold Cape York Expedition on April 9, 1948).

DIAGNOSIS: Preserved specimens of *Sphenophryne pluvialis* may be distinguished from other Australian *Sphenophryne* by the ventral color pattern. In *pluvialis* the chin and chest are more densely pigmented with melanin than the abdomen, and there is a rather sharp change in density at the level of the arms. In the other four species the chin is generally more heavily pigmented than the abdomen, but the transition is gradual (fig. 8C). In living frogs this difference in melanin is somewhat obscured by lighter pigments that are lost in preservative. The presence of a silvery white streak along the canthus rostralis and edge of upper eyelid and red pigment in the iris are good field marks for living *pluvialis*. A much less well-defined light canthal mark is present in some individuals of other species, and some red may occasionally be present in the normally golden iris.

The call is a train of high-pitched notes, averaging about 14 notes in a 1-second call. Other species call at a slower rate, and in the case of *S. robusta,* utter the notes in couplets. For remarks on differences in proportions among species, see the following section on comparisons.

DESCRIPTION

MORPHOLOGY: The largest male is 25.7 mm SV and the largest female 29.3 mm in a sample of over 100 specimens. Males mature at a size at least as small as 21.3 mm, as indicated by calling. The smallest gravid females among 20 examined measure 22.5 and 22.7 mm, whereas two frogs measuring 21.6 and 21.7 mm appear to be immature. Hence, females evidently mature at a body length of about 22 mm.

Head slightly narrower than body; snout bluntly pointed as seen from above, rounded and slightly projecting in profile. Canthus rostralis rounded, loreal region slightly sloping and slightly convex; nares lateral, barely visible from above, about midway between eye and snout tip but appearing much closer to snout tip in profile. Eyelid narrower than interorbital space; corneal outline visible from below. Tympanum obscure or hidden, about half length of orbit. Relative lengths of fingers 3>4>2>1, first half length of second, all with grooved terminal discs, disc on first finger equal to or slightly wider than penultimate phalange, others more distinctly expanded, the third averaging about 1.8 times width of penultimate phalange; subarticular tubercles moderately well developed, distinct inner and middle metacarpal elevations present. Toes unwebbed, relative lengths 4>3>5>2>1, all with grooved discs broader than penultimate phalanges; disc on fourth toe largest, averaging about 1.8 times width of penultimate phalange; subarticular tubercles moderately well developed, an elongate inner metatarsal tubercle but no outer. Skin smooth dorsally and ventrally except for an indistinct, curved, postorbital-supratympanic fold.

COLOR AND PATTERN: The dorsal color in preservative is light brown with darker brown maculation on body and limbs. The loreal region, including the upper lip, is uniform dark brown, bordered above by a weak whitish stripe along the canthus rostralis and edge of the eyelid. The dark loreal color continues through the tympanic region and in some specimens diffusely onto the side of the body, which generally has a darker ground color than the back. There is no distinctive pattern in the groin or on the concealed parts of the thighs, just a continuation of the lateral and dorsal patterns with slightly more dark pigmentation. The chin has a nearly uniform brown ground color relieved by a few light spots. At the level of the arms, the pattern reverses to a pale ground with scattered melanophores, occasionally grouped into small spots in no regular pattern. The undersurfaces of the thighs are patterned much like the abdomen, but the shank and foot are light with dark spots.

A specimen from the vicinity of Kuranda, about 13 km north of the type locality, had the following colors in life: dorsum light gray-brown with a faint pinkish tinge on the hind legs and darker brown mottling on the body; the dark side of the face was bordered above by a light canthal stripe continuing along the edge of the eyelid but fading before reaching the level of the arm; the pupil was edged with red; the throat was pale gray, the abdomen yellower, and the undersurfaces of the hind legs verged on orange. Another from the same locality was similar except that the throat was darker with dull yellow spots. A specimen from the region of Palmerston National Park had a dark brown dorsum with obscure darker mottling and the loreal area black, with this color extending through the eye region to the side of the body. The canthal line was pale, almost white, and the upper part of the iris conspicuously reddish gold. The throat and chest were pinkish gray with a few light flecks, the abdomen greenish yellow, and the undersides of the legs orange-brown. Notes accompanying a specimen from Thornton Peak indicate similar colors in this northern population, including the red pupillary ring and pale canthal line. Color photos in Cogger (1975, fig. 46) and Barker and Grigg (1977, p. 205) show the red iris well.

The abrupt change in pattern in the chest region, so conspicuous in preserved specimens, is not clearly evident in living frogs in which the transition appears more graded.

VARIATION IN PROPORTIONS: See tables 2–4 for variation in selected proportions of adult frogs from two localities: Thornton Peak and Kuranda, areas about 80 km apart. The ratios of HW, EN, and IN to SV are closely similar in adults and the regression lines for the two samples virtually coincide in each instance. Eye size and tibia length show some evidence of geographic variation, with the eyes being larger and legs longer in the northern (Thornton Peak) sample (figs. 60B, 61D). Regression lines for eye size diverge, whereas those for tibia length are essentially parallel. I am not confident that the apparent difference in eye size is meaningful—the measurement is not one of the most reliable ones, and the regression lines are less than 0.2 mm apart at the maximum adult size. Tibia length, however, is a more reliable measurement, and the samples maintain an average difference of about 0.5 mm from small to large body size. It appears that frogs from the area of Thornton Peak usually start with relatively longer legs and maintain the difference throughout life. The amount of differentiation is not great; less than 50 percent of frogs in the combined samples could be allocated correctly to geographic origin on the basis of leg length.

COMPARISONS WITH OTHER SPECIES

Sphenophryne pluvialis is microsympatric with *S. robusta* and *S. fryi* and may exist at one locality with *S. gracilipes*. The differences in pigmentation discussed in the diagnosis should be adequate to permit identification of living or preserved individuals. Some differences in proportions will be discussed briefly.

The chief difference in proportions between *pluvialis* and the two species of similar size—*robusta* and *fryi*—lies in the longer hind legs of *pluvialis*. Only one *pluvialis* among 20 of adult size from Thornton Peak has a TL/SV ratio less than 0.44, whereas only one among 93 adult *fryi* has a ratio that high. Southern *pluvialis*, as exemplified by the sample from the vicinity of Kuranda, are somewhat shorter legged, and there is considerable overlap in the TL/SV ranges of these *pluvialis* with the ranges of *fryi* and *robusta*, which themselves are highly similar. Only slightly more than half the southern *pluvialis* have TL/SV values of 0.44 or greater and can be identified on this character alone. Relative values for eye size, internarial distance, and eye-naris distance all average higher in *pluvialis* than in *robusta* and *fryi*, but the overlaps in ranges are large enough to limit use in diagnoses.

Adult *S. gracilipes* and *S. pluvialis* are similar in having relatively long legs, but in most other respects *gracilipes* differs from *pluvialis* in the same ways as *fryi* and *robusta* do: relative eye size, internarial distance, and eye-naris distance are all greater in *pluvialis*. Head width is narrower in *gracilipes*, but neither this character nor the others mentioned will provide a high degree of separation between *gracilipes* and *pluvialis*. However, the small size of *gracilipes* (maximum size approximately equal to the minimum size of mature *pluvialis*) and characteristics of color pattern should prevent confusion among specimens.

HABITAT AND HABITS

Locality records for *Sphenophryne pluvialis* are in areas mapped by Tracey and Webb (1975) as vine forest, ranging from simple notophyll vine forest to complex mesophyll vine forest (fig. 20). Sites of capture with specific elevational data lie at or below 800 m. Records near Daintree show that the species ranges almost to sea level where the forest has not been destroyed.

Like other rainforest *Sphenophryne*, these frogs may be found beneath surface cover in daytime and, also like the others, they call from the leaf litter at night. My impression is that *S. pluvialis* is less secretive when calling than are *S. fryi* and *S. robusta*, species with which it is microsympatric. It is often

TABLE 7
Call Statistics for *Sphenophryne pluvialis*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Notes per Call Mean (Range)	Notes per sec Mean (Range)	Frequency, Hz	Number of Calls
WH 2188[a]	241	–	19.0	0.98 (0.91–1.22)	13.0 (11–16)	12.8 (12.5–13.0)	3000	5
No spec.[b]	229	–	22.3	1.12 (1.12–1.13)	18.0 (18)	15.7 (15.6–15.7)	2900	5
No spec.[c]	228	–	23.2	1.18 (1.11–1.26)	19.0 (18–20)	15.6 (15.4–15.8)	3050	6
AMNH 111465[d]	229	21.3	23.4	1.26 (1.12–1.46)	21.2 (19–24)	16.5 (16.2–16.7)	3200	10
AMNH 111466[d]	229	21.7	23.4	1.48 (1.31–1.61)	22.4 (20–24)	15.0 (14.7–15.5)	3400	5
No spec.[d]	229	–	23.4	0.99 (0.97–1.05)	16.2 (16–17)	16.0 (15.8–16.1)	3300	5
No spec.[e]	248	–	–	1.10 (1.03–1.17)	17.0 (16–18)	15.5 (14.8–15.9)	2600	5

[a] Majuba Creek, E slope Mt. Bartle Frere, 305 m.
[b] 5.5 km N, 6 km E Tinaroo Dam, 800 m.
[c] 12.5 km S, 13 km E Millaa Millaa, 460 m.
[d] 1 km E, 3 km N Kuranda, 350 m.
[e] Tully Falls.

possible—with sufficient contortions—to see a calling *pluvialis,* whereas finding one of the other species usually involves moving some cover.

Czechura (1978) studied the distribution of *Sphenophryne pluvialis* and *S. robusta* (called *fryi* in his paper) along an altitudinal transect near the headwaters of the Russell River. He found only *pluvialis* from 460 m to about 560 m elevation and only *robusta* above about 580 m, with a zone variably 30 to 50 m wide in which both species called. The situation is, as Czechura suggests, indicative of altitudinal replacement, but the data base of one evening on one transect is insufficient for anything but preliminary speculation. The two species occur together at 800 m northeast of Tinaroo Dam but nearby at 1080 m I heard only *robusta* on brief visits on two evenings.

Brattstrom (1970) attempted to study thermal acclimation in *Sphenophryne pluvialis,*[2] but found that the frogs could not tolerate exposure to 5°C or even 10°C; at the latter temperature 50 percent of his frogs died within 48 hours. The lack of tolerance of low temperature may bear on the species' relatively restricted elevational distribution.

CALL

Sphenophryne pluvialis utters a short train of relatively high-pitched notes (fig. 64A, table 7). The mean call duration ranged from 0.98 to 1.48 seconds in seven individuals, with from 13.0 to 22.4 notes in an average call. Notes are about 0.3–0.5 seconds in length, separated by intervals of similar length, and with a frequency of about 2600–3400 Hz. A slight rise and fall of frequency within each note is evident in some audiospectrograms. The mean number of notes per second ranged from about 12.8 to 16.5. The slowest rate was recorded at the lowest temperature (19°C), as would be expected, but the sample size and temperature range are too small to provide meaningful data on the effect of temperature. The frogs call at irregular intervals; less than a minute to several minutes may elapse between calls.

DISTRIBUTION

The majority of localities for *Sphenophryne pluvalis* lie on or border the Atherton Tableland (fig. 16). The southernmost locality is Wallaman Falls National Park west of Ingham, where Keith McDonald heard and collected the species on February 16, 1984. There is a substantial gap in the known range between this locality and others to the west of Tully on the north. I have seen no specimen from the northern edge of the range in the region between the vicinity of Kuranda and Daintree, about 60 km farther north. However, Dennis and Trenerry (1984) mention the presence of *pluvialis* on the lower slopes of Mt. Lewis, midway in this gap (not plotted in fig. 16).

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[2] Identified as *Sphenophryne* sp., but three voucher specimens deposited in AMNH are *pluvialis.*

The region of Mt. Finnigan, south of Cooktown, has been fairly heavily collected and has produced no *pluvialis*. Hence, it is surprising to find a specimen recorded from Leo Creek in the McIlwraith Ranges more than 300 km from the otherwise northernmost specimens. The frog, QM J28816, is an adult female and in all respects typical of the species. Verification of this northern record would be desirable.

LOCALITY RECORDS AND SPECIMENS EXAMINED: All localities are in Queensland: Leo Creek, NNE of Coen (QM J28816); McDowell Range, ca. 17 km N, 2 km E Daintree, 550 m (QNPWS N14156, N14159, N14177, N14178); Thornton Peak (AM R55078, R56442, R56480–56493, R56510–56513, R56602, R58274–58279, R87917–87919); lowlands S of Thornton Peak (AM R87865–87874); ridge between Thornton Peak and Daintree River (AM R87875–87880); Mt. Windsor (AMNH 118813, 118814); 1.5 km SE Daintree (DU 10121, 10151–10174); 24 km N Miallo (AM R51367); Black Mountain Road, Kuranda State Forest, 10.4 km N Kennedy Highway (AM R87861–87864); 1 km E, 3 km N Kuranda, 350 m (AMNH 111465–111467); Black Mountain Road, Kuranda (QM J28745–28747, J28749, J28750); Kuranda (AMNH 111496–111499; MCZ 7063, 19256; FMNH 29026, 29028–29032); Jumrun Creek, Kuranda (AM R111626, 111627); Kennedy Highway 1.5 km E Barron River Bridge at Kuranda (AM R87830–87845); Kennedy Highway 3 km SE Barron River Bridge at Kuranda (AM R87846–87848); Kuranda State Forest (no specific locality—AM R56291–56303, R56608); 8 km S Kuranda, 600 m (AMNH 85270); Speewah, 460 m (AM R61416–61421; AMNH 54195 [holotype]; MCZ 106115, 106116); 5.5 km N, 6 km E Tinaroo Dam, 800 m (AMNH, tape recording only); Danbulla State Forest, 1.4 km W Kauri Creek picnic area (N side of Tinaroo Lake, AM R87849–87853); Kauri Creek (AM R111628, R111632); 3.9 km E Danbulla State Forest camp and office (AM R87854–87856); Severin Boar Pocket, ca. 13 km E, 1 km S Tinaroo Dam (QNPWS QPA 29); Stallion Pocket, Mulgrave River (QM J30903, J32061, J32148); Lake Eacham (FMNH 29034); Gadgarra State Forest, 6 km N, 11 km E Malanda (QNPWS, 2 uncatalogued specimens); Mt. Bartle Frere (QM J32146); Majuba Creek, E slope Mt. Bartle Frere, 300 m (WH, tape recording only); Tchupala Falls, Palmerston National Park (AMNH 111495); Tchooratippa Creek, Palmerston National Park, 460 m (AMNH 85271, 85272); 12.5 km S, 13 km E Millaa Millaa, 460 m (AMNH 111464); Tully Falls (QM J32149); Koombaloomba Dam (QM J29577–29579); ca. 30 km W Tully (QM J32115); Wallaman Falls National Park, 540–560 m (QNPWS N15603; *fide* Keith McDonald, specimen not examined).

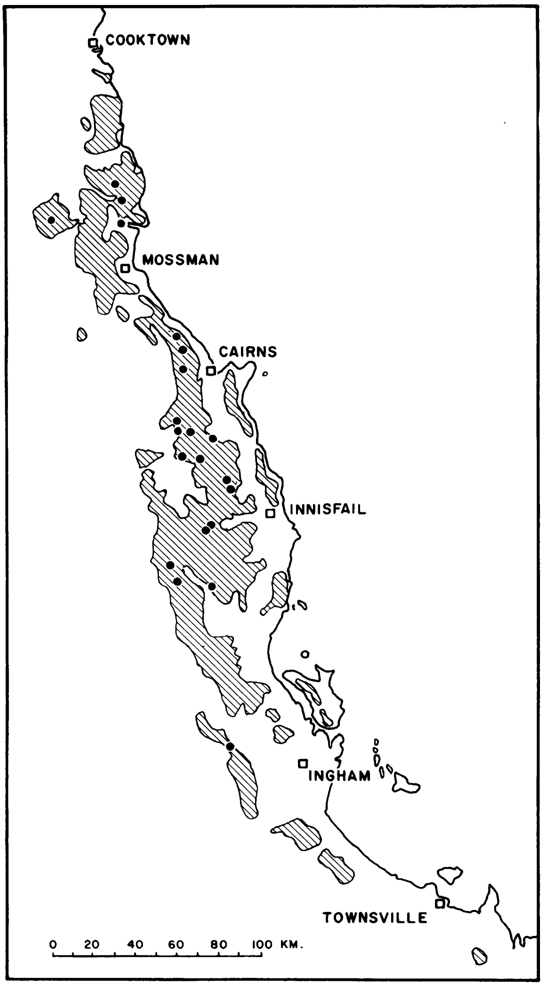

FIG. 16. Distribution of *Sphenophryne pluvialis*. A record far to the north near Coen (see fig. 27) requires confirmation.

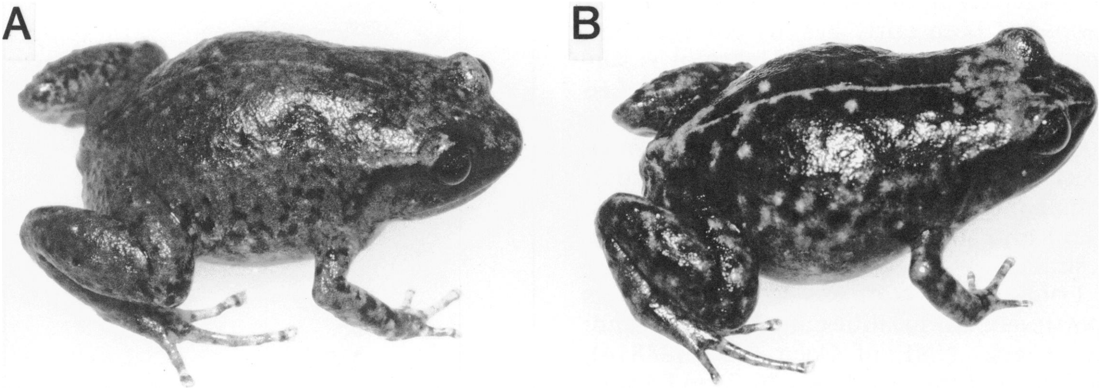

FIG. 17. *Sphenophryne robusta.* **A,** AMNH 111470, near Ravenshoe, adult male, SV 23.5 mm; **B,** AMNH 111472, Bobbin Bobbin Falls, adult female, SV 23.3 mm.

Sphenophryne robusta (Fry)

Figures 17, 18

Austrochaperina robusta Fry, 1912, p. 89 (type locality, "Russell River, North-east Queensland"; holotype, AM R5295, date of collection and collector not recorded). Andersson, 1916, p. 7.

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

Sphenophryne robusta: Parker, 1934, p. 157. Zweifel, 1962, p. 19 (part). Zweifel, 1965, p. 2 (part).

Sphenophryne polysticta: Loveridge, 1935, p. 56 (part).

TYPE LOCALITY: The precise type locality of *Sphenophryne robusta*—a matter of concern because of the possibility of confusion between this species and *S. fryi*—cannot be determined. The Russell River has its origins in creeks on the western slopes of Mt. Bartle Frere and nearby in the vicinity of Lamins Hill on the eastern edge of the Atherton Tableland. It flows eastward, south of Mt. Bartle Frere, and upon reaching the narrow coastal plain turns north for several kilometers before passing to the ocean through a gap in the coastal hills. Without allowing for the numerous twists and turns in the watercourse, the distance from headwaters to mouth is somewhat over 50 km.

The lowest elevation at which *S. robusta* has been found is about 360 m; there are no coastal plain localities for the species. This would seem to restrict the type locality to about the upper 10 percent of the river's course, on the west side of Mt. Bartle Frere or the edge of the Atherton Tableland, an area where *robusta* has been positively identified by its call. Mr. Keith McDonald (personal commun.) has made the reasonable suggestion that the type series may have been taken in the vicinity of Boonjee, where mining operations in the late 19th century provided access to an area otherwise difficult to reach. Future studies may extend the range of *S. fryi* into the immediate area of the type locality of *robusta*—specimens thought to be *fryi,* but not verified by call, are from South Bell Peak, 16 km north northwest of the mouth of the Russell River.

TYPE SPECIMEN: The holotype is a gravid female with the right side of the chest dissected, revealing the generically diagnostic presence of the clavicle. The specimen is bleached, though some dark pigment remains—a canthal dark streak and a streak from the posterior corner of the eye over the tympanum. Measurements are: SV 23.7, TL 9.7, HW 8.3, EYE 2.5, EN 1.4, IN 2.35, width of third finger disc 0.6 (penultimate phalange 0.5), width of fourth toe disc 0.75 (0.45).

It is not possible to say with certainty that the holotype of *robusta* represents the population with which I associate the name and not the sibling species *fryi.* In a following section on comparisons I show that *robusta* and *fryi* have an average difference in the IN measurement, with many *robusta* having higher IN/SV values than any *fryi,* and somewhat fewer *fryi* exceeding *robusta* at the lower end of the scale. Of the eight specimens that I examined in the type series of *robusta,* three have ratios characteristic of *fryi,* one of *robusta,* and four (including the holotype) are indeterminate.

DIAGNOSIS: *Sphenophryne robusta* differs from *S. pluvialis* in that the dark pigmentation of the throat is not abruptly set off from the paler abdominal pigmentation in preserved specimens, but rather there is a gradual transition. Living frogs of these species can generally be distinguished by the lack of a distinct light canthal line and lack of red iris pigment in *robusta. Sphenophryne gracilipes* and *S. adelphe,* which are widely disjunct from *robusta,* are much smaller; their maximum size of about 20 mm SV approximates the minimum size at which *robusta* becomes mature. *Sphenophryne fryi* and *S. robusta* have closely similar morphologies and no character or combinationof characters will allow certain identification of most specimens. See the following section on comparisons for discussion. The call of *robusta*—a series of chirps given in couplets—is unique.

DESCRIPTION

MORPHOLOGY: The largest among more than 300 *robusta* is a female from Henrietta Creek, Palmerston National Park, that measures 32.9 mm SV. Clearly this is an exceptional individual, for the next largest measures only 28.8 mm and frogs as large as 26 or 27 mm are a small minority among about 90 females identified (by dissection) as adult. Females evidently mature at about 21–22 mm SV, for this size range includes individuals that are gravid as well as others that appear to have immature ovaries. Males reach at least 26.5 mm and mature as small as 19.8 mm (calling individual).

Head slightly narrower than body; snout bluntly pointed in dorsal aspect, high, slightly rounded, and projecting only a little past lower jaw in profile; nostrils lateral, barely visible from above, slightly closer to tip of snout than to eye but appearing much closer in profile. Eyes oriented anterolaterally, corneal outline partly visible from beneath, eyelid narrower than interorbital space. Tympanum inconspicuous, one-half length of orbit or a little larger. Relative lengths of fingers 4>3>2>1, first finger slightly less than one-half length of second; all fingers with grooved terminal discs, that of first poorly developed, narrower than penultimate phalange, others broader than penultimate phalanges, that of third about 1.25 times its width; subarticular tubercles low, not prominent; inner metacarpal elevation elongate, only slightly more evident than the low middle and outer metacarpal elevations. Toes unwebbed, relative lengths 4>3>5>2>1, first toe less than half length of second; all toes with grooved terminal discs, that on first toe not broader than penultimate phalange, others broader than penultimate phalanges and broader than finger discs, disc on fourth toe about 1.5 times width of penultimate phalange; subarticular tubercles rounded, slightly prominent, an elongate inner metatarsal elevation but no outer. Dorsal surfaces smooth to finely rugose; a weak to moderately prominent postocular-supratympanic fold.

COLOR AND PATTERN: The ground color in preservative is light brown to dark gray-brown. The dorsum is variably patterned—some individuals are pale with only a few darker flecks; others have more intense dark pigmentation, especially in the middorsal region. Rarely the back is largely dark with a few pale spots. A pale vertebral hairline may be present. The loreal region, including the upper lip, is typically uniform dark brown. A dark streak follows the postorbital fold, and the area beneath the fold may be dark, continuous with the loreal pigmentation. Upper surfaces of the limbs are much like the adjacent dorsal surfaces. The groin and anterior and posterior surfaces of the thighs are not distinctively patterned. The venter may be pale with little dark pigmentation, or may show fairly heavy melanic mottling on the chin and chest, giving way in a gradual transition to a less heavy but coarser abdominal pattern. Such differences are probably influenced by metachrosis.

The dorsal ground color in life is a shade of brown, some frogs with a gray tint, but more often reddish. The diffuse darker spotting partakes of the general shade of the ground, whereas the loreal color is darker, almost black. One peculiarly patterned in-

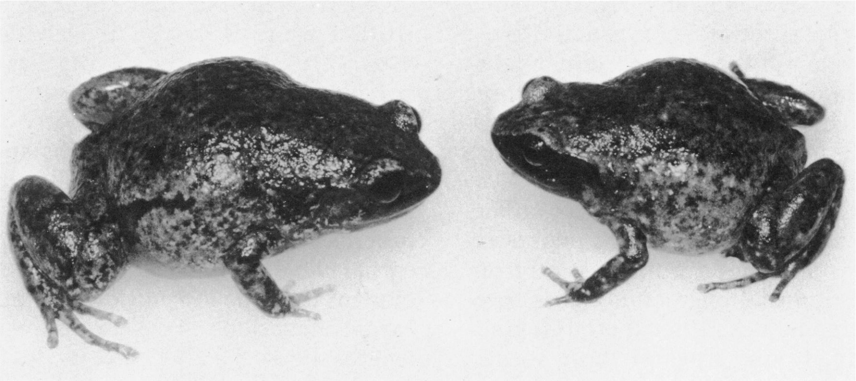

FIG. 18. *Sphenophryne fryi* (left) and *S. robusta,* identified by their calls and captured about 3 km apart northeast of Tinaroo Dam. *S. fryi,* AMNH 111459, adult male, SV 27.0 mm; *S. robusta,* AMNH 111473, adult male, SV 23.1 mm.

dividual (fig. 17B) had the back dark brown with small light spots, a vertebral hairline, and the back of the head light yellowish brown. The ventral color ranges from yellow to orange, rather bright in some instances but more often dulled by darker mottling. This ground color may also be present in the groin and on the concealed parts of the thighs. The iris is dark golden. For an illustration in color, see Barker and Grigg (1977, p. 203). The frog illustrated is identified as *S. fryi,* but from the locality (The Crater) almost certainly it is *S. robusta.*

VARIATION IN PROPORTIONS: Tables 2–4 present statistics on body proportions of adult frogs from three localities: the region of Mt. Spec, a presumably isolated population at the southern limit of the species range; Majors Mountain, 160 km north-northwest of Mt. Spec; the vicinity of Lamins Hill and Boonjee, 30 km northeast of Majors Mountain. The proportions relating TL, EYE, EN, and IN to SV, and the EN/IN ratio show no differences of any consequence among the samples. The mean of the HW/SV ratio is lower in the Boonjee-Lamins Hill sample than in the other two, but its range almost totally overlaps that of the nearby Majors Mountain sample. Average head widths of adult animals, as measured by regression lines, are no more than 0.5 mm apart in the three samples.

COMPARISONS WITH OTHER SPECIES

The geographic ranges of *Sphenophryne robusta* and *S. pluvialis* overlap broadly, and the two may be found calling side by side. Information in the diagnoses and in the comparisons section of the *pluvialis* account should make it possible to identify most specimens, even if the call is not heard.

Sphenophryne fryi and *S. robusta* are parapatric, and identification of many specimens is not possible in the absence of information on the calls of individual frogs or without reliance on geography. *Sphenophryne fryi* is a slightly larger frog than *S. robusta,* but the average difference of about 2 mm in size at attainment of maturity and in maximum size is too small to be useful in identification. Ratios relating the measurements TL, HW, EYE, third finger, and fourth toe discs to snout-vent length provide no means of segregating specimens (tables 2–4). I find nothing in the color pattern of living or preserved frogs that will aid in identification (fig. 18).

In only one measurement (IN) is there a consistent average difference between *robusta* and *fryi,* and even here overlap in ranges precludes effective use in allocating many specimens to species. Figure 19 shows the SV and IN measurements of samples of 50 *robusta* and 57 *fryi.* Large adult specimens of the two species show an average difference (as measured by the regression lines) of only about 0.2 mm in their internarial distance. In a sample of 119 adult *robusta,* the IN/SV ratio equals or exceeds 0.105 in 81 specimens (67%), whereas only 3 of 93 *fryi* have so high a ratio. At the other end of the range, only 3 of 119 *robusta* have a ratio equal to or less

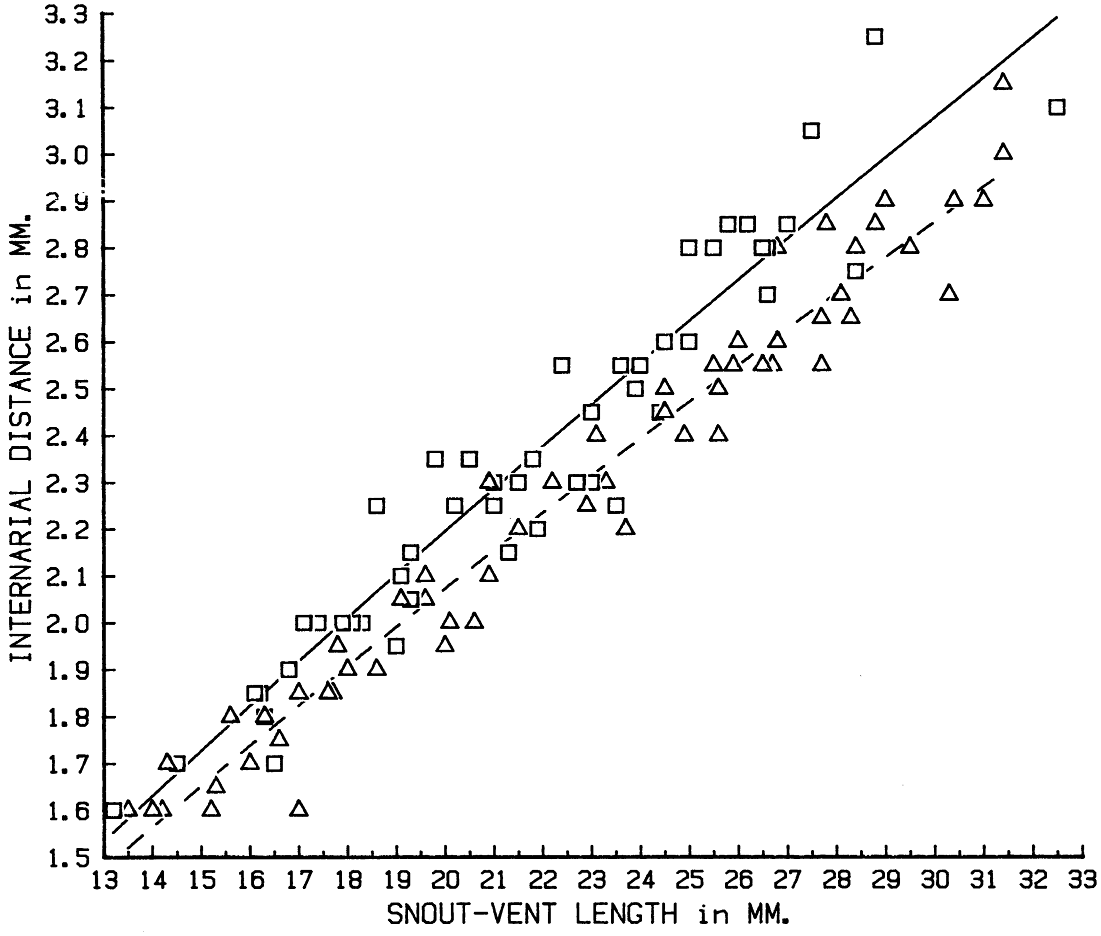

FIG. 19. Comparison of internarial distances in *Sphenophryne robusta* (squares, solid line) and *S. fryi* (triangles, broken line). Regression formulas: *robusta* (n = 50), IN = $0.779SV^{0.790}$, r = 0.964; *fryi* (n = 57), IN = $0.195SV^{0.789}$, r = 0.980.

than 0.96, whereas 45 of 93 *fryi* (48%) have a ratio this small. Thus, it appears that a criterion of IN/SV ≥ 0.105 will correctly allocate about 67 percent of adult *robusta* while IN/SV ≤ 0.96 will correctly identify about 48 percent of *fryi*. The significant proportion of specimens with ratios from 0.97 to 0.104 cannot accurately be identified by morphological criteria. Because the EN measurements of *robusta* and *fryi* are essentially the same for individuals of the same body size, use of the EN/IN ratio affords no better separation of the species than does the IN/SV ratio. (My a priori identification of most of the specimens upon which the above statistics were calculated was based on geography and excluded animals from the area of parapatry.)

HABITAT AND HABITS

Sphenophryne robusta ranges through virtually the entire spectrum of rainforest vegetation types, from complex mesophyll vine forest at 360 m elevation at Henrietta Creek in Palmerston National Park to simple microphyll vine forest thicket atop Mt. Bellenden Ker at 1520 m (figs. 20, 34). Whether it occurs at lower elevations in the few remaining tracts of forest near the coast remains to be determined. As a ground-dwelling species, it would not be expected to be found in forests

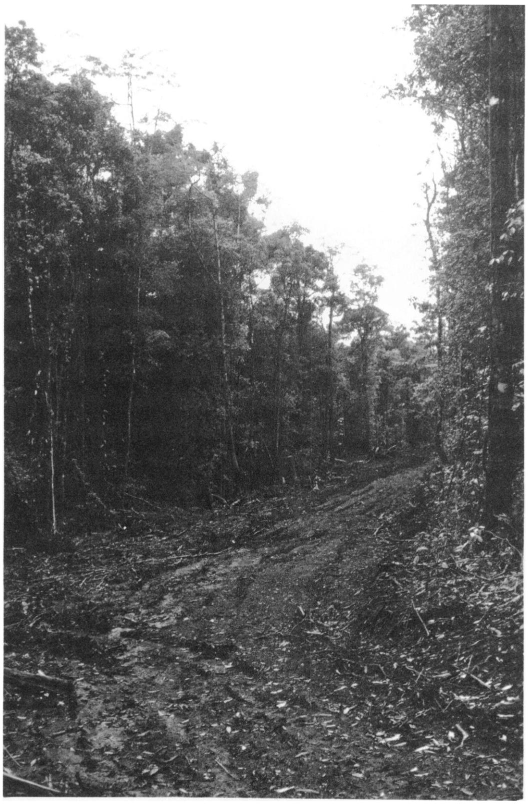

FIG. 20. Swath cut through forest in Palmerston National Park for road construction, January 1981. Microhylids in this area include *Sphenophryne pluvialis, S. robusta, Cophixalus ornatus,* and *C. infacetus.*

that are seasonally flooded, but low, forested hills on the coastal plain may provide suitable habitat.

In the daytime these frogs shelter under surface cover such as rocks and logs and presumably within the leaf litter as well. Males typically call from concealment in the leaf litter—not deeply buried where that is possible (the leaf litter often is quite thin), but generally well hidden. Keith McDonald (field notes) found one calling from within a 2-in. deep hole in a roadbank.

CALL

Sphenophryne robusta utters a series of short (0.04–0.08 sec), high-pitched chirps arranged in couplets (fig. 64C, table 8). Calls range from about 1 to 5 seconds in length, with from 6 to 20 notes per call. The numbers of notes per call (r = +0.503) and note couplets per second (r = +0.589) each show a rather weak correlation with temperature, whereas call duration exhibits no correlation (r = +0.091, T = 18.4–22.4°C). Individual notes apparently begin with an abrupt upward frequency sweep and end with a similarly rapid fall. The body of the note is finely tuned, with the initial note of each couplet typically shifting downward in frequency about 300 Hz through a midpoint frequency of about 3000 Hz. The second note is shorter, with a midpoint frequency about 100 Hz lower.

DISTRIBUTION

The range of *Sphenophryne robusta* probably is continuous in upland rainforest from the region of Mt. Haig and Mt. Edith, north of Tinaroo Lake, southward to the Cardwell Range east of Kennedy. Presumably the populations in the forest blocks west and south of Ingham (fig. 21) are isolated from the main body of the range to the north. The northern limit of the range remains to be determined, but it may lie in the 30-km stretch between Kuranda (northwest of Cairns) and present records near Mts. Edith and Haig. A considerable number of *Sphenophryne* (mostly *pluvialis,* some *fryi* but no *robusta*) have been collected in the vicinity of Kuranda. On my two nights in the forest near Kuranda I heard only *pluvialis* and *fryi.*

Sphenophryne robusta has not yet been found in any coastal situation, the lowest elevation of record being 360 m at Henrietta Creek in Palmerston National Park. Keith McDonald and I obtained a specimen at 1520 m on Centre Peak, Mt. Bellenden Ker, which represents the maximum known elevation for the species. It reaches at least 1280 m on Mt. Bartle Frere (Wm. Hosmer, collector).

The ranges of *Sphenophryne fryi* and *S. robusta* approach closely north of Tinaroo Lake, about 20 km northeast of Atherton, and evidently overlap slightly. We investigated this area on the evenings of February 1 and 2, 1981, and tape recorded and collected both species, though not in precise sympatry. Verified records for *fryi* (frogs heard or tape recorded) are at 4.5 km E, 2 km N Tinaroo Dam (680 m) and at 6.5 km E, 4 km

N Tinaroo Dam (720 m). The latter record is on Forest Road B, which leaves the road bordering Tinaroo Lake and winds 8.7 km north to the ridge that includes Mt. Haig and Mt. Edith. Along this road we heard *S. robusta* at three places at elevations of 800, 880, and 1080 m. The first of these localities is only 1.5 km from the closest spot for *fryi* verified by call. *Sphenophryne pluvialis* occurs here together with both species.

Although positive identification of these species is possible only for calling males, the value of the IN/SV ratio permits tentative assignment of many specimens (see foregoing section on comparisons). Seven specimens (AM R87889–87891, R87896–87898, R87926) collected along the north and east sides of Tinaroo Lake and three from Lake Barrine (AM R29512, R29513, R73668) have ratios characteristic of *fryi* and rarely if ever attained by *robusta*. In contrast to these apparent *fryi*, a sample of six specimens from 5.1 km up Forest Road B, elevation about 880 m, evidently contains both species. Two specimens (AM R87892, R87893) are too small to classify, but three have IN/SV ratios typical of *robusta* (AM R87894, R87895, R87927) and one of *fryi* (AM R87928). The range of IN/SV ratios in these adult speci-

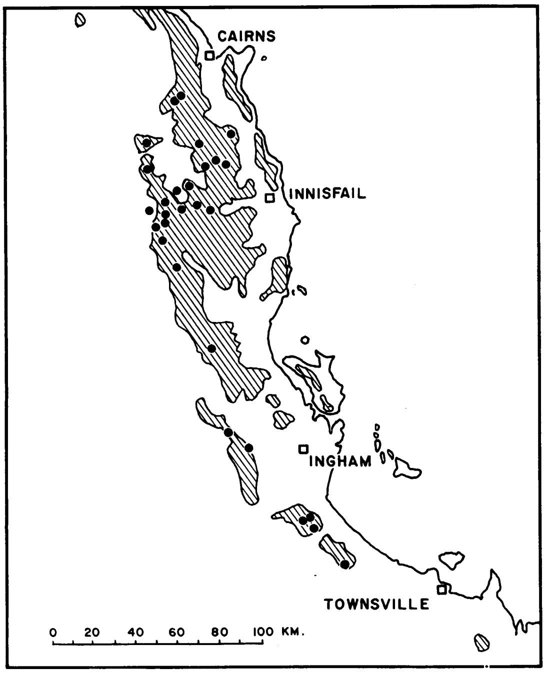

FIG. 21. Distribution of *Sphenophryne robusta*. Shading delimits major areas of rainforest. See figure 12 for complementary distribution of *S. fryi*.

TABLE 8

Call Statistics for *Sphenophryne robusta*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Notes per Call Mean (Range)	Note Couplets per sec Mean (Range)	Frequency, Hz[a]	Number of Calls
AMNH 111468[b]	228	19.6	18.4	3.26 (2.18–3.98)	11.4 (8–14)	1.53 (1.4–1.7)	3200–3100	7
No spec.[c]	202	—	20.0	2.57 (2.12–3.38)	11.0 (9–12)	1.95 (1.6–2.2)	3200–3100	10
WH 1170[d]	241	—	20.0	3.93 (3.74–4.41)	12.4 (12–14)	1.40 (1.4)	3000–2900	5
AMNH 111469[e]	228	25.7	20.2	2.79 (1.03–4.20)	12.8 (6–18)	2.13 (2.0–2.4)	2650–2650	5
AMNH 111470[e]	228	23.6	20.6	3.81 (1.73–4.82)	14.4 (8–18)	1.73 (1.5–1.9)	3000–2750	5
No spec.[f]	239	—	21.8	3.23 (1.84–4.20)	12.0 (8–14)	1.71 (1.6–1.8)	2700–2600	3
No spec.[g]	229	—	22.3	3.01 (2.75–3.44)	14.7 (14–16)	2.20 (2.1–2.3)	2750–2600	3
No spec.[g]	230	—	22.3	2.82 (1.92–3.80)	11.3 (8–14)	1.90 (1.7–2.1)	2900–2750	3
AMNH 111471[h]	228	19.7	22.4	4.18 (3.90–4.29)	19.5 (18–20)	2.17 (2.1–2.2)	3300–3100	4
No spec.[i]	239	—	—	2.67 (2.41–2.91)	11.0 (10–12)	1.80 (1.6–1.9)	3050–3000	4
No spec.[c]	248	—	—	2.53 (2.52–2.54)	10.0 (10)	1.69 (1.69)	2700–2500	3

[a] Midpoint frequencies of first and second notes of each couplet.

[b] Paluma.

[c] Mt. Spec.

[d] Lamins Hill.

[e] North side of Majors Mountain.

[f] The Crater National Park.

[g] 5.5 km N, 6 km E Tinaroo Dam.

[h] Millaa Millaa Falls.

[i] Henrietta Creek, Palmerston National Park.

mens, 0.087–0.109, virtually assures that both species are present.

The specimens from Lake Barrine are the southernmost tentatively identified *fryi*, and those from the north side of Tinaroo Lake the southernmost firmly identified ones. Two specimens collected by Keith McDonald on South Bell Peak, Malbon Thompson Range (QNPWS N28741, N28742) are of large size (SV 29 mm) and have moderately low IN/SV ratios, suggesting that *fryi* extends virtually to the coast at this latitude but at a relatively high elevation (860 m).

Locality Records and Specimens Examined: 6.5 km N, 4.5 km E Tinaroo Dam, 880 m (AMNH 111473); Forest Road B, 5.1 km N of road around Tinaroo Lake (AM R87892–87895); Mt. Haig, 14 km N Tinaroo Dam (AMNH 111518); Mt. Edith, 3 km N Tinaroo Dam (AMNH 111519–111521); 11 km W Atherton, 1200 m (LACM 58020); Baldy Mountain Road, SW of Atherton (QM J39151, J39154, J39156, J39157, J39159); Carrington (MCZ 17806); Mt. Bellenden Ker, Centre Peak, 1520 m (AMNH 111401); Mt. Bellenden Ker [east side], Cable Tower no. 3 (QM J37635, J37636); Bellenden Ker Range (MCZ 18501, 18504); 5 km N Hypippami Crater [The Crater National Park] (AM R61434); 8 km W The Crater National Park (WH 1245, 1247–1249); The Crater National Park (AM R61427–61433; FMNH 97824; QNPWS A808); 2 km E The Crater (QM J32074); Lamins Hill, 800 m, 2.5 km SSW Butchers Creek Township (AMNH 111476–111478; WH 1119–1124, 1168, 1169, 1643, 1644, 2356–2359, 2361, 2362, 2365, 2367–2373, 2375); Boonjee, 790 m (QM J30979, J30980, J30994–31003; QNPWS N28118–28126); near junction of Russell River and Kiandra Creek (QM J32151); Russell River (AM R5295 [holotype], R5296 [paratype], R30827–30832 [paratypes, formerly Macleay Museum R53]); Mt. Bartle Frere, 1280 m (AMNH 67403); Mt. Bartle Frere, west face, 1000–1400 m (QM J39148, J39149); Bobbin Bobbin Falls, west side of Mt. Bartle Frere, 640 m (AMNH 111472); Palmerston Highway near Millaa Millaa (QM J32111); Millaa Millaa (AM R71671; FMNH 97826–97828; MCZ 18378, 18379); Millaa Millaa Falls, 780 m (AM R87914–87916; AMNH 111471; WH 1348, 1349); 2.5 km NW Palmerston Highway on Theresa Creek Road (AM R87909–87913); Zillie Falls, 16 km E Millaa Millaa (AMNH 111516, 111517); Elinjah Creek near Millaa Millaa (FMNH 97829–97831); 3 km N Ravenshoe (WH 1653); Mt. Fisher, 1220 m (QM J31241–31251; QNPWS N28183–28185); Sluice Creek Road, Mt. Fisher (WH 1548, 1549, 2023); 1.8 km N Sluice Creek Road (AMNH 111474; WH 1565, 1567, 1568, 1570; Malanda-Atherton Road, ca. 30 km S Malanda (QM J32110, J32116); Massey Creek, Palmerston Highway (AM R87860, R87906–87908); Maalan State Forest (QM J31138–31144, J31164, J31165, J31167); Miyee Creek, 620 m, Palmerston National Park (AM R61143–61146; WH 1714–1717); Palmerston Highway ca. 30 km W Innisfail (QM J32152); Palmerston Highway 25 km E Millaa Millaa (QM J25578–25580); Palmerston Highway near Henrietta Falls (QM J32071); Henrietta Creek, Palmerston National Park, 360 m (AMNH 111475, 111512–111515; QNPWS N14245, N14246; WH 1774, 1775); Tschupalla Falls, Palmerston National Park (AMNH 111511); Vine Creek, 4 km W, 8 km S Ravenshoe (MCZ 18380–18382; WH 1395, 1458–1461, 2411, 2412, 2425, 2426); Charmillin Creek at Tully Falls Road, 900 m (AM R87901–87905, R94435–94443; QM J34433–34451); north side of Majors Mountain, 950 m, 4.5 km E, 3 km S Ravenshoe (AMNH 111469, 111470; QM J31062–31064, J31091–31100, J31107–31110, J31116–31120, J31131; QNPWS N28134–28136, N28152–28157, N28163–28165, N28174–28177); Tully Falls Road, 20.5 km S Kennedy Highway at Ravenshoe (AM R87900); Tully Falls Road, 21.1 km S Kennedy Highway at Ravenshoe (AM R87889); Tully Falls Road (AM R87858, R87859); Koombaloomba Creek, 12 km E, 27 km S Ravenshoe (AMNH 65429–65436); Smoko Creek at Kirrima State Forest Road, 22 km W, 2 km N Kennedy (AM R87884–87888; UMMZ 132721 [5 specimens]); Ingham-Wallaman Falls Road ca. 32 km WNW Ingham (DU 9995, 9996); Mt. Spec, 890 m (UMMZ 132718 [7 specimens], 132722, 132723; DU 9969, 9983, 10000–10003); Shay's Clearing, 5 km N Lake Paluma (DU 10004); 2 km SE Paluma Dam (AM R87881); Birthday Falls, 5.5 km W, 3.5 km N Paluma (UMMZ 132719, 132720); 4 km SE Paluma Dam (AM R87882, R87883); Cloudy Creek, vic. Paluma (UMMZ 132724, 132725); Paluma, 900 m (AMNH 111468; QM J32086; QNPWS N14231–14234; DU 9968); 3 km E, 8 km S Mt. Halifax, Paluma Range (K. McDonald, *in litt.*); 1 km E, 11 km S Mt. Halifax, Paluma Range (K. McDonald, *in litt.*).

GENUS *COPHIXALUS* BOETTGER

DIAGNOSIS: Genyophrynine microhylid frogs (*sensu* Zweifel, 1971, for Sphenophryninae) lacking procoracoids and clavicles, with a normal (not narrow and elongate) snout region, alary process of premaxilla typically slender and not merging insensibly into the body of the bone, and lacking a hypertrophied serous gland on the snout.

Sphenophryne, the only other Australian genus of microhylids, is readily distinguished from *Cophixalus* by its possession of clavicles and procoracoids (see preceding section on identification). Two genyophrynine genera besides *Cophixalus* also lack these structures: *Copiula* and *Choerophryne.* These last two genera had been synonymized in *Cophixalus* by Parker (1934) but were revived by Menzies and Tyler (1977). *Choerophryne rostellifer* (Wandolleck), the only member of its genus, is a most peculiar looking tiny frog with a narrow, elongate snout (and appropriate modifications of the underlying skeleton) and extensive sacrococcygeal fusion. Menzies and Tyler also listed as differences from *Cophixalus* the presence of a tiny sesamoid bone at the tibiotarsal articulation and larger toe discs than finger discs. I have not found a sesamoid bone in Australian *Cophixalus* but have not surveyed extralimital species. The digital disc character is invalid; several species of *Cophixalus* (mostly described herein) have toe discs smaller than those on the fingers.

Menzies and Tyler (1977, p. 434) gave the following "major features distinguishing *Copiula* from *Cophixalus*": (1) The alary process of the premaxilla is slender in *Cophixalus,* arising abruptly from the dorsal surface of the bone, but in *Copiula* it is much broader and dilated at the base, merging insensibly with the body of the bone; (2) *Copiula* possesses and *Cophixalus* lacks a hypertrophied serous dermal gland distinguished externally by a translucent white, and sometimes uptilted, tip to the snout; (3) digital discs of *Copiula* are small and those on the toes are larger than those on the fingers, compared to customarily large ones in *Cophixalus,* with finger discs invariably broader.

The three species of *Copiula* are morphologically almost indistinguishable (one is larger than the others, and calls differ) but look rather different from *Cophixalus.* There is, however, a paucity of objective characters to support the generic distinction. The difference in shape of the premaxillary bone is at least partly bridged in *Cophixalus* (see Osteology), and the character involving the relative widths of digital discs does not hold up (see foregoing comment on *Choerophryne*). The rostal gland is not found in any *Cophixalus* that I know of, though *Sphenophryne* has something at least superficially similar. One possibly useful character is the shape of the prevomer. In *Copiula* the anterior arm is slender, not expanded as it is in *Cophixalus* (Menzies and Tyler, 1977, fig. 1; Zweifel and Allison, 1982, fig. 3).

COMMENT: Menzies, Tyler, and Zweifel (1980) showed that the type species of the genus *Cophixalus* is congeneric with species referred to *Oreophryne.* Strict application of the rules of nomenclature would lead to extensive and potentially very confusing rearrangements of taxonomy on both generic and specific levels. As a result of an appeal to the International Commission on Zoological Nomenclature, these generic names were placed on the Official List of Generic Names in Zoology (Melville, 1984), thereby maintaining accustomed usage.

Cophixalus bombiens, new species
Figure 22

HOLOTYPE: QM J42060 (formerly AMNH 111432, Field No. RZ 11479), collected on January 21, 1981, by R. Zweifel and K. McDonald on the southern side of Mt. Windsor Tableland, elevation about 900 m, approximately 40 km west-northwest of Mossman, Queensland.[3]

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[3] Owing to the lack of an up-to-date map, the exact type locality cannot be stated more precisely. The site is by a forestry camp located 41 km along a road that intersects the Cooktown Road 15 km west of Mt. Carbine, probably the same road beside which the Australian Museum paratypes were taken.

TABLE 9
Body Proportions in Fourteen Samples of the Genus *Cophixalus*

Sample	TL/SV Mean ± σ_m	TL/SV Range	TL/SV n	HW/SV Mean ± σ_m	HW/SV Range	HW/SV n
C. bombiens	0.451 ± 0.003	(0.40–0.48)	36	0.364 ± 0.002	(0.34–0.39)	36
C. concinnus[a]	0.399 ± 0.003	(0.37–0.44)	30	0.391 ± 0.003	(0.35–0.44)	30
C. crepitans	0.499 ± 0.004	(0.47–0.54)	18	0.365 ± 0.005	(0.33–0.40)	14
C. exiguus	0.445 ± 0.004	(0.40–0.49)	30	0.394 ± 0.004	(0.36–0.46)	30
C. hosmeri	0.398 ± 0.004	(0.34–0.45)	39	0.393 ± 0.003	(0.36–0.44)	39
C. infacetus[b]	0.481 ± 0.006	(0.44–0.55)	22	0.380 ± 0.005	(0.33–0.42)	22
C. infacetus[c]	0.451 ± 0.003	(0.43–0.46)	6	0.405 ± 0.006	(0.39–0.42)	6
C. mcdonaldi	0.411 ± 0.004	(0.37–0.44)	23	0.401 ± 0.005	(0.36–0.45)	23
C. neglectus[d]	0.356 ± 0.004	(0.32–0.40)	26	0.385 ± 0.004	(0.35–0.43)	26
C. neglectus[e]	0.377 ± 0.006	(0.31–0.42)	18	0.400 ± 0.004	(0.36–0.43)	17
C. ornatus[f]	0.418 ± 0.004	(0.37–0.47)	30	0.365 ± 0.004	(0.32–0.41)	30
C. ornatus[g]	0.457 ± 0.003	(0.41–0.48)	28	0.376 ± 0.002	(0.35–0.41)	28
C. peninsularis	0.41 —	(0.40–0.42)	2	0.39 —	(0.38–0.40)	2
C. saxatilis	0.480 ± 0.007	(0.44–0.50)	12	0.384 ± 0.005	(0.36–0.42)	15

[a] Combined sample, Thornton Peak and Mt. Lewis.
[b] Palmerston Park and vicinity.
[c] Crystal Cascades, Cairns.
[d] Mt. Bellenden Ker.
[e] Mt. Bartle Frere.
[f] Upland sample.
[g] Lowland sample.

Paratypes: AMNH 111431, 111433–111440, QM J42063, same data as holotype; AM R62557–62599, R62626–62628, collected by A. Greer, H. Cogger, P. Webber, and E. Cameron on July 13–14, 1977, on the southwest side of Mt. Windsor Tableland along a forest road 31.5 to 34 km northeast of the Cooktown Road.

Etymology: The name *bombiens,* Latin for "buzzing," is descriptive of the male frog's call.

Diagnosis: The features that in combina-

TABLE 10
Body Proportions in Fourteen Samples of the Genus *Cophixalus*

Sample	EYE/SV Mean ± σ_m	EYE/SV Range	EYE/SV n	EN/IN Mean ± σ_m	EN/IN Range	EN/IN n
C. bombiens	0.128 ± 0.001	(0.109–0.139)	36	0.747 ± 0.006	(0.69–0.83)	36
C. concinnus[a]	0.127 ± 0.001	(0.109–0.146)	30	0.851 ± 0.010	(0.76–1.00)	30
C. crepitans	0.144 ± 0.001	(0.134–0.155)	17	0.724 ± 0.009	(0.65–0.78)	16
C. exiguus	0.135 ± 0.001	(0.125–0.152)	30	0.838 ± 0.011	(0.72–0.94)	30
C. hosmeri	0.132 ± 0.001	(0.118–0.145)	39	0.764 ± 0.007	(0.70–0.85)	39
C. infacetus[b]	0.129 ± 0.002	(0.113–0.140)	22	0.800 ± 0.011	(0.72–0.93)	21
C. infacetus[c]	0.120 ± 0.001	(0.117–0.123)	6	0.798 ± 0.012	(0.75–0.84)	6
C. mcdonaldi	0.120 ± 0.001	(0.108–0.130)	23	0.824 ± 0.010	(0.73–0.95)	23
C. neglectus[d]	0.116 ± 0.001	(0.103–0.132)	27	0.729 ± 0.010	(0.65–0.88)	27
C. neglectus[e]	0.117 ± 0.002	(0.096–0.129)	17	0.715 ± 0.009	(0.66–0.77)	18
C. ornatus[f]	0.120 ± 0.001	(0.100–0.125)	30	0.918 ± 0.006	(0.86–0.98)	30
C. ornatus[g]	0.125 ± 0.001	(0.114–0.139)	28	0.886 ± 0.011	(0.70–1.00)	28
C. peninsularis	0.138 —	(0.138–0.139)	2	0.67 —	(0.67)	2
C. saxatilis	0.123 ± 0.002	(0.113–0.136)	15	0.902 ± 0.015	(0.81–1.00)	15

[a] Combined sample, Thornton Peak and Mt. Lewis.
[b] Palmerston Park and vicinity.
[c] Crystal Cascades, Cairns.
[d] Mt. Bellenden Ker.
[e] Mt. Bartle Frere.
[f] Upland sample.
[g] Lowland sample.

TABLE 9
Continued

HAND/SV			FOOT/SV		
Mean ± σ_m	**Range**	**n**	**Mean ± σ_m**	**Range**	**n**
0.212 ± 0.002	(0.19–0.23)	36	0.428 ± 0.003	(0.39–0.46)	36
0.225 ± 0.002	(0.21–0.25)	30	0.405 ± 0.003	(0.37–0.46)	30
0.216 ± 0.002	(0.20–0.23)	17	0.456 ± 0.004	(0.43–0.48)	18
0.220 ± 0.002	(0.19–0.24)	26	0.437 ± 0.004	(0.40–0.50)	26
0.211 ± 0.002	(0.18–0.23)	39	0.397 ± 0.004	(0.34–0.44)	39
0.220 ± 0.002	(0.20–0.25)	22	0.444 ± 0.006	(0.40–0.49)	21
0.207 ± 0.004	(0.19–0.22)	6	0.424 ± 0.006	(0.41–0.45)	6
0.225 ± 0.002	(0.20–0.25)	23	0.421 ± 0.004	(0.38–0.46)	23
0.213 ± 0.002	(0.19–0.24)	26	0.377 ± 0.004	(0.34–0.42)	25
0.235 ± 0.005	(0.19–0.27)	16	0.416 ± 0.009	(0.35–0.46)	16
0.263 ± 0.002	(0.23–0.29)	28	0.415 ± 0.003	(0.39–0.46)	28
0.252 ± 0.002	(0.23–0.27)	28	0.413 ± 0.003	(0.38–0.45)	28
0.195 —	(0.19–0.20)	2	0.38 —	(0.36–0.40)	2
0.255 ± 0.003	(0.24–0.27)	11	0.432 ± 0.005	(0.40–0.46)	11

tion distinguish *Cophixalus bombiens* are its small size (males to 14 mm SV, females to 17 mm), short first finger lacking a disc, moderately long legs, and low average EN/IN ratio. The call is a brief buzz. Comparison is needed only with species of similar size, three of which have quite different calls (the call of *exiguus* is unknown).

Cophixalus exiguus has the first finger longer than in *bombiens* and it bears a distinct though small disc (fig. 6A); the EN/IN ratio is usually less than 0.79 in *bombiens* and 0.79

TABLE 10
Continued

EN/SV			IN/SV		
Mean ± σ_m	**Range**	**n**	**Mean ± σ_m**	**Range**	**n**
0.076 ± 0.001	(0.070–0.085)	36	0.101 ± 0.001	(0.084–0.115)	36
0.076 ± 0.001	(0.068–0.083)	30	0.090 ± 0.001	(0.073–0.106)	30
0.079 ± 0.001	(0.072–0.085)	15	0.109 ± 0.001	(0.103–0.122)	16
0.077 ± 0.001	(0.067–0.087)	30	0.093 ± 0.001	(0.084–0.099)	30
0.073 ± 0.001	(0.064–0.088)	39	0.096 ± 0.001	(0.085–0.111)	39
0.083 ± 0.001	(0.074–0.092)	22	0.104 ± 0.001	(0.092–0.112)	21
0.081 ± 0.001	(0.078–0.083)	6	0.101 ± 0.002	(0.096–0.111)	6
0.077 ± 0.001	(0.070–0.083)	23	0.094 ± 0.001	(0.080–0.103)	23
0.065 ± 0.001	(0.060–0.074)	27	0.090 ± 0.001	(0.079–0.099)	27
0.068 ± 0.001	(0.058–0.077)	17	0.097 ± 0.002	(0.086–0.107)	17
0.080 ± 0.001	(0.072–0.090)	30	0.087 ± 0.001	(0.078–0.098)	30
0.082 ± 0.001	(0.068–0.088)	28	0.092 ± 0.001	(0.084–0.102)	28
0.067 —	(0.066–0.069)	2	0.101 —	(0.099–0.104)	2
0.084 ± 0.002	(0.073–0.096)	15	0.094 ± 0.001	(0.088–0.100)	15

FIG. 22. *Cophixalus bombiens,* QM J42060 (holotype), Mt. Windsor Tableland; adult male, SV 13.3 mm.

or greater in *exiguus*. A criterion of TL/SV greater than 0.42 in *bombiens* and less than 0.43 in *hosmeri* will allocate more than 80 percent of specimens correctly. *Cophixalus infacetus* has larger finger and toe discs than *bombiens* (fig. 6D). *Cophixalus crepitans* has an extremely short first finger compared to *bombiens* (fig. 6F) and longer legs: TL/SV 0.48 or greater for *crepitans* and 0.47 or less for *bombiens* will correctly allocate about 85 percent of the specimens.

DESCRIPTION OF HOLOTYPE: Adult male (calling when captured) with the following measurements and proportions: SV 13.3, TL 6.0, HW 4.8, EYE 1.8, EN 1.0, IN 1.35, disc of third finger 0.55 (penultimate phalange 0.4), disc of fourth toe 0.65 (0.45), HAND 2.9, FOOT 5.8; TL/SV 0.451, HW/SV 0.361, EYE/SV 0.135, EN/SV 0.075, IN/SV 0.101, EN/IN 0.741, third finger disc/SV 0.041, fourth toe disc/SV 0.049, HAND/SV 0.218, FOOT/SV 0.444.

Snout bluntly rounded, almost truncate viewed from above, vertical but rounded in profile; canthus rostralis rounded, loreal region flat, nearly vertical, nostrils lateral, much closer to tip of snout than to eye, internarial distance greater than eye-naris distance. Eyes moderately large, corneal outline prominent in ventral view, eye approximately equal to snout length. Tympanum small, obscure. Relative lengths of fingers, 3>4>2>1, first much less than one-half length of second; grooved terminal discs on second to fourth fingers weakly developed, scarcely broader than penultimate phalanges, smaller than toe discs; first finger bluntly rounded terminally, without a disc; subarticular elevations scarcely evident, no distinct metacarpal elevations. Toes unwebbed, relative lengths 4>3>5>2>1, first less than one-half length of second; all toes with grooved, expanded terminal discs, that on first toe least broadened; subarticular elevations scarcely evident, no distinct metatarsal tubercles. Skin smooth dorsally and ventrally except for faintly indicated W-shaped scapular fold, but slight pustulosity evident in life (fig. 22).

In preservative the dorsum is brown, the side of the head mottled and somewhat darker than the back but without a distinct mask effect. An indistinct darker mark passes from the posterior corner of the eye, curving down behind the tympanum. The lateral body surface is spotted with brown on a ground color lighter than that of the dorsum, and the darker brown is more concentrated along a dorsolateral line that curves downward toward the inguinal region. The hind limbs show dark and light spots on a brown background, the groin and anterior surfaces of the thighs are mottled, and there is a dark brown seat patch with its triangular apex above the vent. The chin and chest are brown broken by irregular lighter marks. The abdomen is paler, with brown markings on a light background. The undersurfaces of the hind legs are mottled with brown and light tan.

VARIATION IN THE TYPE SERIES: Averages and ranges of selected proportions are in tables 9–11. Females mature between 13 and 14 mm SV and attain at least 17.2 mm. Among 14 specimens sexed by dissection, two measuring 13.3 and 13.5 mm appear to be immature, whereas one at 13.6 mm is adult, as are all larger individuals. The 17.2 mm female is the largest among 40 specimens measured. Males are adult at least as small as 11.9 mm SV (calling individual) and reach 14.9 mm (sample of seven sexed).

The sample (and known range) is restricted to one small area, so nothing can be determined of geographic variation. With respect to growth trends, *Cophixalus bombiens* resembles many other Australian *Cophixalus* in that the size of most body parts relative to body length does not keep pace with growth

TABLE 11
Digital Disc Proportions in Fourteen Samples of the Genus *Cophixalus*

	Third Finger Disc/SV			Fourth Toe Disc/SV		
Sample	Mean ± σ_m	Range	n	Mean ± σ_m	Range	n
C. bombiens	0.034 ± 0.001	(0.028–0.041)	36	0.045 ± 0.001	(0.039–0.055)	36
C. concinnus[a]	0.040 ± 0.001	(0.032–0.053)	30	0.041 ± 0.001	(0.034–0.049)	30
C. crepitans	0.042 ± 0.001	(0.036–0.049)	15	0.045 ± 0.001	(0.032–0.052)	17
C. exiguus	0.034 ± 0.001	(0.023–0.045)	30	0.043 ± 0.001	(0.037–0.053)	30
C. hosmeri	0.036 ± 0.001	(0.031–0.042)	39	0.042 ± 0.001	(0.035–0.050)	38
C. infacetus[b]	0.044 ± 0.001	(0.034–0.052)	20	0.050 ± 0.001	(0.038–0.059)	20
C. infacetus[c]	0.043 ± 0.001	(0.040–0.046)	6	0.051 ± 0.002	(0.048–0.059)	6
C. mcdonaldi	0.038 ± 0.001	(0.034–0.044)	23	0.040 ± 0.001	(0.034–0.044)	23
C. neglectus[d]	0.036 ± 0.001	(0.032–0.041)	26	0.041 ± 0.001	(0.036–0.046)	26
C. neglectus[e]	0.038 ± 0.001	(0.028–0.042)	16	0.042 ± 0.001	(0.032–0.048)	16
C. ornatus[f]	0.059 ± 0.001	(0.050–0.077)	30	0.044 ± 0.001	(0.038–0.052)	30
C. ornatus[g]	0.052 ± 0.001	(0.045–0.063)	28	0.044 ± 0.001	(0.039–0.052)	27
C. peninsularis	0.045 —	(0.044–0.046)	2	0.045 —	(0.044–0.046)	2
C. saxatilis	0.060 ± 0.001	(0.050–0.067)	15	0.043 ± 0.002	(0.030–0.050)	14

[a] Combined sample, Thornton Peak and Mt. Lewis.
[b] Palmerston Park and vicinity.
[c] Crystal Cascades, Cairns.
[d] Mt. Bellenden Ker.
[e] Mt. Bartle Frere.
[f] Upland sample.
[g] Lowland sample.

in body length: TL, HW, EYE, EN, IN, HAND, and FOOT all have coefficients well under unity (tables 9–11). Disc widths are an exception, but the finger discs of *bombiens* are among the smallest seen in Australian *Cophixalus*. The ratio EN/IN, useful in some diagnostic species comparisons, remains virtually constant with growth as the two component measurements have similar coefficients.

Preserved specimens resemble the holotype, though many tend to be more gray than brown, and the facial pattern more often shows a concentration of dark pigment beneath the eye rather than a diffuse mask effect. A faint lumbar ocellus may be present, and occasional individuals have a light middorsal band with a diffuse dark border, presumably an instance of polymorphism. In life the dorsum of two specimens was reddish brown with the dark markings nearly black and the undersides gray with light flecks. A specimen with a middorsal light band had the band and the upper part of the iris light bronze.

COMPARISONS WITH OTHER SPECIES

Cophixalus bombiens is known to be sympatric with no other *Cophixalus* and coexists with only one other microhylid, *Sphenophryne fryi*. Should *bombiens* be found outside of its known range, confusion with the geographically closest species would be likely. *Cophixalus exiguus* should be distinguishable on the basis of its long first finger and EN/IN ratio, as given in the diagnosis, and it also has a broader head on the average. In the absence of information on the calls, it could be more difficult to separate *bombiens* and *hosmeri*, especially if geographic variation rendered the distinction in leg length (see Diagnosis) ineffective. The head averages narrower in *bombiens*, but there is much overlap in ranges of variation.

HABITAT AND HABITS

The area from which *Cophixalus bombiens* is known is mapped by Tracey and Webb (1975; see also Tracey, 1982) as simple microphyll vine-fern forest. In the daytime we found frogs under debris on the floor of the forest. Males calling at night were close to ground level concealed on some small elevation. One was in a hollow at the broken end of a fallen branch; others called from the shelter of leaves resting on logs or branches. The Australian Museum paratypes were found under roadside debris beside a small creek in kauri forest in daytime; none called at night (H. Cogger, personal commun.).

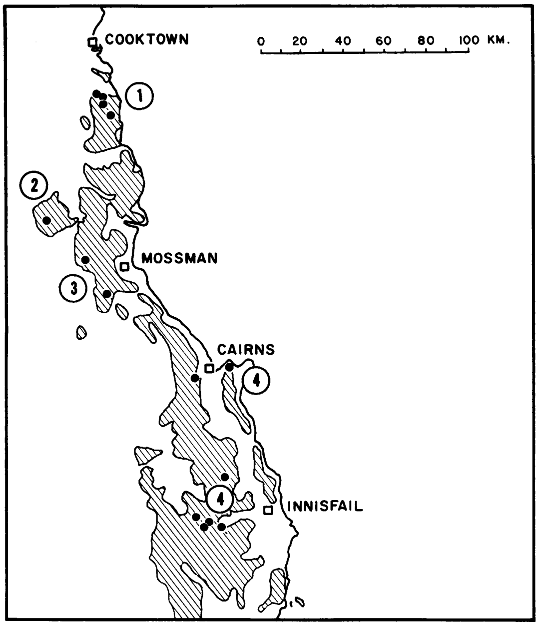

FIG. 23. Distribution of four species of *Cophixalus*. **1,** *C. exiguus*; **2,** *C. bombiens*; **3,** *C. hosmeri*; **4,** *C. infacetus*. Shaded areas indicate rainforest but do not necessarily imply wider distributions than the spots indicate.

CALL

The call is a brief buzz, averaging slightly less than one-half second (table 12, fig. 65A). The average interval between the start of one call and the start of the next in the four frogs recorded was 7.6, 8.7, 10.7, and 7.1 seconds, with a grand range of 4.5–17.1 seconds for 76 intervals tabulated. The mean pulse rate over the whole note ranges from about 150 to 200 pulses per second. The pulse rate at midcall is about double that at the beginning, and the rate drops off toward the end of the note. There is no clear peak of frequency dominance, but a broad area between 4000 and 5500 Hz evidently contains much of the energy.

DISTRIBUTION

Cophixalus bombiens is known only from the Mt. Windsor Tableland, west-northwest of Mossman, Queensland, at an elevation of about 900 m (fig. 23). Specimens examined are listed above under holotype and paratypes.

Cophixalus concinnus Tyler

Figure 24

Sphenophryne polysticta: Loveridge, 1935, p. 57 (some specimens from Mt. Spurgeon).

Cophixalus sp.: Zweifel, 1962, pp. 13–14 (some specimens from Mt. Spurgeon).

Cophixalus concinnus Tyler, 1979b, p. 119 (type locality, "at an elevation of 1,250 m on Thornton Peak [16°12′; 145°20′], Cape York Peninsula, Queensland, Australia"; collected by J. Winter on November 15, 1973).

DIAGNOSIS: *Cophixalus concinnus* is distinguished from other Australian *Cophixalus* by the following combination of characters: size moderate, adult males 15–22 mm SV, adult females 18–23 mm (rarely to 26 mm); digital discs well developed, that on the third finger slightly smaller to slightly larger than that on the fourth toe (both ontogenetic and geographic variation); tip of first finger disclike with terminal groove, but not or little expanded; call a series of 11 or 12 clicks uttered over a period of about 0.8–1.2 seconds.

TABLE 12
Call Statistics for *Cophixalus bombiens*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Pulses per Call Mean (Range)	Pulses per sec Mean (Range)	Frequency, Hz	Number of Calls
AMNH 111431[a]	229	11.9	20.8	0.43 (0.40–0.45)	66.7 (64–72)	154.6 (150–161)	5400	10
QM J42060[a,b]	229	13.3	20.6	0.46 (0.45–0.48)	83.4 (79–88)	179.5 (173–185)	4950	10
AMNH 111433[a]	229	13.9	20.6	0.45 (0.43–0.48)	69.9 (66–73)	152.5 (147–158)	5150	10
QNPWS N28771[a]	239	12.5	20.6	0.43 (0.40–0.46)	88.9 (84–94)	207.2 (198–217)	5300	10

[a] Mt. Windsor Tableland.

[b] Holotype.

Cophixalus mcdonaldi and *C. neglectus*, species similar in size to *C. concinnus*, both differ from *concinnus* in the same ways: they have the first finger relatively short and discless, and the disc of the third finger is usually (*mcdonaldi*) or consistently (*neglectus*) narrower than that of the fourth toe. *Cophixalus saxatilis* is much larger than *concinnus* (minimum size of adult males about 29 mm SV) and has truncate finger disks much larger than those of the toes. See following section on comparisons for distinctions between *concinnus* and the sympatric or nearly sympatric species *exiguus, hosmeri,* and *ornatus.*

DESCRIPTION

MORPHOLOGY: The size range of adult females is approximately 18–26 mm SV. Specimens measuring 18.3 and 19.0 mm appear to be subadult, whereas one of 18.6 mm is gravid, as are others of 19 mm or greater length. The largest individual, the female holotype, is exceptional at 26.3 mm, for none other of more than 50 females measures as much as 24 mm. The largest among 15 males measures 21.8 mm; individuals of 15.0 and 18.5 mm were calling.

Head slightly narrower than body. Snout bluntly rounded in dorsal view, nearly vertical and slightly projecting in profile; canthus rounded, slightly curved, loreal region oblique and almost flat; nostrils much closer to tip of snout than to eye, directed laterally (scarcely visible from above), internarial distance greater than eye-naris distance. Eyes large, visible from directly beneath, protrude beyond margin of jaw; interorbital space broader than upper eyelid. Tympanum small, scarcely visible. Relative lengths of fingers 3>4>2>1, first less than one-half length of second; broadened, terminally grooved discs on second to fourth fingers, tip of first disclike and grooved but not or scarcely expanded; subarticular, inner, and outer metacarpal tubercles low and rounded; no tubercles on palm. Relative lengths of toes 4>3>5>2>1; all toes with expanded, grooved discs, those of third and fourth largest, varying between slightly larger to slightly smaller than largest finger discs; subarticular tubercles low, rounded, and inconspicuous; a low, rounded inner metatarsal tubercle but no outer one; no tubercles on sole. Skin of head, body, and limbs smooth dorsally and ventrally.

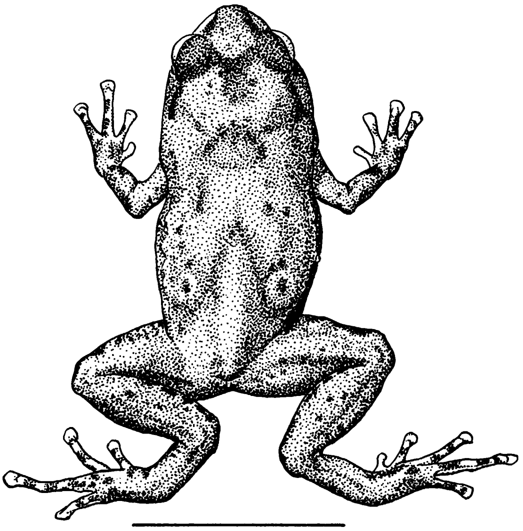

FIG. 24. *Cophixalus concinnus,* AMNH 117290, adult male, Mt. Lewis. Scale line represents 10 mm.

VARIATION IN PROPORTIONS: For average proportions of adults, see tables 9–11. Regression analysis shows that body proportions are variably influenced by growth. Foot length and tibia length are relatively some 5–10 percent shorter compared to body length in large adults than in small subadults. Eye size, narial distances, and hand size also decrease relative to body size but less strikingly so—under 2 percent in most cases. Toe discs tend to maintain their relative size or reduce less than 1 percent, and finger discs increase slightly (see below).

In most proportions samples from the four distribution areas—Mt. Finnigan, Thornton Peak, Mt. Spurgeon, and Mt. Lewis—do not appear to differ from one another. Regression lines for the following measurements are highly similar in slope and placement: TL, HAND, FOOT, EN, IN, and width of fourth toe disc. There is somewhat more variation in maximum size, eye size, and width of finger discs (fig. 57B).

The holotype from Thornton Peak has a snout-vent length of 26.3 mm and one of the paratypes measures 23.4 mm; there are 18 specimens in all from this locality. Among

68 specimens from the other localities there are only 5 greater than 22 mm SV, and the largest at 23.5 mm is notably smaller than the holotype.

Eye size is similar among small individuals of all samples, but the Thornton Peak adults tend to have larger eyes than frogs of comparable size from the other samples. Individual eye size measurements for all specimens greater than 20 mm SV from samples other than Thornton Peak fall below the Thornton Peak regression line, though there is some overlap in ranges.

In none of 53 frogs of all sizes from Mt. Lewis and Mt. Spurgeon is the disc of the third finger wider than that of the fourth toe, though the discs are of equal width in six and nearly so in many others. Among nine specimens from Mt. Finnigan the proportion of frogs with relatively large finger discs is greater: two specimens SV 17.6 and 23.5 mm have finger discs slightly broader; three at 17.6, 18.6, and 21.7 mm have equal disc measurements; whereas one at 22.4 mm and three less than 16 mm have smaller finger discs. The situation is similar among 16 specimens from Thornton Peak: three have the finger discs larger (20.6–26.3 mm SV), two are equal (20.8, 21.8 mm), and 11 have smaller finger discs (13.3–21.6 mm). Two additional specimens (19.2, 20.8 mm) whose toe discs cannot be measured with sufficient accuracy have finger discs of large size, larger than the toe discs of other frogs of similar body size.

The size of the disc on the fourth toe stays the same relative to body size (slope coefficient = 1, Mt. Lewis) or decreases slightly (slope coefficient < 1, Thornton Peak and Mt. Finnigan) with growth, whereas the relative size of the third finger disc increases in all samples. Finger discs average smaller than toe discs in juveniles of all samples, but with differences in relative growth the regression lines for the two cross at about SV 20 mm for the Thornton Peak and Mt. Finnigan samples, whereas for the Mt. Lewis sample they intersect only when extrapolated to about 30.5 mm, a greater size than the species is known to attain. Although measurements of digital discs are subject to spurious variability (because of their small size and because of variation introduced in preservation and storage), I think that the differences seen among these samples do reflect both ontogenetic and geographic variation.

COLOR AND PATTERN: Notes by the collector, J. Winter, provide information on the colors in life of the holotype and five paratypes that I paraphrase and condense here: dorsal surfaces brown, uniform or with yellowish brown to orange markings; chin with brown lattice markings and orange to yellow spots marginally; abdomen white to yellowish green, uniform or with orange spots or brown dendritic marks; groin and anterior surfaces of thighs orange; iris brown to black, sometimes with white or gray speckles in upper half.

The dorsal ground color in preservative is brown with the top and sides of the snout and eyelids often darker brown and a dark postorbital streak passing over the ear. Indistinct darker markings and lumbar ocelli may be visible on the back. Presumably polymorphic variations include a pale vertebral hairline, a broad, pale vertebral stripe diffusely edged in dark brown, or the dorsal area largely dark brown, contrasting with the paler sides and emphasizing the lumbar ocelli. The chin may appear dark with an indistinct median hairline, or may be largely pale with dark pigment concentrated around the margin of the jaw. Probably this is metachrotic variation, because a general stippling of melanophores is visible over the chin in pale individuals. Similarly, the abdomen may be largely pale or may have a considerable encroachment of dark pigment from the lateral and posterior margins. Some specimens have a dark spot on the chest near the base of each forelimb. There is dark pigment on the soles and palms.

COMPARISON WITH OTHER SPECIES

Cophixalus concinnus is sympatric with *C. hosmeri* and *C. ornatus* on Mt. Lewis and Mt. Spurgeon. *Cophixalus concinnus* is a larger frog than *C. hosmeri,* there being no overlap in sizes of adult males or females of the two species. Average TL/SV ratios of adults of the two species are virtually identical, but because of ontogenetic change in tibia length, *concinnus* within the size range of adult *hosmeri* are conspicuously longer legged. Among 12 *concinnus* from Mt. Lewis in the size range 15–17 mm SV, the TL/SV mean is 0.421 ± 0.005 (0.400–0.460), compared to 0.374 ± 0.005 (0.341–0.407). If TL/SV equal to or greater than 0.40 is used as a criterion for identifying *concinnus,* more than 95 percent of the specimens in this sample will be identified correctly. The two species also differ significantly in the EN/IN ratio, which changes much less with growth than does TL/SV. There is more overlap in the ranges of EN/IN, but if the criterion EN/IN equal to or greater than 0.79 is used to identify *concinnus,* 83 percent of the specimens in the mixed sample of 24 will be identified correctly. With sexual maturity as a primary consideration, seconded by the proportions discussed, there should be little difficulty in distinguishing between sympatric adult *hosmeri* and *concinnus.* Differences between the calls of the two species are subtle and need to be better quantified when more recordings become available.

Cophixalus ornatus, the other sympatric *Cophixalus* on Mt. Lewis and Mt. Spurgeon, differs markedly in its short, unpulsed (to the human ear) call, contrasted to the series of clicks uttered by *concinnus.* The most conspicuous morphological difference is the size and shape of the digital discs. In *concinnus* the disc of the third finger is larger than that of the fourth toe only in some of the larger individuals, whereas in *ornatus* only rare individuals, usually of relatively small size, have the finger disc as narrow as that on the toe. Also, the finger discs of *ornatus* tend to be more nearly truncate rather than rounded and are larger than those of *concinnus* of comparable size.

I have no records of sympatry between *Cophixalus exiguus* and *C. concinnus,* though the two occur within less than 7 km of one another—*exiguus* on Mt. Hartley and *concinnus* on Mt. Finlay and Mt. Finnigan. The chief difference between the two is size, with the maximum size of male (SV 15.7 mm) and female (19.1 mm) *exiguus* about equal to the minimum known sizes at maturity for *concinnus* (15 and 18 mm). The two are quite similar in proportions, especially in the size range of small *concinnus* with which *exiguus* might be confused. Average differences that exist in some proportions (e.g., greater TL/SV in *exiguus*) are not great enough to be of much diagnostic use. Unfortunately, the call of *exiguus* has not been recorded.

HABITAT AND HABITS

Meager information available to me shows this to be a scansorial species. Notes by the collector of the type series, J. Winter, mention individuals calling "from hollow branch in shrub thicket 2 m. high . . . from hole in tree trunk 2 m. off ground . . . from vegetation 1 m. off ground." The female holotype was "collected at night in rain forest on palm frond 1 m. off ground," and another male was on a "fallen palm frond over fern mat." A male reported as calling and "found hiding under a leaf" was associated with a call unlike that otherwise attributed to *concinnus* (see section on call).

Localities for *C. concinnus* on Thornton Peak and on Mt. Finnigan are in areas mapped by Tracey and Webb (1975) as simple microphyll vine-fern thicket, and the Mt. Lewis locality is in simple microphyll vine-fern forest. See the section on distribution for comments on elevations of collecting sites.

CALL

I know the call of this species from three recordings made on Mt. Lewis: one with a voucher specimen and air temperature provided by William Hosmer; the other two provided by Glen Ingram but without specimens or temperatures. I do not question the identities of the unvouchered frogs, as Ingram differentiated this species in the field from its smaller but similar sympatric congener, *Cophixalus hosmeri.*

The call (fig. 66B, table 13) is a series of clicks, each call comprised of 11–26 clicks uttered in a space of about 0.6–2.8 seconds. There are frequency peaks at about 2000 and 4400 Hz in one call, whereas in the others only a lower harmonic of 2800 or 3300 Hz is emphasized. The pulse (click) rate is about 8 to 12 per second. One frog initiated ten calls within a period of about 2.5 minutes, the interval from the beginning of one call to

TABLE 13
Call Statistics for *Cophixalus concinnus*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Pulses per Call Mean (Range)	Pulses per sec Mean (Range)	Frequency, Hz	Number of Calls
AMNH 117290[a]	236	18.5	22.0	0.92 (0.83–0.99)	11.6 (11–12)	11.5 (11.1–12.0)	2000, 4000[b]	10
No spec.[a]	248	—	—	2.24 (2.00–2.49)	23.2 (21–26)	10.0 (9.6–10.1)	3300	5
No spec.[a]	248	—	—	2.45 (1.75–2.77)	21.6 (16–24)	8.4 (8.2–8.6)	2800	7

[a] Mt. Lewis.
[b] Two principal peaks.

that of the next ranging from 11.6 to 30.2 seconds (mean 17.09 ± 1.97, N = 9).

The call is closely similar to that of *Cophixalus hosmeri* in most respects. The only trenchant difference appears to be in pulse rate, and here the data are few. The pulse rate of the single *concinnus* at 22° (11.5/sec) is slightly below the rates of two *hosmeri* recorded at 18.8° (12.2/sec) and 19.3° (12.6/sec). Mr. Hosmer recorded what he identified as the call of *hosmeri* within a few minutes of making his recording of *concinnus* (the calling *hosmeri* could not be found), and at the same temperature. This call was given at a pulse rate of 17.7 per second compared to 11.5 per second for *concinnus*. The difference between the pulse rates of the presumptive *hosmeri* at 22° and vouchered *hosmeri* at about 19° is consistent with the expected effect of temperature, so I think it likely that the call of *hosmeri* undocumented by a specimen is correctly attributed.

Dr. J. Winter (field notes) characterized the call of a paratype of *Cophixalus concinnus* as "a short rattle about 2 sec long." The description agrees with the call recorded on Mt. Lewis. A call he attributed to another of the paratypes was verbalized as "a high pitched di-di-da-di (long)." This is unlike any *Cophixalus* call otherwise reported in Australia and requires verification. The specimen was "found hiding under a leaf," so it is possible that the frog captured did not actually produce the call attributed to it.

REMARKS

Dr. P. J. Darlington first collected *Cophixalus concinnus* on Mt. Spurgeon in 1932. Loveridge (1935, pp. 56–57) included Darlington's specimens under the name *Sphenophryne polysticta* along with several other species of *Cophixalus* and *Sphenophryne*. Zweifel (1962, pp. 13–14) examined the Mt. Spurgeon specimens and identified them as *Cophixalus* distinct from *C. ornatus* and *C. neglectus* (the only other Australian species then known) but left them in indeterminate status pending acquisition of more material. It was a decade before additional specimens were taken—first by David Liem on Mt. Lewis in 1972, then by William Hosmer on Mt. Spurgeon and by J. Winter (the type series) on Thornton Peak in 1973. Subsequent activity by Hosmer on Mt. Lewis, by Glen Ingram and C. Corben on Mt. Lewis and Mt. Finnigan, by Winter on Thornton Peak, by Harold Cogger and Allen Greer on Thornton Peak, and by J. Covacevich and K. McDonald on Mt. Finnigan provided the material now available.

In view of the geographic variation in morphology seen among apparently disjunct populations, it may be questioned whether only one species is covered by the name *concinnus* as I apply it. Unfortunately, the voice is known only from recordings from one locality (Mt. Lewis) and from verbal descriptions (Thornton Peak), so this criterion of relationship cannot be applied objectively. I view the morphological similarities as outweighing the differences for taxonomic purposes, but recommend the problem as worthy of more study with special emphasis on obtaining a broad geographic sample of calls.

A specimen (AMNH 111490) that I identify as *C. concinnus* and received from Dr. David Liem is said to have been taken at an elevation of 3000 ft on Mt. Elliot, where Dr. Liem collected a series of *Cophixalus mcdonaldi.* Mt. Elliot is the southernmost point in Australia where microhylid frogs are known to occur and is more than 350 km south of Mt. Lewis, the southernmost verified locality for *concinnus.* The only collection of microhylids other than Liem's made on Mt. Elliot comprised only *Cophixalus mcdonaldi.* In view of the relatively restricted distributions of most other species of Australian *Cophixalus* and the absence of any records for *concinnus* in the area between Mt. Lewis and Mt. Elliot, I think that the data and the specimen may be erroneously associated. There was opportunity for such an error, because Dr. Liem collected *concinnus* on Mt. Lewis only a few days before visiting Mt. Elliot.

DISTRIBUTION

Present records indicate that *Cophixalus concinnus* is distributed at relatively high elevations in rainforest areas from Mt. Finnigan, 40 km south of Cooktown, to Mt. Lewis, 20 km south-southeast of Mossman (fig. 25). Elevations of capture with reasonably precise data range from 975 to 1250 m. Probably the distribution is disjunct, for collections made at lower elevations within the range (e.g., on Thornton Peak, where the species occurs at 1000–1250 m) produced no specimens.

LOCALITY RECORDS AND SPECIMENS EXAMINED: All localities are in Queensland: Mt. Finnigan, 975–1100 m (QM J24810–24812, J25302–25305, J27260, J27261, J27272, J27273, J27290, J27291); Mt. Finlay (QM J27263); Thornton Peak, 1000 m (AM R56592–56596, R57777–57780); Thornton Peak, 1190 m (QNPWS 017 + 1 untagged); Thornton Peak, 1250 m (QM J30743 [holotype], J30744–30746 [paratypes]; SAMA 16375, 16376 [paratypes]); east-west ridge between Thornton Peak and Daintree River (AM R87976). Mt. Spurgeon, 910–1500 m (MCZ 18374, 18375); Mt. Spurgeon, 1060 m (WH 1801, 1802, 1835–1838); Mt. Lewis, 1040–1060 m (AMNH 111386–111389, 111481–111484, 117290; AM R97577, R97578; WH 1389, 1497, 1498, 1633, 1634, 1713, 1864, 2096, 2099, 2101, 2103, 2104, 2106, 2107, 2113, 2118–2120, 2133, 2213, 2277, 2285, 2287, 2290, 2292–2295, 2297, 2302, 2513); Mt. Lewis (QM J29603, J29604, J37284–37286).

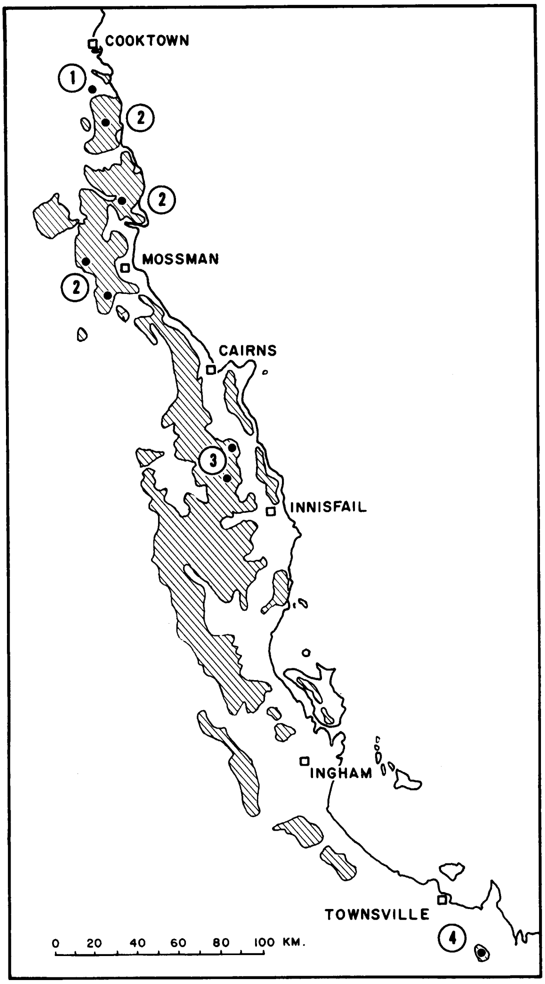

FIG. 25. Distribution of four species of *Cophixalus.* **1,** *C. saxatilis*; **2,** *C. concinnus*; **3,** *C. neglectus*; **4,** *C. mcdonaldi.* Shaded areas are rainforest but do not necessarily imply wider distributions than the spots indicate.

Cophixalus crepitans, new species
Figure 26

HOLOTYPE: QM J28817, collected July 2, 1976, by Paul Filewood at Leo Creek, McIlwraith Range, northeast of Coen, Cape York Peninsula, Queensland.

PARATYPES: QM J41650, J41651, SAMA R23873, collected by J. W. Winter and R. G. Atherton on May 15, 1978 at Rocky Scrub,

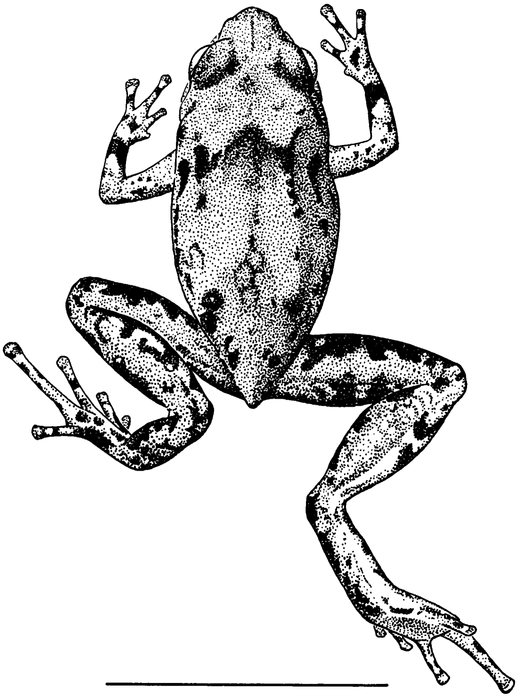

FIG. 26. *Cophixalus crepitans,* QM J28817 (holotype), Leo Creek, McIlwraith Range. Scale line represents 10 mm.

28 km NE Coen (13°44'30", 143°20'30"), 520–540 m; QM J41652, J41653, AMNH 116917, collected by J. W. Winter and R. G. Atherton on May 18, 1978 at Rocky Scrub, 29 km NE Coen (13°44'30", 143°21'30"), 520–540 m; QM J41649, SAMA R23874, same data as QM J41652 except collected on November 16, 1978; QM J41643–41647, AMNH 116918, 116919, SAMA R23875, collected by R. G. Atherton, K. McDonald, P. A. Matthew, and J. W. Winter on March 16, 1979 at Weather Station, 19 km ENE Mt. Croll (13°42'30", 143°18'30"), 380–400 m; QM J41648, collected by Keith McDonald on March 18, 1979, at Leo Creek Road about 1.5 km past Weather Station Creek, Rocky Scrub.

ETYMOLOGY: The Latin adjective *crepitans* means "rattling," and refers to the sound of the frog's call.

DIAGNOSIS: A *Cophixalus* of small size (males to 14 mm SV, single female specimen of the same size) with the following diagnostic combination of characters: hind legs relatively long; EN/IN ratio relatively low; first finger discless and extremely short; call a rattle about 2 seconds long, composed of paired clicks.

Cophixalus hosmeri differs from *C. crepitans* in having much shorter hind legs: maximum TL/SV in *hosmeri,* 0.451; minimum in *crepitans,* 0.466. The relatively long first finger with a small disc distinguishes *C. exiguus* from *crepitans* with its extremely short first finger (fig. 6F). Most specimens can also be differentiated on the basis of the ratios EN/IN (less than 0.79 in *crepitans,* 0.79 or greater in 90% of *exiguus*) and TL/SV (0.47 or greater in *crepitans,* less than that in 80% of *exiguus*). The criterion of TL/SV equal to or greater than 0.48 in *crepitans* and less than that in *bombiens* will correctly allocate 85 percent of specimens examined. *Cophixalus infacetus* differs from *crepitans* in its average higher EN/IN ratio—greater than 0.75 in 80 percent of *infacetus* specimens, less than that in the same percent of *crepitans.*

DESCRIPTION OF HOLOTYPE: Adult female with the following measurements and proportions: SV 14.1, TL 7.35, HW 5.2, EYE 1.95, EN 1.05, IN 1.45, disc of third finger 0.6 (penultimate phalange 0.35), disc of fourth toe 0.7 (0.4), HAND 2.9, FOOT 6.3; TL/SV 0.521, HW/SV 0.369, EYE/SV 0.138, EN/SV 0.074, IN/SV 0.103, EN/IN 0.718, third finger disc/SV 0.042, fourth toe disc/SV 0.050, HAND/SV 0.206, FOOT/SV 0.447.

Head scarcely narrower than body, legs relatively long. Snout blunt in dorsal view, slightly rounded; loreal region flat and nearly vertical, canthus rostralis slightly rounded; nostrils lateral, much nearer tip of snout than eye, internarial distance greater than eye to naris. Eyes large, about equal to snout length, projecting beyond jaw margin viewed from beneath; interorbital space wider than upper eyelid. Tympanum small, scarcely visible. Relative lengths of fingers 3>4>2>1, the first extremely short; second to fourth fingers with enlarged, grooved discs smaller than those on toes, first finger tip bluntly rounded; subarticular and metacarpal elevations scarcely visible. Toes unwebbed, relative lengths 4>3>5>2>1, the first less than one-half the length of the second and without a disc; terminal grooves and discs on all other toes, but disc of fifth toe scarcely enlarged; no distinct

TABLE 14
Call Statistics for *Cophixalus crepitans*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Pulses per Call Mean (Range)[a]	Notes per sec Mean (Range)	Frequency, Hz	Number of Calls
QM J41643[b]	224	12.4	22.6	1.87 (1.82–1.98)	33.0 (32–35)	17.3 (17.2–17.3)	5000	4
No spec.[b]	224	—	22.6	2.37 (2.10–2.53)	41.2 (37–44)	17.1 (16.9–17.3)	4700	4
QM J41648	239	13.1	24.4	1.68 (1.37–1.89)	33.3 (31–37)	19.4 (19.2–19.6)	5100	8

[a] Each note includes two discrete pulses.

[b] Leo Creek Road, McIlwraith Range.

metatarsal or subarticular elevations. A weak postocular fold over upper edge of tympanum, dorsal and ventral skin otherwise smooth.

The dorsal ground color in preservative is gray-brown with darker markings including streaks above and below the tympanum, an incomplete W-shaped mark in the scapular region, and dark spots in the lumbar region that contribute to obscure lumbar ocelli. The lower arm has a dark crossband, and the upper surfaces of the hind legs are light brown with irregular darker brown markings. The anterior and posterior surfaces of the thighs are dark with lighter spots, coarser on the posterior side. The chin and chest have a fairly uniform wash of brown interrupted by small pale spots. The underside of the thigh is similar, the abdomen more mottled than spotted. There is no information on the color in life.

VARIATION IN THE TYPE SERIES: Statistics for selected proportions are in tables 9–11. The only female in the type series is the holotype, SV 14.1 mm. The remaining 17 specimens are all adult males (calling when captured) and range from 11.6 to 14.0 mm SV. The geographic restriction of the sample precludes study of geographic variation.

The range of body size in the type series—11.6 to 14.1 mm—is so small that the calculated coefficients are probably inadequate descriptors of ontogenetic change. This species is notable for having the longest legs relative to body length of any Australian *Cophixalus,* though the difference from *C. infacetus* and *C. saxatilis* may not be significant. Among 15 specimens which are preserved well enough to compare the discs of the fingers and toes, the disc on the fourth toe is larger than that on the third finger in 11, the two are equal in three, and in only one is that of the third finger broader.

There are no notable variations of pigmentation in the type series. Keith McDonald (field notes) recorded that a frog was "burnt orange in color along with the brown markings."

COMPARISONS WITH OTHER SPECIES

Cophixalus crepitans is sympatric with *C. peninsularis*; see the account of that species for comparisons. As for the other four small species, there is little to add to what is presented in the diagnosis. There are average differences between *crepitans* and the other species in some features of morphology (e.g., larger finger discs than in *bombiens, hosmeri,* and *exiguus*), but because of broad overlap in ranges of variation such differences, although they may be statistically significant, are of little or no diagnostic use.

HABITAT AND HABITS

The habitat of *Cophixalus crepitans* in the McIlwraith Range is one of the few areas of rainforest on Cape York Peninsula north of Cooktown. Webb and Tracey, writing in Pedley and Isbell (1971, p. 55), state that the area "supports a variety of vine-forest vegetation associated with differences in aspect, rainfall distribution, and the nature of the soil parent materials." Collectors' field notes document the habit common to other small Australian *Cophixalus* of calling from elevated sites close to the ground: "Calling from between 5 cm. and 45 cm. above ground," and "calling from logs and sticks about 30 cm. off the forest

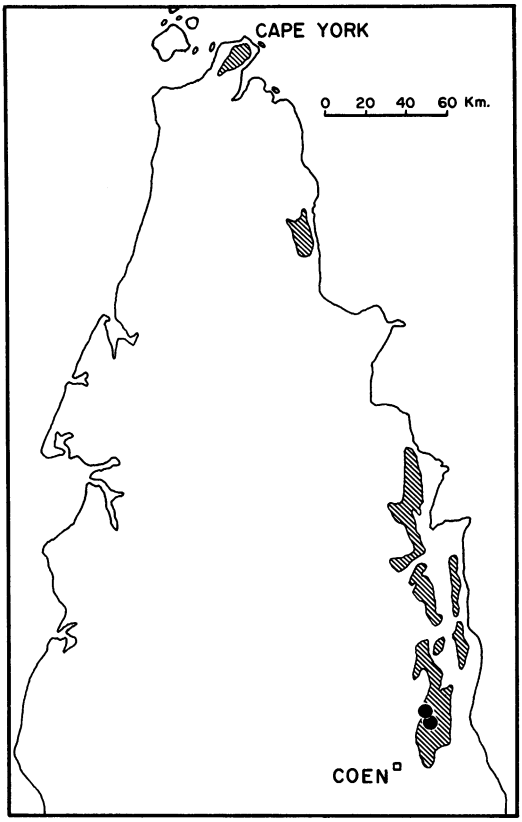

FIG. 27. Locality records for *Cophixalus crepitans* (both spots) and *C. peninsularis* (southern spot only). Shaded areas mark larger patches of rainforest, suggesting other potential sites for *Cophixalus* in northern Cape York Peninsula.

floor." In two instances frogs were calling "on ground."

CALL

The call is a rattling sound, possibly given that characteristic because each of its series of notes includes a pair of clicks (fig. 65C). Calls sampled include from 31 to 44 of these double-pulsed notes and average about 2 seconds in length (table 14). Frequency dominance is in the area of 4700–5100 Hz, but the call is not finely tuned.

REMARKS

Records for *Cophixalus crepitans* are restricted to a small area in the McIlwraith Range. Rainforest presumably indicative of habitat suitable for *Cophixalus* also occurs in the Iron Range area, north of and narrowly disjunct from the McIlwraith tract (Pedley and Isbell, 1971; Hynes and Tracey, 1980). This and other smaller areas of rainforest near Cape York and east of McDonnell should be investigated in the rainy season by someone with a keen ear for and appreciation of tiny, nondescript frogs; see figure 27 and vegetation maps in Kikkawa, Monteith, and Ingram (1981) and Pedley and Isbell (1971, also postscript, p. 71). Two other species of frogs—*Cophixalus peninsularis* (described herein) and *Litoria longirostris* Tyler and Davies (1977) are known only from the same area as *C. crepitans*.

DISTRIBUTION

Cophixalus crepitans is known only from localities in the McIlwraith Range northeast of Coen on the eastern side of the Cape York Peninsula, Queensland (fig. 27). Specimens examined are listed under holotype and paratypes.

Cophixalus exiguus Zweifel and Parker

Figures 28, 29

Cophixalus exiguus Zweifel and Parker, 1969, p. 2 (type locality, "at an elevation of between 1800 and 2000 feet on Mt. Hartley, 23 miles south and 5 miles east of Cooktown, Queensland"; holotype, SAMA R10311, collected by Fred Parker on June 10, 1968).

DIAGNOSIS: *Cophixalus exiguus* differs from its Australian congeners in the combination of small size (males to 15.7 mm SV, females to 19.1 mm), high EN/IN (mean 0.838), long first finger with terminal disc, and moderately long legs (TL/SV mean 0.398). The call is not known.

Among *Cophixalus* of similar size, *C. exiguus* is distinguished as follows: from *bombiens* by the higher EN/IN ratio of *exiguus* (0.79 or greater in most *exiguus* and less than that in most *bombiens*); from *hosmeri* by the greater leg length of *exiguus* (SV 0.43 or greater in 80% of *exiguus,* less than that in *hosmeri*); from *crepitans* by that species' much lower EN/IN ratio (less than 0.79 in all specimens), short and discless first finger, and longer legs (TL/SV 0.47 or greater in *crepitans,* less than that in 80% of *exiguus*);

from *infacetus* by that species' larger finger and toe discs, except that the first finger of *exiguus* is longer with a better developed disc.

DESCRIPTION

MORPHOLOGY: Based on a sample of 19 dissected specimens, adult females range in size from 15.8 to 19.1 mm SV; the last is the largest among 41 specimens measured, males included. Males in a sample of six range from 14.0 to 15.7 mm, but because calling data are absent, the range in adult size cannot be specified.

Head as wide as body or slightly narrower. Snout rounded to almost truncate viewed from above, high and rounded and projecting slightly past lower jaw in profile; canthal region rounded, not well defined; loreal area flat, nearly vertical; nostrils directed laterally, much closer to tip of snout than to eye, internarial distance greater than eye-naris distance. Eyes large, corneal margin visible from beneath, upper lid narrower than interorbital distance. Tympanum small, inconspicuous. Relative lengths of fingers, 3>4>2>1, first well developed, almost one-half length of second, all with grooved discs but disc of first only equal to or scarcely wider than penultimate phalange; inconspicuous, low, rounded subarticular, inner and outer metacarpal tubercles present. Toes unwebbed, relative lengths 4>3>5>2>1, all with enlarged, grooved discs broader than those on the fingers; subarticular tubercles low, rounded, inconspicuous; inner metatarsal tubercle elongate, low, rounded, about one-half length of first toe or a little longer, conspicuous only if it lacks pigment; no outer metacarpal tubercle. Dorsum smooth anteriorly, warty posteriorly and on hind legs in some individuals; weak postorbital fold sometimes present; W-shaped scapular fold more or less developed.

VARIATION IN PROPORTIONS: See tables 9–11 for average proportions of adults. Regression analysis shows marked decreases in tibia length and foot length relative to body length (7.7% and 5.1%, respectively) between juvenile and large adult individuals, whereas hand size decreases much less (1.6%). Other proportions decrease very little (EYE 1.1%, IN 1.1%, EN 0.7%) or scarcely at all (third finger and fourth toe disc widths 0.2%). Because all specimens come from the same general region, nothing can be said of geographic variation.

FIG. 28. *Cophixalus exiguus,* SAMA R10311 (holotype), Mt. Hartley; adult female, SV 18.3 mm.

COLOR AND PATTERN: The dorsal color of preserved specimens is a shade of brown, some individuals having scattered darker spots or paired dark tubercles on the posterior part of the back. The scapular mark may be prolonged posteriorly into dorsolateral streaks, separating the darker middorsal region from the paler sides. One specimen had a light vertebral hairline, and another a pale yellowish middorsal band, obscurely dark edged (fig. 29). The lumbar ocelli are typically faint, but are distinct in a very dark specimen. The upper sides of the hind legs may be virtually unmarked, or may have discrete black spots. The side of the head may be little different from the top, or there may be a dark face-mask effect and a dark supratympanic streak. The pattern of the chin and chest ranges from a pale, even stippling of melanophores to a dark, mottled pattern. The abdomen shows a similar range, but is always lighter than the chin and chest. The anterior and posterior surfaces of the thighs may be

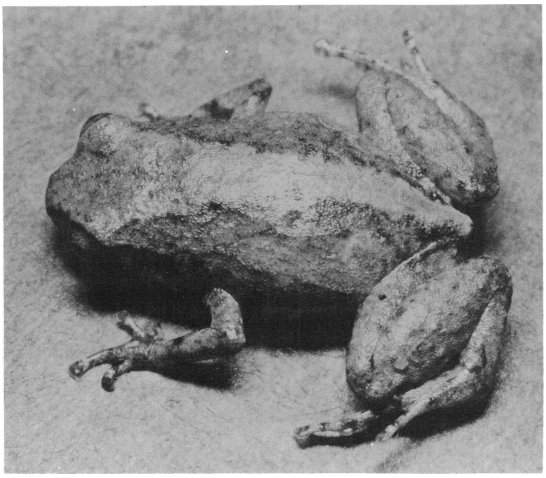

FIG. 29. *Cophixalus exiguus*, MCZ 73290, Mt. Hartley; adult female, SV 17.8 mm. Photograph by Fred Parker.

relatively lightly pigmented or darker and somewhat mottled. The undersides of the hind limbs are spotted to mottled, sometimes heavily.

In life the dorsal ground color is gray-brown with paler areas (e.g., the dorsal band seen in fig. 29) yellow brown. The ventral surfaces are translucent yellowish brown to brown with some opaque white and yellow spots, with concentrations of melanophores mainly under the head and legs. All specimens had a deep red blotch in the groin and in some there were scattered melanophores there. The iris is silvery to pale yellow above and below the horizontal pupil, with a deep red area at both anterior and posterior edges of the eye.

COMPARISON WITH OTHER SPECIES

Cophixalus exiguus is not known to be sympatric with any other species of *Cophixalus*, though it and *C. concinnus* have been taken less than 7 km apart. Except for size there is little to distinguish the two, the call of *exiguus* being unknown (see account of *concinnus*). In view of the considerable difference in size, there being almost no overlap between the smallest adult *concinnus* and the largest *exiguus* of each sex, I do not doubt that they are different species.

In the absence of knowledge of the call, which so readily differentiates the four other similar, small species of *Cophixalus*, the case for specific distinctness of *exiguus* at present must rest on morphology. The differences between *exiguus* and the others, though slight, enable the proper segregation of the great majority of specimens and are of similar kind and magnitude to those that characterize the other species among themselves. The features mentioned in the diagnosis point up the best ways of differentiating *exiguus* from the other similar species, but there are other average differences of less use on the diagnostic level but real nonetheless: *Cophixalus bombiens* has a narrower head, and the first finger is shorter and discless; *C. hosmeri* has a lower EN/IN ratio and a discless first finger; *C. infacetus* has longer legs; *C. crepitans* has larger finger discs. If *C. exiguus* were not considered a species apart, it would be extremely difficult to justify allying it with one of the other clearly distinct forms.

HABITAT AND HABITS

"All specimens were found under logs, stones, and leaf litter in primary rain forest, both near to, and away from, waterways. All were found by day; none was discovered in the open on either wet or dry nights. When uncovered, these small frogs rapidly attempted to escape into leaf litter and under other cover. No call was heard that could be traced to this species" (Zweifel and Parker, 1969, pp. 8–9). Localities for *Cophixalus exiguus* are within areas mapped by Tracey and Webb (1975) as mesophyll vine forest, simple notophyll vine forest, and simple microphyll vine-fern thicket.

REMARKS

Nothing has been added to our knowledge of this species since it first was collected by Fred Parker in 1968. I have seen only one specimen, a topotype, that was not in the type series. Roads made impassible by heavy rains frustrated an attempt by Keith McDonald, William Hosmer, and myself to reach the habitat of *exiguus* in January 1981. Recordings of the call of *exiguus* are greatly needed.

DISTRIBUTION

Cophixalus exiguus has been found only in rainforested uplands between the Annan and Bloomfield rivers, south of Cooktown, Queensland, at elevations between 180 and 610 m (fig. 23).

LOCALITY RECORDS AND SPECIMENS EXAMINED: All localities in Queensland; some specimens that were examined only in the course of the original description are listed: Mungumby Creek, 460 m, 28 km S, 1 km E Cooktown (MCZ 73288 [paratype]); Big Tableland, 610 m, 29 km S, 3 km E Cooktown (SAMA R9832 [paratype]); Home Rule, Slaty Creek, 180 m, 32 km S, 5 km E Cooktown (MCZ 75131 [paratype]); Mt. Hartley, 550–610 m, 36 km S, 9 km E Cooktown (AM R26842–26845; AMNH 81308–81310; MCZ 73278–73287, 73289–73297; NMV D13170–13172; SAMA R9732, R9796 [all the foregoing are paratypes], R10311 [holotype], R10035–10040 [paratypes]); Mt. Hartley (QM J24861).

Cophixalus hosmeri, new species

Figure 30

Sphenophryne polysticta: Loveridge, 1935, p. 57 (part, specimen from Mt. Spurgeon).
Cophixalus sp.: Zweifel, 1962, pp. 13–14 (part, specimen from Mt. Spurgeon).

HOLOTYPE: QM J42058 (formerly QNPWS N14302), collected on February 15, 1977, by Keith McDonald on Mt. Lewis, 6 km west and 9 km north of Mt. Molloy (town), Queensland, elevation 980 m.[4]

PARATYPES: AMNH 111444–111446, same locality as holotype, collected by K. McDonald and R. Zweifel on January 25–26, 1981; QM J37281–37283, same locality as holotype, collected by G. Ingram and C. Corben on January 26, 1980; AMNH 111441–111443, AM R97574–97576, WH 1408, 1537, 1785, 2111, 2112, 2114–2117, 2123, 2127, 2134, 2135, 2138, 2139, 2141, 2214, 2272, 2276, 2278, 2280, 2282, 2284, 2286, 2313–2315, Mt. Lewis, 1060 m, collected by William Hosmer; MCZ 18386, Mt. Spurgeon, 910–1520 m, collected by P. J. Darlington in July 1932; WH 1803, Mt. Spurgeon, collected by W. Hosmer on July 27, 1973; WH 1839, Mt. Spurgeon, 1370 m, collected by W. Hosmer on August 4, 1973.

FIG. 30. *Cophixalus hosmeri,* AMNH 111445, Mt. Lewis; adult male, SV 12.1 mm.

ETYMOLOGY: This species is named for William Hosmer, in recognition of his many contributions to Australian herpetology, which include collecting the majority of the specimens of this species.

DIAGNOSIS: *Cophixalus hosmeri* is a small species (males to 14 mm SV, females to 17 mm), distinguished from others of similar size in its combination of short hind legs, low EN/IN ratio, and short, discless first finger. The call is a series of about 15 clicks uttered over a period of about 1 second.

The most consistent morphological character for distinguishing *C. hosmeri* from its congeners of similar size is its relatively short hind legs. The TL/SV ratios of *hosmeri* (maximum 0.451) and *crepitans* (minimun 0.466) do not overlap at all, and 95 percent of *hosmeri* and *infacetus* will be correctly allocated if specimens with TL/SV less than 0.44 are identified as *hosmeri.* More than 80 percent of *bombiens* and *hosmeri* are separable on the basis of TL/SV greater than 0.42 in *bombiens* and less than 0.43 in *hosmeri. Cophixalus exiguus* differs similarly, with 80 percent of specimens examined having TL/SV 0.43 or greater.

DESCRIPTION OF HOLOTYPE: Adult male (calling when captured) with the following measurements and proportions: SV 13.2, TL 5.7, HW 5.2, EYE 1.85, EN 1.05, IN 1.35, disc of third finger 0.5 (penultimate phalange

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[4] The locality is by a forestry camp 11.7 km along a road that passes west from a junction 3 km north of Julatten on the Mossman to Mt. Molloy Road.

0.3), disc of fourth toe 0.55 (0.3), HAND 2.75, FOOT 5.4; TL/SV 0.432, HW/SV 0.394, EYE/SV 0.140, EN/SV 0.079, IN/SV 0.102, EN/IN 0.778, third finger disc/SV 0.038, fourth toe disc/SV 0.042, HAND/SV 0.208, FOOT/SV 0.409.

Head narrower than body, hind legs relatively short. Snout bluntly rounded, almost truncate viewed from above, vertical and slightly rounded in profile; canthus rostralis rounded, lores flat, nearly vertical; nostrils lateral, much nearer end of snout than eyes, internarial distance greater than eye-naris. Eyes large, same length as snout, corneal outline projecting beyond jaw margin in ventral aspect; interorbital distance greater than width of upper eyelid. Tympanum small, scarcely visible beneath skin. Relative lengths of fingers, 3>4>2>1, first much shorter than second (fig. 6B); second to fourth fingers with grooved, slightly broadened discs smaller than those of toes, first finger tip bluntly rounded with no clear disc or groove; subarticular and metacarpal elevations low, rounded, scarcely visible. Toes unwebbed, relative lengths, 4>3>5>2>1, first less than one-half length of second; toes two to five with grooved, expanded discs, tip of first toe somewhat disclike but not expanded; subarticular and inner metatarsal elevations barely indicated, no outer metatarsal elevation. Skin largely smooth above and beneath but with some slight dorsal pustularity and with a trace of a scapular fold.

In preservative the dorsum is brown with indistinct darker markings, the most evident being a dark inverted "V" in the scapular region and a dark postorbital streak. The eyelids are darker than the top of the snout or postorbital dorsum, and a narrow band of dark pigment crosses the interorbital space. The upper surfaces of the hind limbs bear a few small dark spots. The chin is dark brown with light speckles, the chest slightly darker but abruptly different from the almost unpigmented abdomen. A dark streak on the anterior side of the thigh from groin to knee abuts the unpigmented undersurface of the thigh, which in turn contrasts with the brown lower surface of the shank. On the posterior surface of the thighs there is a dark line that passes through the vent. In life the dorsal color was gray-brown, the throat gray with the midchest area darker, the pale areas of the abdomen and thighs dirty yellow, the undersides of the shanks gray, and the upper part of the eye golden (K. McDonald, field notes).

VARIATION IN THE TYPE SERIES: Averages and ranges of selected proportions are presented in tables 9–11. Females mature at about 13–14 mm SV and attain 17.0 mm. The sample of 32 specimens sexed by dissection includes two apparently immature ones at 13.0 and 14.1 mm and four of 13.3 to 13.6 mm that are adult. Four adult males (the three smallest calling when captured) are 12.1–13.8 mm.

The two localities for the species—Mt. Lewis and Mt. Spurgeon—are less than 30 km apart, and there is no indication of difference in morphology between the small sample of three adult females from Mt. Spurgeon and the much larger topotypic series. In all measurements the Mt. Spurgeon specimens fall within the range of variation of the topotypes.

The relative lengths of all standard measurements decrease with increasing snout-vent length—TL, FOOT, EYE, EN, and IN most markedly, HW and HAND less so. Only the widths of finger and toe discs come close to keeping pace with SV growth, and the finger discs of *hosmeri* are among the smallest of Australian *Cophixalus* to begin with. The rates of change in EN and IN are almost identical; therefore the EN/IN ratio remains essentially constant with growth.

In some specimens the tip of the first finger appears more flattened and disclike than in others and there may be a vestige of a terminal groove. However, there is never a clearly defined disc.

The top of the snout and eyelids may be dark, in contrast to the holotype which has dark pigment in this region confined to the eyelids and a narrow interorbital band. Lumbar ocelli show faintly in some preserved specimens. The dorsal band morph exists in this species as in most other Australian *Cophixalus*. In one specimen there is a pale dorsal band, diffusely edged with darker pigment, from the posterior edge of the eyelids to the vent. Another has this same pattern and superimposed on it a paler vertebral hairline that meets a similar line running along the posterior upper sides of the thighs and above the vent. The undersides of most specimens do not show the contrast of dark throat and unpigmented abdomen seen in the holotype, but are more uniformly pigmented on all surfaces—a dusting of melanin with a hint of lighter spotting. The specimen illustrated (fig. 30) had in life a reddish brown dorsum with obscure darker markings and golden-tipped warts in the postsacral region. The upper quadrant of the eye was the same as the dorsum, and the undersides were gray.

Comparisons with Other Species

Cophixalus hosmeri is sympatric with *C. ornatus* and *C. concinnus* on Mt. Lewis and Mt. Spurgeon. Greater body size and enlarged, truncate digital discs with those on the fingers larger than those on the toes amply distinguish *ornatus*. *Cophixalus concinnus* also is larger than *hosmeri*, but the two are similar in many respects and juveniles of *concinnus* could be confused with *hosmeri*. See the account of *concinnus* for a detailed comparison.

Other than the differences in leg length pointed out in the diagnosis, there are average differences between *hosmeri* and the other small species that point to its distinctiveness but are not great enough to be of diagnostic value. For example, the EN/IN ratio averages significantly lower than in *exiguus*, the first finger is less well developed than in *exiguus* but larger than in *crepitans*, and the discs of the fingers and toes average smaller than in *infacetus*.

Habitat and Habits

Tracey and Webb (1975) map the vegetation of the collection site on Mt. Lewis as simple microphyll vine-fern forest, and Tracey (1982, fig. 13) diagrams a cross section of this vegetation on Mt. Spurgeon. The holotype was found calling from the axil of a palm frond about 1 m above ground level (Keith McDonald, field notes). The individual I tape recorded was hidden beneath a dead leaf on a branch 3 cm in diameter lying across a palm frond 150 cm above the leaf litter. Frogs also have been found under surface debris in the daytime.

Other species of *Cophixalus* found on Mt. Lewis and Mt. Spurgeon are the larger *C. concinnus* and *C. ornatus*. The last is at the northern end of its range, whereas *concinnus* is at its southern extreme. At no other site are more than two species of Australian *Cophixalus* known to coexist.

Call

I have recordings of the calls of three individuals, two documented by specimens and one identified by inference. The call is a series of 15–17 clicks uttered over a span of 0.78–1.24 seconds, with a mean pulse rate ranging from 12.1 to 17.7 pulses per second (fig. 66A, table 15). In two calls most of the energy is in the region of about 4000–5000 Hz, whereas in the third there is also a peak at about 2000 Hz. The call is most similar to that of sympatric *Cophixalus concinnus*, but evidently differs in its slower pulse rate at corresponding temperatures; see the account of *concinnus* for elaboration. Dennis and Trenerry (1984, p. 3) stated that the call of *concinnus* on Mt. Lewis "is a short rattle whereas the other [*hosmeri*] has a slow tapping call which starts off soft and very slow and increases in volume and speed before tapering off and stopping."

Remarks

Like *Cophixalus concinnus*, this species was first collected by P. J. Darlington on Mt. Spurgeon in 1932 and, like *concinnus*, it was confused by Loveridge (1935, p. 57) with five other species of *Sphenophryne* and *Cophixalus* under the name *Sphenophryne polysticta*. (This last species is a Papuan one not known to occur in Australia.) Zweifel (1962, pp. 13–14) treated the MCZ specimen of this species and those of *C. concinnus* as *Cophixalus* sp. without distinguishing between them. Evidently there were no collections of *C. hosmeri* made following Darlington's until William Hosmer obtained specimens on Mt. Spurgeon more than 40 years later in 1973. Subsequently Hosmer collected a large series on Mt. Lewis, and other collectors added specimens from there too.

Distribution

This species has been found only at relatively high elevations on Mt. Lewis and Mt.

TABLE 15
Call Statistics for *Cophixalus hosmeri*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Pulses per Call Mean (Range)	Pulses per sec Mean (Range)	Frequency, Hz	Number of Calls
No spec.[a]	236	–	22.0	0.84 (0.76–0.96)	15.9 (15–17)	17.7 (16.7–18.7)	2000–4500[b]	10
AMNH 111444[a]	229	13.0	19.3	1.11 (0.93–1.24)	14.7 (13–17)	12.6 (11.8–13.0)	4100–5350[c]	10
QM J42058[a,d]	239	13.2	18.8	1.14 (1.06–1.21)	14.6 (13–15)	12.1 (11.2–13.1)	4600	10

[a] Mt. Lewis.
[b] Two codominant peaks.
[c] Four codominant peaks within this range.
[d] Holotype.

Spurgeon to the southwest and west, respectively, of Mossman, Queensland (fig. 23). Reasonably precise records of elevation are 960–1000 m on Mt. Lewis and 1370 m on Mt. Spurgeon. All specimens examined are listed under holotype and paratypes.

Cophixalus infacetus, new species
Figure 31

HOLOTYPE: QM J42059 (formerly AMNH 111447, field number RZ 11427), collected January 17, 1981, by R. G. Zweifel and Keith McDonald, 12.5 km south and 13.0 km east of Millaa Millaa, Queensland, elevation 460 m.[5]

PARATYPES: AMNH 111448, 111449, same data as holotype; WH 2149, Palmerston National Park Camp Area (Henrietta Creek?), collected by W. Hosmer, April 21, 1975; AM R97579, WH 2150, 2396, 2397 + 2 untagged, same data as WH 2149, no date; SAMA R23872, Henrietta Creek, Palmerston National Park, 360 m, collected by K. McDonald and R. Atherton, February 11, 1977; QM J41461,[6] same data as SAMA R23872, collected by Keith McDonald on February 13, 1980; QM J41639, J41640, Park Ranger's Residence, Palmerston National Park, collected by K. McDonald on October 6, 1980; AM R28458, Palmerston National Park, 48 km from Innisfail, collected by H. Cogger, October 2, 1969; QM J29728, J29729, Palmerston National Park, 34 km west of Innisfail, collected by G. Ingram and G. Roberts on January 17, 1977; AMNH 116920, SAMA R24080, Palmerston National Park, collected by K. McDonald on February 16, 1977; DU 10005, ca. 32 km west of Innisfail along Palmerston Highway, collected by Arnold Gaunt, June 29, 1971.

ETYMOLOGY: The Latin adjective *infacetus*—meaning rude, unmannerly—refers to the sound of the frogs' call.

DIAGNOSIS: *Cophixalus infacetus* is a small species (females to 17.6 mm SV, males slightly smaller) that differs from others of similar size in the following combination of characters: long hind legs, moderately high EN/SV ratio, well-developed digital discs, but first finger without a distinct disc. The call is a series of closely spaced clicks, about 60–100 in a 1-second call.

Cophixalus hosmeri is well distinguished from *infacetus* in leg length, with 95 percent of specimens separable on the basis of TL/SV equal to or greater than 0.45 in *infacetus*. *Cophixalis crepitans* has a lower EN/IN ratio than *infacetus*, less than 0.75 in 80 percent of *crepitans* and greater than 0.75 in 80 percent of *infacetus*. The latter also has a better developed first finger (fig. 6D). *Cophixalus exiguus* has a longer first finger than *infacetus*, with a feebly developed disc (fig. 6A). *Cophixalus bombiens* does not differ from *C. infacetus* in any morphological feature that would be of much use in identifying specimens, though the digital discs of *infacetus* often are larger (fig. 6C, D).

DESCRIPTION OF HOLOTYPE: Adult male (calling when captured) with the following measurements and proportions: SV 15.2, HW 5.6, TL 6.7, EYE 2.0, EN 1.25, IN 1.6, third finger disc 0.75 (penultimate phalange 0.4),

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[5] The locality is in State Forest 1276, 5.7 km southwestward along a road that joins the Palmerston Highway in Palmerston National Park opposite Tchupala Falls.

[6] A clutch of eggs found with paratype QM J41641 is registered as QM J41642.

fourth toe disc 0.85 (0.55), HAND 3.2, FOOT 6.7; TL/SV 0.441, HW/SV 0.358, EYE/SV 0.132, EN/SV 0.082, IN/SV 0.105, EN/IN 0.781, third finger disc/SV 0.049, fourth toe disc/SV 0.056, HAND/SV 0.210, FOOT/SV 0.441.

Head slightly narrower than body, hind legs relatively long. Snout bluntly rounded seen from above, vertical but well rounded in profile; canthus rostralis rounded, loreal region vertical and flat; nostrils lateral, closer to tip of snout than to eye, internarial span greater than eye-naris distance. Eyes large, same length as snout, projecting beyond margin of jaw as seen from directly beneath; interorbital span greater than width of an upper eyelid. Outline of tympanum scarcely visible beneath undifferentiated overlying skin. Relative lengths of fingers, 3>4>2>1, first less than half length of second; second to fourth fingers with well-developed grooved discs, slightly smaller than those of toes, that of third finger almost twice width of penultimate phalange, tip of first finger rounded, not disclike; subarticular and metacarpal elevations low and rounded, scarcely evident. Toes unwebbed, relative lengths 4>3>5>2>1, first less than half length of second; all toes bear grooved discs, but that of first toe not wider than penultimate phalange; subarticular and inner metatarsal elevations present but low and indistinct. Dorsal and ventral surfaces smooth—no obvious folds or wartiness.

The dorsal ground color in preservative is brown, paler laterally, with darker brown markings: a broad dark area beneath the eye, attenuated beneath the tympanum; a dark canthal streak; a postorbital-supratympanic streak, barely disconnected from an elongate dark mark over the base of the arm; eyelids darker than top of head; a faint, W-shaped scapular marking; diffuse small dark spots on the back; sides mottled. The upper sides of the hind legs are dark spotted, verging on reticulate. The anterior surfaces of the thighs are dark with a few light spots, the posterior surfaces similar but even less spotted. A conspicuous dark transverse mark crosses the lower arm. The chin is brown with irregular lighter spots, the abdomen paler and more mottled. The undersides of the legs are brown with irregular lighter spots.

FIG. 31. *Cophixalus infacetus,* QM J42059 (holotype), 12.5 km S, 13 km E Millaa Millaa; adult male, SV 15.2 mm.

In life, the holotype was golden brown in the shoulder and posterior head region and more gray-brown elsewhere, with dark brown markings. The iris was deep gold and not conspicuous. The undersides were dark gray, the chin somewhat darker than the abdomen and with a few light flecks.

VARIATION IN THE TYPE SERIES: See tables 9–11 for means, averages, and ranges of selected proportions. Six adult males in the type series measure 14.5–15.8 mm SV; the smallest was calling when captured. Two gravid females measure 16.8 and 17.6 mm SV; the latter is the largest specimen of the species.

The type series comes from a relatively restricted region, and there are only eight specimens from outside of the immediate area of the type locality. Hence, material is insufficient to investigate geographic variation (see Remarks). Leg length of *infacetus* is proportionally among the longest in Australian *Cophixalus,* and the toe and finger discs average larger than in the other small species. However, the fourth toe disc is consistently larger than the third finger disc, in contrast to the larger scansorial species *ornatus* and *saxatilis* which have the finger disc larger. Only in occasional small *infacetus* are the toe and finger discs equally expanded. The toe and finger discs increase in width relative to body length with growth, as does head width to a lesser degree. Other proportions follow the more common trend expressed as a growth coefficient less than unity.

The only variation in pattern noted among the frogs examined is the presence of a strong vertebral stripe such as is seen as a presumably polymorphic variant in other species.

COMPARISONS WITH OTHER SPECIES

Cophixalus infacetus is sympatric with *C. ornatus* in Palmerston National Park and vicinity, where *ornatus* is distinguished by its larger size and larger digital discs, the disc of the third finger being broader than that on the fourth toe in *ornatus.* For comparisons with the small-bodied lowland population of *ornatus* (allopatric to the range of *infacetus* as known at present), see the account of *ornatus.*

Among the small species, *Cophixalus infacetus* is perhaps the least distinctive morphologically. In almost all proportions the ranges of variation in *infacetus* extensively overlap those of the other species, with only *hosmeri* being well differentiated in leg length and *crepitans* somewhat less well by the EN/IN ratio (see Diagnosis). The digital discs are larger in *infacetus,* but this character is difficult to use without well-preserved comparative material at hand. Differences in the length of the first finger that distinguish *infacetus* from *exiguus* and *crepitans* are no doubt real but again are difficult to utilize for identification without comparative material. None of this casts doubt on the specific distinctness of *infacetus,* which is amply indicated by its call.

HABITAT AND HABITS

The region of Palmerston National Park (fig. 20) and adjacent State Forest where this species occurs is mapped as complex mesophyll vine forest (Tracey and Webb, 1975). Tracey (1982, p. 14), referring to the subdivision of this vegetation type in Palmerston, states that it "represents the optimum development of rainforest in Australia under the most favourable conditions of climate and soil in the tropical humid lowlands."

Males called from sheltered, slightly elevated situations. One called from beneath a branch lying across a log, two others from between and beneath leaves lying on logs, and a fourth from a leaf on a low shrub, but concealed by an overlying leaf. William Hosmer (field notes) found one calling "from a small hole in rotting timber on the forest floor," and heard others in "low vegetation three to four feet above ground." Specimens taken near Cairns (see Remarks) were "calling from beneath litter . . . in rainforest by small creek" (collector's notes).

Keith Mcdonald (*in litt.*) furnished information on breeding of *C. infacetus* in an open-air fern house at the Ranger's Residence in Palmerston Park. A clutch of eight eggs attended by an adult was under a staghorn fern on July 7, at which time no embryonic development was apparent. Pigmented embryos were evident on August 4, and the eggs had hatched when next examined on August 25. In another instance, an adult male and an apparently immature female (SV 12 mm, I examined both frogs) were associated with what evidently were two clutches of 10 and 11 eggs. Two hatchlings from the group of 11 found on October 6 measure about 5 mm snout to vent. The eggs had been tended, probably by the male captured, for at least a month prior to hatching.

CALL

The call is a series of clicks lasting about 1 second with the mean pulse (click) rate varying from about 60 to 110 per second in the sample of six individuals (fig. 66C, table 16). Typically, the pulse rate increases during each call and slows down slightly near the end. The dominant frequency is in the area from 3200 to 4400 Hz, but the call is not finely tuned and the band of dominance may be several hundred Hertz broad. Variation in the emphasized frequency band is not introduced by variations in the recording or analyzing equipment, for on one of the tapes (recorded by Wm. Hosmer) two frogs calling side-by-side have the midpoints of their frequency bands 900 Hz apart.

The rate at which calls are repeated varies considerably both in successive calls of the same individual and among different frogs. One frog initiated calls on the average of every 8.5 seconds (N = 4, range 5.6–9.9 sec), whereas another called every 24.5 seconds (6, 10.9–38.1). Two others with larger samples (N = 12 and 14) had intermediate averages (14.6 and 11.2) and similar ranges (ca. 8–17). Variation in this and other features of the call

TABLE 16
Call Statistics for *Cophixalus infacetus*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Pulses per Call Mean (Range)	Pulses per sec Mean (Range)	Frequency, Hz	Number of Calls
QM J42059[a,b]	228	15.2	23.4	1.02 (0.99–1.06)	63.7 (62–65)	62.5 (60–64)	4300	10
No spec.[a]	228	—	23.6	0.97 (0.86–1.04)	99.6 (98–114)	111.5 (102–120)	4400	10
SAMA R23872[a]	239	14.6	—	1.11 (1.10–1.12)	74.2 (71–76)	67.0 (63–69)	4100	5
WH 2149[a]	241	14.5	21.0	0.89 (0.87–0.91)	76.8 (75–99)	86.3 (85–88)	4400	5
No spec.[a]	236	—	—	0.95 (0.85–1.02)	72.6 (67–77)	76.7 (75–78)	3200	5
No spec.[a]	236	—	—	0.92 (0.88–0.95)	78.0 (74–82)	84.8 (83–86)	4100	5

[a] Palmerston National Park and vicinity.

[b] Holotype.

(table 16) is not explicable in terms of temperature, body size, or geography. Disturbance by the recordist or unobserved interactions with other frogs may have been involved.

REMARKS

The description is based on specimens from a small area close to the Palmerston Highway. There are, in addition, eight specimens that I associate with *Cophixalus infacetus* but without sufficient confidence to include them among the paratypes upon which the species is based. The mating call of these additional specimens is unrecorded and they come from localities apart from the established range. The only realistic alternatives to their being *C. infacetus* are that they represent *C. ornatus* or are undescribed.

One of these is QM J30915, collected on Mt. Bartle Frere (exact locality and elevation not specified) in January 1977 by Gregory Czechura. The locality is about 20 km north of the Palmerston sites. The specimen (unsexed) measures 16.1 mm SV and so approaches the upper size limit of *infacetus*. In several proportions, *C. ornatus* and *C. infacetus* of this body size are sufficiently alike that a difference based on one specimen would be meaningless—these include HW, EYE, EN, and IN. With a TL of 7.8 mm, the specimen is well within the range of *infacetus* but barely within that of *ornatus*. The specimen has the relative finger and toe disc sizes of *infacetus*, but the discs are much smaller than expected for that species. The size of the hand (3.5 mm) is exactly on the regression line for *infacetus* and smaller than that predicted for lowland (4.0 mm) or highland (5.1 mm) *ornatus* of the same size.

Another specimen, QM J37280, is from the Cairns–Yarrabah Road at the boundary of the Yarrabah Aboriginal Reserve, about 65 km north of the Palmerston localities, collected by Glen Ingram in January 1980. At 16.6 mm SV, the unsexed specimen approaches the largest female from Palmerston. As in the specimen from Bartle Frere, the disc on the fourth toe is larger than that on the third finger, and both are smaller than expected in *ornatus* or in *infacetus*. Hand size, 3.5 mm, is as expected in *infacetus* and smaller than expected in either lowland or highland *ornatus*.

Six males from Crystal Cascades, near Cairns (AM R106927–106932, 15.6–16.7 mm SV) agree in all pertinent characters with *infacetus*, though again the finger discs average slightly smaller than in the Palmerston sample.

At my request, Mr. William Hosmer kindly visited the Crystal Cascades locality to look for these frogs. Though unable to make recordings, Mr. Hosmer (*in litt.*, Oct. 1984) reports that he "did hear calls of the same species as heard at Palmerston" and is "sure beyond doubt that the Crystal Cascades frogs are the same species as at Palmerston. The same call has been heard also on the Whitfield Range, west of Cairns, also at Babinda Boulders."

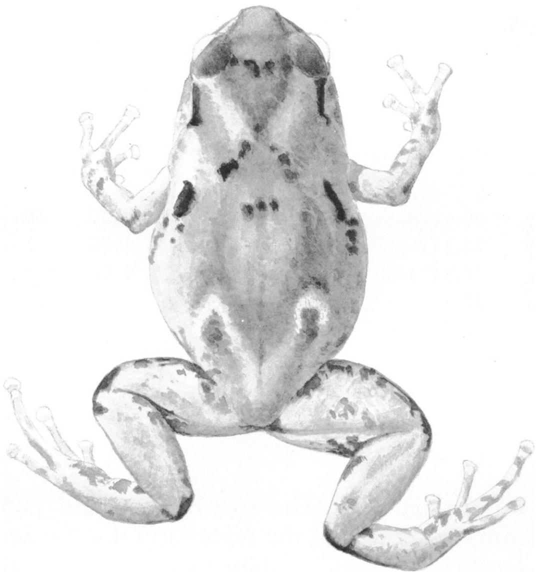

FIG. 32. *Cophixalus mcdonaldi,* QM J42064 (holotype), Mt. Elliot; adult female, SV 25 mm.

The sizes of the hands and relative sizes of finger and toe discs are sufficient to exclude the questionable specimens from *Cophixalus ornatus,* and there are no positive data to suggest undescribed taxa. Confirmation of their assignment to *infacetus* awaits recording of vocalizations.

Cophixalus infacetus was collected at least as early as 1969. William Hosmer was, in 1975, evidently the first to recognize *infacetus* as an undescribed form. Subsequent collections by Keith McDonald and Glen Ingram, who also independently recognized the species as undescribed, contributed substantially to the material available.

DISTRIBUTION

Most records for this species are clustered in an area along the Palmerston Highway, in or adjacent to Palmerston National Park, about 30 km west-southwest of Innisfail, Queensland, at elevations between 360 and 460 m (fig. 23; localities and specimens listed under holotype and paratypes). Eight specimens from outside this area are tentatively assigned to the species (see Remarks): QM J30915, Mt. Bartle Frere; QM J37280, Yarrabah Aboriginal Reserve, on boundary of Reserve on Cairns–Yarrabah Road; AM R106927–106932, Crystal Cascades, 4 km S, 9 km W Cairns.

Cophixalus mcdonaldi, new species

Figure 32

HOLOTYPE: QM J42064 (formerly AMNH 111489, field no. D. Liem 6352), collected June 8, 1972 by David S. S. Liem at an elevation of about 900–1000 m on Mt. Elliot, 30 km southeast of Townsville, Queensland.

PARATYPES: AMNH 111485–111488, same data as holotype[7]; QM J42040–42057, SAMA R24945, R24946, Mt. Elliot summit, collected by John W. Winter, Robert G. Atherton, and R. Taylor on July 4–7, 1977.

ETYMOLOGY: This species is named for Keith McDonald of the Queensland National Parks and Wildlife Service in recognition of his important collections of microhylid frogs, and of his generosity in sharing his specimens, time, and information with me and with others who have studied the Queensland herpetofauna.

DIAGNOSIS: A species of moderate size (males to 23 mm SV, females to 26 mm), *Cophixalus mcdonaldi* differs from species of similar or larger size in the following combination of characters: disc of third finger usually narrower than that of fourth toe; first finger relatively short, without a terminal groove or disc; EN/SV and TL/SV ratios moderate, lying between the extremes reached by other species. The call is not known.

Cophixalus neglectus resembles *C. mcdonaldi* in the relative sizes of toe and finger discs and in the discless nature of the first toe, but has shorter legs and a lower average EN/IN ratio: 87 percent of *mcdonaldi* have TL/SV equal to 0.40 or greater, whereas the same proportion of *neglectus* have a shorter ratio; 87 percent of *mcdonaldi* have an EN/IN ratio greater than 0.78, compared to 89 percent of *neglectus* with a lower ratio. *Cophixalus ornatus* and *C. saxatilis* have enlarged, truncate digital discs, that of the third finger

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[7] AMNH 111488 (D. Liem 6349) bears a tag reading "Mt. Edith 2-6-72," but data furnished with the specimen indicate it came from Mt. Elliot. The specimen is typical of *C. mcdonaldi* in all respects and unlike *C. ornatus,* the only *Cophixalus* known from Mt. Edith (at the northern side of the Atherton Tableland).

broader than that on the fourth toe, and have the first finger relatively long, with a conspicuous disc. *Cophixalus concinnus* has a better developed first finger with a small, grooved disc.

Description of Holotype: Adult female (gravid) with the following measurements and proportions: SV 25.0, TL 9.6, HW 9.6, EYE 2.85, EN 1.75, IN 2.25, third finger disc 1.0 (penultimate phalange 0.65), fourth toe disc 1.1 (0.65), HAND 5.3, FOOT 10.2; TL/SV 0.384, HW/SV 0.384, EYE/SV 0.114, EN/SV 0.070, IN/SV 0.090, EN/IN 0.778, third finger disc/SV 0.040, fourth toe disc/SV 0.044, HAND/SV 0.212, FOOT/SV 0.408.

Head narrower than body, legs short. Snout seen in dorsal view bluntly pointed, not truncate, rounded and slightly projecting in profile; canthus rostralis slightly rounded, loreal region sloping, flat; nostrils lateral, closer to tip of snout than to eye, internarial distance greater than eye-naris distance. Eyes moderately large, about equal to snout length; corneal outline projects beyond jaw margin viewed from below; upper eyelid considerably narrower than interorbital span. Tympanum about half diameter of eye, but scarcely visible externally. Relative lengths of fingers 3>4>2>1, first very short, scarcely reaching subarticular tubercle of second; second to fourth with grooved discs smaller than those on toes, tip of first finger rounded, not disclike or grooved; subarticular and metacarpal elevations low, rounded, indistinct. Toes unwebbed, relative lengths 4>3>5>2>1, first very short, not reaching subarticular tubercle of second toe; second to fifth toes with grooved, enlarged terminal discs, that of fifth toe scarcely broader than penultimate phalange, tip of first toe rounded and somewhat disclike but not expanded; subarticular tubercles low, rounded, inconspicuous; inner metatarsal tubercle low, rounded, elongate; no outer tubercle. Dorsal and ventral skin surfaces smooth with only a faint postocular-supratympanic fold.

The dorsal ground color in preservative is pale tan. Darker markings include canthal and supratympanic streaks, small spots anteriorly on the back, and a few scattered marks on the arms and legs. Lumbar ocelli are indistinct. The side of the head is slightly darker than the dorsum, giving an indistinct mask effect that includes the margin of the lower jaw. The groin and anterior surface of the thigh are mottled, as is the region behind the knee, though most of the posterior surface of the thigh is more lightly and uniformly pigmented. A dark spot surrounds the vent. The ventral surfaces are pale with stippling anteriorly gradually becoming more of a network on the abdomen and then mottled distally on the thighs and shanks.

Variation in the Type Series: See tables 9–11 for statistics of selected proportions. The 11 females in the type series are adult and measure from 21.0 to 26.1 mm SV. Thirteen males range from 16.1 to 23.3 mm, but there is no information on size at maturity.

The relative increase with growth of all standard measurements lags behind increase in body length. Finger and toe discs are similar in size, but in most instances (19 of 25 specimens) the disc of the fourth toe is slightly broader than that of the third finger. In only two frogs is the third toe broader, whereas in three they are the same. Growth coefficients for finger and toe discs are relatively high (above 0.9) and similar, so the width of the discs relative to body size changes less than other body parts, and their size relative to one another does not change. Growth coefficients of EN and IN are sufficiently similar that the ratio EN/IN does not change significantly with growth.

There is no information on color in life. The dorsal ground color includes a range of shades from the pale tan of the holotype to, less commonly, dark brown. Variation in markings is slight. A dark streak above the arm is common to all specimens and in some extends irregularly along the side. The slightly darker facial region, canthal stripe, and postocular streak are present in all; the last may curve downward behind the tympanum. Some specimens have an ill-defined interocular bar, with the area anterior to it somewhat paler than the general ground color. Ventral surfaces in most specimens are as described for the holotype. In only one does dark pigment predominate.

Comparisons with Other Species

Cophixalus mcdonaldi is not known to be sympatric with any other microhylid. *Co-*

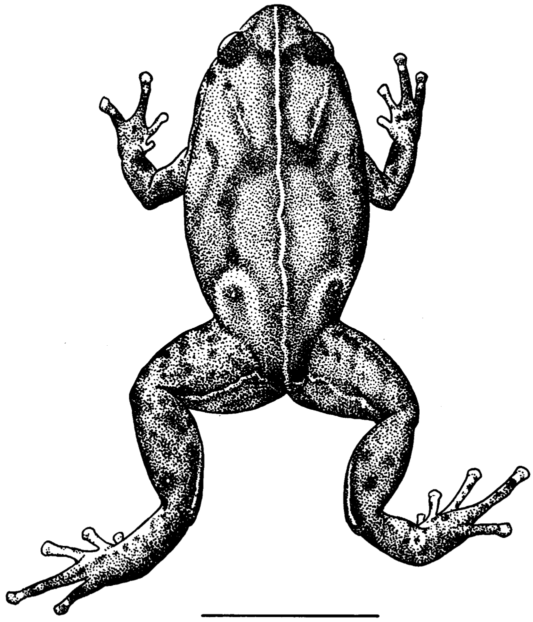

FIG. 33. *Cophixalus neglectus,* AMNH 111396, adult male, Centre Peak, Mt. Bellenden Ker. Scale line represents 10 mm.

phixalus concinnus and *C. mcdonaldi* do not differ significantly in most proportions useful in distinguishing among species of Australian *Cophixalus*; only the better developed first finger of *concinnus* compared to the discless, short finger of *mcdonaldi* is a useful key character. *Cophixalus mcdonaldi* averages larger than *concinnus*; 8 of 11 female *mcdonaldi* are greater than 23 mm SV, whereas only 4 of 37 adult females of *concinnus* attain this or a greater length. I consider the differences in size and finger morphology adequate reasons for recognizing *mcdonaldi* as a species distinct from *concinnus,* especially considering the isolation of *mcdonaldi* on a mountaintop 360 km from the closest known population of *concinnus.* Data on the call of *mcdonaldi* could prove especially useful in testing this hypothesis of level of relationship.

HABITAT AND HABITS

Mt. Elliot, the only known locality for *Cophixalus mcdonaldi,* rises from the coastal lowlands southeast of Townsville to an elevation of 1240 m. In their discussion of rainforest refugia, Webb and Tracey (1981, p. 655) mention Mt. Elliot among "moist upland refugia." Other than the location of the specimens high on the mountain (900 m or higher), nothing specific is on record concerning habitat or habits. There is no recording or description of the call.

REMARKS

First collected by Dr. David Liem in 1972, *Cophixalus mcdonaldi* has been obtained only once subsequently that I know of. It has the distinction of being the southernmost microhylid in Australia.

DISTRIBUTION

The species is known only from 900 m or higher on Mt. Elliot, 30 km southeast of Townsville, Queensland (fig. 25). Specimens examined are listed under holotype and paratypes.

Cophixalus neglectus Zweifel
Figure 33

Sphenophryne polysticta: Loveridge, 1935, p. 56 (part).

Cophixalus neglectus Zweifel, 1962, p. 15 (type locality, "Bellenden Ker Range, Queensland"; holotype, MCZ 18505, collected by W. E. Schevill in 1932; see below for a more precise statement of the type locality).

TYPE LOCALITY: The type locality given in the original description, "Bellenden Ker Range," is relatively imprecise and does not distinguish between two probably disjunct populations (see section on distribution). Through the courtesy of the collector, Mr. William E. Schevill (*in litt.,* January 1982), it is possible to define the type locality with greater precision. Mr. Schevill writes that the frog was collected on April 5, 1932 (possibly a day earlier or later) on the northeasterly slopes of the center peak of Mt. Bellenden Ker at an elevation of 4000 ft or more, perhaps 1000 ft below the summit (summit elevation 1520 m; 5000 ft).

DIAGNOSIS: A *Cophixalus* of moderate size (males to 23 mm SV, females to 28 mm), distinguished from other Australian species of similar or larger size by the following combination of characters: digital discs poorly developed, that on the third finger narrower than that on the fourth toe; first finger short with tip rounded, not disclike; legs short (mean TL/SV 0.356); EN/IN low (mean 0.729). The call is a buzz about one-half second long.

Cophixalus saxatilis and *C. ornatus* are immediately distinguished from *C. neglectus* in having enlarged, truncate digital discs, those on the fingers conspicuously larger than those on the toes. *Cophixalus concinnus* also has larger digital discs than *neglectus,* though the difference is less marked. In *concinnus* the disc on the third finger is usually almost equal to that on the fourth toe and sometimes exceeds it, and the first finger bears a disc. *Cophixalus mcdonaldi* differs from *neglectus* in its longer legs (TL/SV greater than 0.38 in most specimens) and higher EN/IN ratio (greater than 0.77 in most). *Cophixalus peninsularis* probably is a smaller species (two male specimens measure 17 and 18 mm SV), and has moderately enlarged digital discs, that on the third finger equal to that on the fourth toe.

DESCRIPTION

MORPHOLOGY: The largest among 12 male frogs measures 23.1 mm SV. Maturity is attained by at least as small as 20.4 mm, judged by calling. Among 32 females dissected, the largest measures 28.5 mm, and eight others are 26 mm or larger. Females evidently mature at about 22 mm. Six frogs measuring between 17.5 and 20.7 mm are immature, whereas 26 measuring 22.1 mm or larger have enlarging ova or other indications of maturity.

Head slightly narrower than body. Snout bluntly rounded seen from above, more nearly truncate but slightly rounded in profile, projecting only slightly beyond lower jaw; canthal region rounded; loreal area steeply sloping, flat to shallowly concave; nostrils much closer to end of snout than to eye, directed anterolaterally, scarcely visible from above; internarial distance greater than eye-naris distance. Eyes moderate, corneal outline visible from beneath, upper eyelid narrower than interorbital distance. Tympanum small, indistinct. Relative lengths of fingers 3>4>2>1, first finger much less than half length of second; fingers 2 to 4 with grooved discs slightly wider than their penultimate phalanges, tip of first finger rounded, not disclike; subarticular tubercles low, rounded; metacarpal elevations scarcely evident. Toes unwebbed, relative lengths 4>3>5>2>1; first toe very short; all toes with enlarged, grooved discs, but disc of first toe scarcely broader than penultimate phalange; subarticular tubercles low, rounded; an indistinct slightly elongate elevation in position of inner metatarsal tubercle. Dorsal surfaces of head and back largely smooth, some individuals with faint)(-shaped folds and small warts on lower back and hind legs; ventral surfaces smooth.

The dorsal color of preserved frogs ranges from light grayish tan to dark brown. Darker dorsal markings are usually small and obscure. A dark line on the scapular folds may extend posteriorly as a diffuse band angled slightly downward, and the area below the line may be paler than the middorsal region. Lumbar ocelli are absent or weakly developed. Occasional individuals have a midvertebral hairline from nose to cloacal opening, where it meets a similar line along the upper posterior part of the thigh. All but the darkest specimens have the side of the head darker than its top, producing a poorly defined face-mask effect. Usually this is coupled with a dark postorbital streak. Ventral surfaces typically are pale with little pattern evident to the naked eye, but occasional specimens are heavily pigmented, including the undersides of the limbs. In life the dorsum may be any of a variety of shades of brown, sometimes quite orange. The venter ranges from yellow to orange.

VARIATION IN PROPORTIONS: The range of *Cophixalus neglectus,* though small, comprises two probably disjunct units centered on Mt. Bellenden Ker and Mt. Bartle Frere (see Distribution). Samples from these two mountains differ slightly but consistently in several respects. Tables 9–11 give average proportions of adults. Eye and disc sizes are sufficiently close in the two samples that I attribute no significance to the differences, but in all other proportions the frogs from Mt. Bartle Frere consistently average larger for a given body size than do those from Mt. Bellenden Ker. As estimated by the regression equations (tables 20, 21, figs. 56, 57), large adult males (23 mm SV) show the following average differences (in mm): HW 0.40, TL 0.55, FOOT 1.03, HAND 0.52, IN 0.16, EN 0.09. Although these differences are small, they approach or exceed average interspecific differences for several species pairs (figs. 56, 57), so I regard them as evidence for differentiation between the presumably disjunct populations.

COMPARISONS WITH OTHER SPECIES

Cophixalus ornatus, the only sympatric congener, is abundantly distinct from *C. neglectus* in several aspects of morphology additional to toe disc size as brought out in the diagnosis.

The species most closely similar morphologically to *C. neglectus* is *C. mcdonaldi,* found 270 km south-southeast of *neglectus* and, like that species, a montane isolate. The two are much alike in body size, internarial distance, hand and digital disc size, and in their short, discless first fingers. *Cophixalus mcdonaldi* has significantly longer legs and a longer eye-naris distance. With TL/SV 0.38 or less as a criterion of *neglectus,* more than 90 percent of specimens in a mixed sample will be identified correctly. About 88 percent will be identified correctly using EN/IN 0.78 or greater as the criterion for *mcdonaldi.*

HABITAT AND HABITS

The habitat of *Cophixalus neglectus,* atop the highest peaks of Queensland, has one of the highest yearly rainfalls of any place in Australia. A relatively brief (six-year) record from Centre Peak of Mt. Bellenden Ker gave an annual average of 8529 mm (almost 28 ft), and this station holds the Australian record for 24 hours—1140 mm (Tracey, 1982, pp. 4–9). The sensitivity of this species to rainfall was well demonstrated to Keith McDonald and me on January 19–20, 1981. As we ascended Centre Peak through clouds and rain on the cable lift that services the microwave communications facility there, we could hear *Sphenophryne robusta* calling in the forest below. At about 1000 m elevation, calls that proved to be those of *C. neglectus* replaced those of *robusta,* and these continued as we approached the peak. When we arrived at the peak at 15:00 hours, rainfall ceased and so did most calling. In the evening the sky cleared and almost no calling occurred—a 1.5 hour vigil in an attempt to record a frog that was heard to call once was fruitless. At about 02:20 hours we were awakened by a light rain to which numerous frogs also responded, and it then was possible to locate and tape record several individuals.

In the daytime the frogs may be found under surface debris—fallen branches and the like—in the forest. Frogs we tape recorded were hidden within or exposed beside grass clumps in the man-made clearing around the building on the peak. A frog recorded by William Hosmer on Mt. Bartle Frere was calling in the fronds of a small palm tree.

On our brief visit to Mt. Bellenden Ker, Keith McDonald found a clutch of eggs, accompanied by a frog, concealed by an overlying fallen branch on the upper side of a rotten log. The 14 eggs were in chains of two to five, the individual eggs connected by mucilaginous cords about 1.3 mm long and 0.5 mm in diameter. The outer egg capsule (preserved) measures 5.5 mm, with a 4.8-mm capsule enclosing a 4.3-mm capsule next to the unpigmented and elongate embryo. It is likely that the groups of eggs are fragments of an originally continuous chain. The accompanying frog appears (by dissection) to be a male, although the sexing is not as certain as I would like. Its size (SV 21.6 mm) is within the range of adult males but fractionally less than the known minimum size for adult females.

We found frogs of three other species atop Mt. Bellenden Ker: a *Cophixalus ornatus* calling from the side of the building; a *Sphenophryne robusta* collected under surface cover in the daytime but not distinguished from *C. neglectus* until several months after it had been preserved; and the myobatrachid *Mixophyes schevillii* Loveridge found in a stream a short distance below the summit.

Many *Cophixalus neglectus* are infested by the chigger *Vercammenia zweifelorum* (Domrow, Loomis, and Lester, 1983).

Our experience in attempting to transport living *neglectus* suggests an intolerance for warmth. Upon reaching the base of the mountain, we divided our specimens (held in plastic bags) between two foam plastic boxes, for one of which we had a small amount

FIG. 34. Clearing atop Centre Peak, Mt. Bellenden Ker, 1520 m. *Cophixalus neglectus* lives in the forest and clearing; *C. ornatus* and *Sphenophryne robusta* also taken here.

of ice. Within little more than an hour—the time it took in late morning to drive through the coastal lowlands to Cairns—all *neglectus* in the uniced container had died, and the other *neglectus* died within a few hours. In contrast, the single specimens of *Cophixalus ornatus* and *Sphenophryne robusta* collected and transported with *neglectus* survived.

Tracey (1982, p. 36, fig. 37) used the vegetation of the summit of Mt. Bellenden Ker as an example of simple microphyll vine-fern thicket and characterized the forest: "Dense streamlined canopy. 10–12 m with wind-sheared emergents *Leptospermum wooroonooran* to 15 m . . . two distinct tree layers . . . ground cover mostly ferns including tree ferns." See figure 34.

CALL

The call of *Cophixalus neglectus* is known from five recordings made by Keith McDonald and myself on Mt. Bellenden Ker and one by William Hosmer made on Mt. Bartle Frere. It is a buzzing sound with an average duration of about one-half second (fig. 65B, table 17). Most of the energy tends to be confined to a band about 1 kHz in width, but the rather ill-defined region of dominance may be as low as 2600 or as high as 3400 kHz. The pulse rate is rather more variable than might be expected, with individual calls ranging from as low as 95 to as high as 168 pulses per second. The variation in dominant frequency and pulse rate cannot be attributed to temperature or body size variation, since body sizes (four of five individuals measured) have a span of only 1.2 mm, and the temperature range is within one degree. The individual from Mt. Bartle Frere has the lowest pulse rate and the longest call duration of six frogs recorded, possibly indicative of minor geographic variation.

DISTRIBUTION

Cophixalus neglectus is known only from the high regions of the Bellenden Ker Range, between Cairns and Innisfail, Queensland (fig. 25). Localities on Mt. Bartle Frere range from about 900 m elevation to about 1460 m, but it is likely that the species extends to the summit at around 1600 m. Most specimens from Mt. Bellenden Ker come from the vicinity of

TABLE 17
Call Statistics for *Cophixalus neglectus*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Pulses per Call Mean (Range)	Pulses per sec Mean (Range)	Frequency, Hz	Number of Calls
AMNH 111393[a]	229	21.3	18.2	0.44 (0.42–0.47)	60.8 (59–63)	136.9 (132–143)	3200	9
AMNH 111392[a]	229	20.9	18.2	0.52 (0.49–0.57)	57.9 (56–61)	111.5 (107–116)	2950	8
No spec.[a]	229	–	18.2	0.45 (0.42–0.48)	52.9 (51–55)	118.8 (115–126)	3400	10
QNPWS N28768[a]	239	20.4	18.2	0.39 (0.35–0.42)	56.2 (52–63)	144.6 (142–154)	3350	10
QNPWS N28769[a]	239	18.2	18.2	0.47 (0.43–0.48)	78.0 (72–80)	166.3 (165–168)	3200	10
WH 2170[b]	241	20.4	19.0	0.71 (0.63–0.77)	69.4 (62–76)	97.8 (95–101)	2600	9

[a] Mt. Bellenden Ker.
[b] Mt. Bartle Frere.

the Telecom facility on Centre Peak, elevation about 1520 m, though the type series came from about 300 m lower. The northern (Bellenden Ker) and southern (Bartle Frere) populations are almost certainly disjunct—the intervening divide between the East Mulgrave River and North Babinda Creek lies at only 320 m. If the lower elevational limit of this species is at about 900 m, the populations are disjunct by only about 8 km airline distance.

LOCALITY RECORDS AND SPECIMENS EXAMINED: All localities in Queensland: Mt. Bellenden Ker, Centre Peak, ca. 1520 m (AMNH 111392–111400, 111402–111405; AM R97582–97584, R97585 [eggs]; QM J35667–35676, J37864; QNPWS N14001–14007, N28768, N28769); northeast slope, Mt. Bellenden Ker, Centre Peak, ca. 1200 m (MCZ 18502, 18503 [paratypes], 18505 [holotype]). Mt. Bartle Frere, western side, 900 m (AMNH 111391; AM R97581; WH 2376, 2386, 2389, 2391, 2392, 2394, 2395, 2398, 2399, 2401–2405, 2408, 2410, 2415, 2420); Mt. Bartle Frere, western side, 1070 m (WH 2170); Mt. Bartle Frere, 1280 m (AMNH 67401, 67402 [paratypes]); Mt. Bartle Frere, 1460 m (AMNH 111390; AM R97580; WH 2081); Mt. Bartle Frere, northwest peak summit, 1440 m (QM J39160, J39161).

Cophixalus ornatus (Fry)
Figure 35

Austrochaperina ornata Fry, 1912, p. 91 (type locality, "twenty-five miles inland from Cairns, North-east Queensland"; holotype, AM R222, collected in 1888 by E. J. Cairn and R. Grant; see Zweifel, 1962, p. 6).

Phrynixalus reginae Andersson, 1916, p. 4 (type localities, "Malanda in the jungles" and "Cedar Creek" [Queensland]; syntypes, NHRM [Naturhistoriska Riksmuseet, Stokholm] 1615 [4 specimens], NHRM 1616, MCZ 17805, BMNH 1929.5.17.1, 4 of 11 original syntypes not located [Cogger, Cameron, and Cogger, 1983, p. 53], collected in February 1913 [Malanda] and April 1913 [Cedar Creek]).

Sphenophyrne variabilis: Procter, 1923 (*non* Boulenger, 1896), p. 1071 (fide Parker, 1934, p. 173).

S[phenophryne]. ornata: Nieden, 1926, p. 48 (new combination).

Cophixalus ornatus: Parker, 1934, p. 173 (new combination). Loveridge, 1935, p. 55, footnote.

Phrynomantis ornata: Loveridge, 1935, p. 55 (new combination).

TYPE LOCALITY: Taken literally as distance inland (west) of Cairns, the stated type locality would fall outside the rainforest area in a region where *ornatus* probably does not occur. The distance was likely an estimate of road or trail mileage. Fortunately there are no taxonomic problems that require determining the exact type locality.

DIAGNOSIS: *Cophixalus ornatus* differs from all other Australian species except *C. saxatilis* in having enlarged, relatively truncate digital discs, the disc on the third finger almost always broader than that on the fourth toe. *Cophixalus saxatilis* is a much larger species, with the minimum known sizes of adult males (29 mm SV) and females (39 mm) above the maxima known for *ornatus* (27

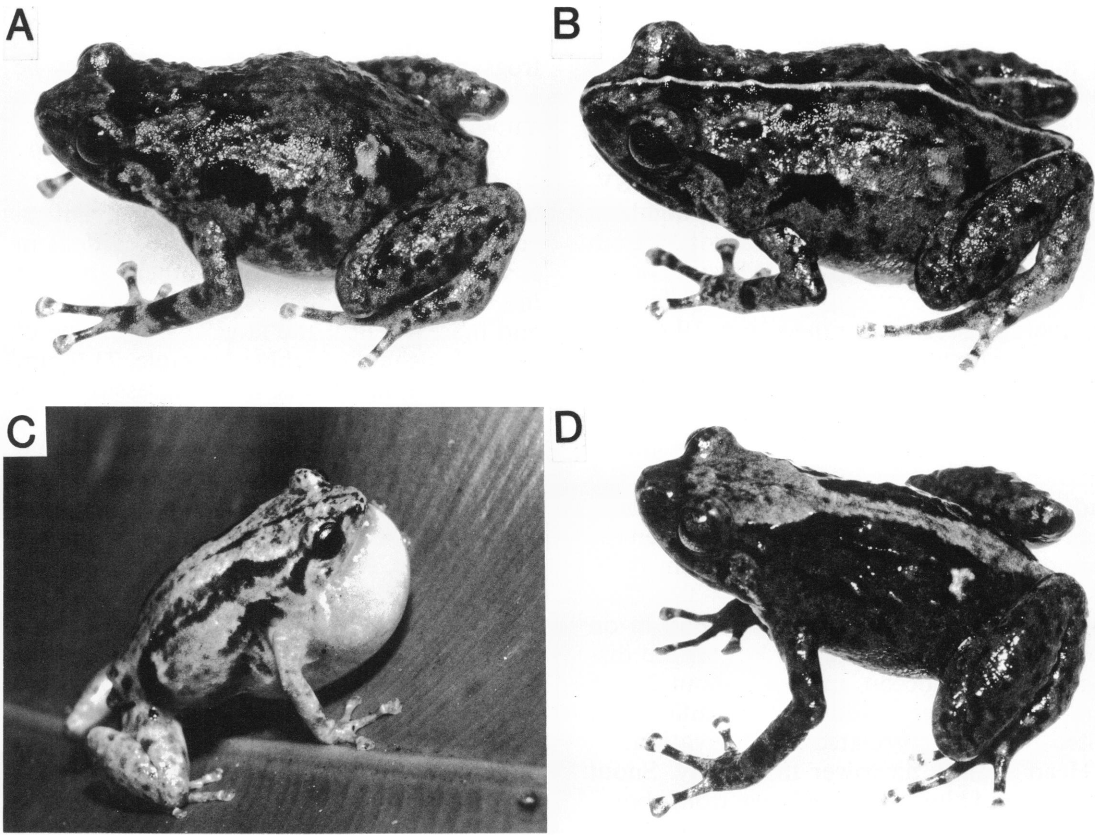

FIG. 35. *Cophixalus ornatus,* showing dorsal color pattern polymorphism. **A,** AMNH 111418, Mt. Lewis, adult male, SV 23.9 mm.; **B,** AMNH 111422, Tinaroo Dam vicinity, adult male, SV 20.6 mm; **C,** frog from Mt. Lewis, introduced into and photographed in a garden in Machan's Beach, Queensland; **D,** no voucher specimen, Henrietta Creek, Palmerston National Park.

and 30 mm). *Cophixalus saxatilis* also is longer legged, with TL/SV equal to or greater than 0.49 in individuals in the size range of *ornatus,* compared to 0.45 or less in adult *ornatus.* The call of *ornatus,* a short "beep," sounds unlike that known for any other Australian *Cophixalus.*

DESCRIPTION

MORPHOLOGY: Geographic variation necessitates treating size and maturity in two parts. Upland areas, constituting the majority of the range of the species, are treated first, coastal areas in the vicinity of Tully second.

Seventeen upland males that were calling when captured, and therefore were sexually mature, range from 18.9 to 25.9 mm SV. Among 23 additional males sexed by dissection, the largest measures 26.9 mm. No geographic variation is evident in this sample—the smallest mature frog (18.9 mm) and a relatively large one (25.2 mm) came from the same locality.

I dissected 18 females that, on the basis of enlarged, yolked ova, were sexually mature. The smallest of these measured 21.7 mm (ova more than 1 mm in diameter), whereas one measuring 21.0 mm appeared to be immature. The largest *ornatus* is a female 30.3 mm long from Mt. Spurgeon. It is exceptional not only in size, but in being the only specimen of its species from the northernmost locality for the species. The three next-largest females measure 27.0–27.1 mm. In addition to the specimens sexed, I measured nearly 100 *ornatus*; the largest of these measures less than 26 mm.

Frogs from the coastal lowlands in the vicinity of Tully at elevations of less than 40 m mature at a smaller size than do those living at higher elevations on the Atherton Tableland and surrounding peaks. Four calling males that Keith McDonald and I collected measure 17.3 (2) and 18.0 (2) mm SV, all smaller than the smallest adult highland male examined. Males in a series of 19 from Lacey's Creek, northwest of Mission Beach at a probable elevation of no more than 40 m, average 17.7 mm, range 16.6–19.4 mm. Bayard Brattstrom, who participated in the collecting of these specimens, informed me (*in litt.*) that the frogs were calling, so they were mature at this small size. Two gravid females from nearby lowlands measure 19.6 and 20.9 mm SV, and so are slightly smaller than the smallest gravid upland specimen examined. The single insular specimen, from Hinchinbrook Island, also is small—17.7 mm. Two males from an elevation of 860 m on South Bell Peak, less than 3 km airline distance from the ocean, measure about 25–26 mm, which suggests that the size differences noted truly are correlated with elevation.

Head slightly narrower than body. Snout truncate and bluntly pointed seen from above, nearly vertical and slightly rounded seen laterally, projecting slightly beyond lower jaw; loreal area nearly vertical, shallowly concave; canthus rounded; nostrils much closer to tip of snout than to eye, scarcely visible from above, internarial distance greater than eye-naris distance; eyes large, projecting well beyond edge of jaw when seen from beneath; interorbital distance broader than upper eyelid. Tympanum small, inconspicuous to virtually hidden. Relative lengths of fingers 3>4>2>1, first slightly less than half length of second; fingers 2 to 4 with large, grooved, somewhat truncate discs, larger than disc on fourth toe; disc on first finger scarcely or not broader than penultimate phalange; subarticular and metacarpal tubercles low and rounded. Toes unwebbed, relative lengths 4>3>5>2>1, first almost half length of second, all with expanded discs, those of first and fifth toes only slightly broader than penultimate phalanges; subarticular tubercles low and rounded; inner metatarsal tubercle rounded, elongate, not prominent; no outer metatarsal tubercle. Dorsum smooth between scattered warts that are less conspicuous in preserved specimens than in living frogs; scapular and postorbital folds may be indistinctly indicated; ventral surfaces smooth.

VARIATION IN PROPORTIONS: See tables 9–11 for average proportions of adults in the highland and lowland populations. Differences between these samples are evident in some proportions but not in others. In most instances the differences involve allometry and merely reflect the larger average size of individuals in the highland sample, 21.9 mm SV vs. 17.9 mm. Thus, if the regression lines for the lowland sample are extrapolated to the average snout-vent length of the highland frogs (or if the two samples are compared at the average size of the lowland frogs), the proportional differences disappear or become insignificant. This is true of the following ratios: EYE/SV, EN/IN, HW/SV, and third finger disc width/SV. Where there are no apparent differences between the ratios of adult highland and lowland frogs, the regression coefficients are close to 1.0 and the size relationships of the dependent measurements (FOOT, fourth toe disc) do not change significantly with growth. Slope coefficients for hand length are closely similar and slightly greater than unity in the lowland and highland samples. The data seemingly point to a slightly greater hand length in highland frogs, but the size ranges overlap so broadly that it would take a much larger sample to be convincing.

In one measurement—tibia length—there is a clear difference that is not attributable to allometry: adult *ornatus* from the lowland sample have longer legs than highland frogs of similar size, and the difference increases with growth (fig. 57D).

COLOR AND PATTERN: A typical preserved specimen is gray to brown dorsally with a dark spot in the lumbar region bordered anteriorly by a pale, crescent-shaped area, a dark interocular band distinct from the lighter eyelids and snout, and a more or less well-developed dark W-shaped mark in the scapular region. Other dorsal markings are quite variable and may include, in various combinations: an anteriorly directed Λ-shaped mark associated with the lumbar spots; dark speckles or larger spots scattered over the dorsal surfaces; a pale vertebral hairline from snout to vent, with or without a corresponding line on top of the thigh; and a broad, pale dorsal band. The chin, chest, and abdomen are gray to brown, generally finely mottled with a paler shade but sometimes more distinctly light spotted. This pattern is usually uniform and includes the undersides of the legs, but rarely the chin may be darker or the thighs may be partly unpigmented.

Some of the variation in dorsal pattern is illustrated in figure 35. The ground color in life is brown or some closely related shade—field notes by Keith McDonald and my notes and photographs indicate shades ranging from orange-brown to dark brown. Light color present atop the snout, anterior to the lumbar dark spot, or in a vertebral stripe or band is generally yellowish tan, rarely with more of an orange tint. The chin, chest, and abdomen are gray to gray-brown with light flecking or mottling. There are no bright flash colors in the groin or on the thighs. The iris is dark, flecked with golden pigment.

In the frogs illustrated in figure 35A and B the ground color was gray-brown and the darker markings black. Light areas associated with the lumbar dark spots were pale yellowish tan. The calling frog in figure 35C, photographed at night, had pale gray-brown sides, a yellowish tan dorsal band, and darker brown markings. The frog in figure 35D was dark brown with a yellowish tan dorsal band and darker virtually black markings.

The several dorsal patterns seen in *Cophixalus ornatus* probably constitute a polymorphism of the sort seen in other microhylids and in frogs of several other families. Zweifel (1962, pp. 8–9) described the variation in a large local sample of *C. ornatus.*

COMPARISONS WITH OTHER SPECIES

Cophixalus ornatus is sympatric with four other *Cophixalus*: in the Palmerston National Park region with *C. infacetus*; on Mt. Lewis and Mt. Spurgeon with *C. concinnus* and *C. hosmeri*; atop Mt. Bellenden Ker with *C. neglectus.* Even without taking calls into account, there is little likelihood that *ornatus* would be confused with the other sympatric species; see the various diagnoses for details.

Cophixalus ornatus from the population in the coastal lowlands near Tully could be confused with *C. infacetus,* because lowland *ornatus* males mature at less than 17 mm SV and *infacetus* males attain at least 15.8 mm. Lowland *ornatus* and *infacetus* are not known to be sympatric, but the inland extent of the distribution of the coastal type of *ornatus* is poorly known and the two forms may coexist. Though differences in sizes of finger and toe discs are less marked in lowland *ornatus* than in the larger highland frogs, relative disc size remains a good diagnostic character. Among 24 lowland *ornatus* the third finger disc is larger than the fourth toe disc in 22, whereas the two are equal in the two other specimens. The fourth toe discs are the larger in 23 *infacetus* and the two are equal in one specimen. Hand size is another distinctive feature. The ratio HAND/SV is 0.24 or greater in 23 *ornatus* but is 0.23 or less in 25 of 26 *infacetus.* The best diagnostic character is, of course, the call.

HABITAT AND HABITS

Cophixalus ornatus probably occurs throughout the entire spectrum of rainforest vegetation types recognized in north Queensland (Tracey, 1982). Near South Mission Beach, at an elevation of less than 20 m, it lives in poorly drained mesophyll vine forest (fig. 36; type 3b of Tracey, 1982; see his fig. 8 for a diagram of forest structure at an *ornatus* locality). In Palmerston National Park (fig. 20), in well-drained uplands at around 400 m, it occurs in complex mesophyll vine forest (type 1a of Tracey, 1982), a formation that Tracey states "represents the optimum development of rainforest in Australia." The range extends in elevation to the highest peaks of Queensland as at 1520 m on Mt. Bellenden Ker, Centre Peak (fig. 34; see account of *C. neglectus*). In addition to the vegetation types mentioned above, I have collected *ornatus* in areas mapped by Tracey and Webb (1975) as mesophyll vine forest, complex notophyll vine forest, and simple microphyll vine-fern forest.

In the daytime *Cophixalus ornatus* shelters under logs on the leaf litter, under loose bark, and in other similar situations. William Hosmer (unpublished MS) found an aggregation estimated at several hundred individuals in

FIG. 36. Habitat of *Cophixalus ornatus* in lowland rainforest near South Mission Beach.

a termite-infested, decayed, but still standing tree trunk about 5 ft in height. To what extent females climb is not recorded, but male *ornatus* call from elevated situations at an average height of slightly less than a meter above ground surface, occasionally as high as 2 m, less often as low as 15–20 cm. Descriptions taken from my field notes exemplify typical situations: on a leaf lodged in tall grass at roadside, 30 cm above ground; on a leaf resting about 30 cm above ground level on a tangle of branches and leaf litter; about 20 cm above ground on upper surface of leaf in a shrub, partly concealed by another leaf; on upper surface of a broad leaf about 60 cm above ground; amidst sprouts from a chopped-off sapling about one meter above ground level; where a branch leaves a tree trunk about 45 cm above ground; about 45 cm above ground in a crotch in a small tree; in head-up position on tree trunk, diameter 30 cm, partly concealed by leaf of a vine 2 m above ground; about 1.5 m up on trunk of a sapling, sheltered by large leaf of a climbing vine; about 75 cm up in slight crevice in trunk of large forest tree. The frogs do not seem to be particularly secretive, though they evidently take advantage of available cover in the relatively exposed situations from which they call. They do not appear to go high in the trees—at least, I never heard any calling from higher than about 2 m.

TERRITORIAL BEHAVIOR: Keith McDonald (field notes, personal commun.) observed an apparent territorial confrontation between two frogs, probably males but not sexed. When first observed on a tree trunk, a frog giving a peculiar "squeaky" call was approached by another and retreated, walking backwards down the trunk. Close approach (but not actual contact), calling, and movement continued until both frogs were on the ground, whereupon the calling frog hopped off, followed by the other. The frogs were still continuing this behavior when McDonald terminated his observations after about one-half hour. The impression was of one frog being driven off by the other, rather than of one following another. I did not hear the "squeaky" call in the field, but I have heard a recording made by William Hosmer of what probably was the same sort of call. Hosmer stated that this occurred in the densest calling population of *ornatus* in his experience. Glen Ingram recorded what I assume is the same call (fig. 68), and though the frog escaped, Ingram observed it and identified it as *ornatus*. The note is initially much harsher than the typical advertisement call of *ornatus*, but changes in midcall to a purer, rising tone.

COURTSHIP BEHAVIOR: The following few notes are the only information on courtship in a sphenophrynine microhylid of which I am aware, so despite their incompleteness they are worth putting on record.

On Mt. Lewis on January 25, 1980, Keith McDonald and I sought a calling *C. ornatus* and were surprised to find it sitting on the leaf litter rather than in the usual situation on an elevated perch. Another *ornatus* (which proved to be a gravid female) was on a fern frond about 15 cm above the leaf litter a few centimeters from where the male called. As

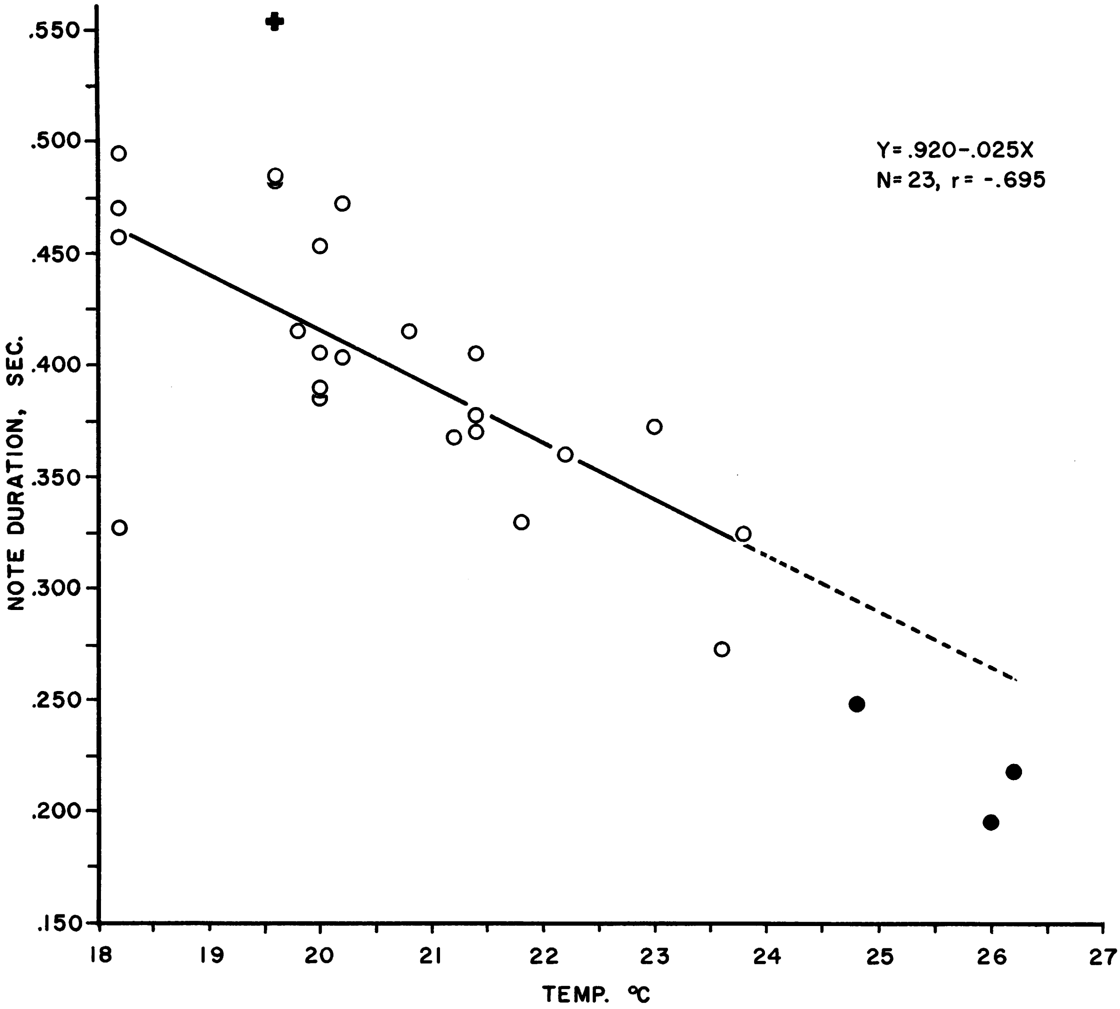

FIG. 37. Relationship between call note duration and temperature in *Cophixalus ornatus*. Regression line fitted to open circles (average call durations for individuals from highland populations); closed circles represent lowland individuals, cross is courting male (see text).

we watched with flashlights dimmed, the second frog hopped down from its perch and approached the calling male, going around him on a radius of about 75 mm before finally touching him. At this he jumped about 90 mm to a hole in the adjacent vertical road bank and went in, still calling. (It was then necessary to capture the second frog to verify its sex.) The hole into which the male moved had a diameter of about 90 mm, but widened to at least 50 cm and was at least a meter deep. It was irregular in shape and probably formed by soil slumping. The male went out of sight deep in the hole and continued to call.

I infer that the male had been calling from the usual elevated site and had attracted the female. When we came upon the scene, he had already hopped down to the ground and was in the process of leading the female to the underground nest site when we interrupted her. The evening was rainless, air temperature about 20°C.

The male's call, which we tape recorded, did not differ qualitatively from calls of males not seen to be courting, but differed quanti-

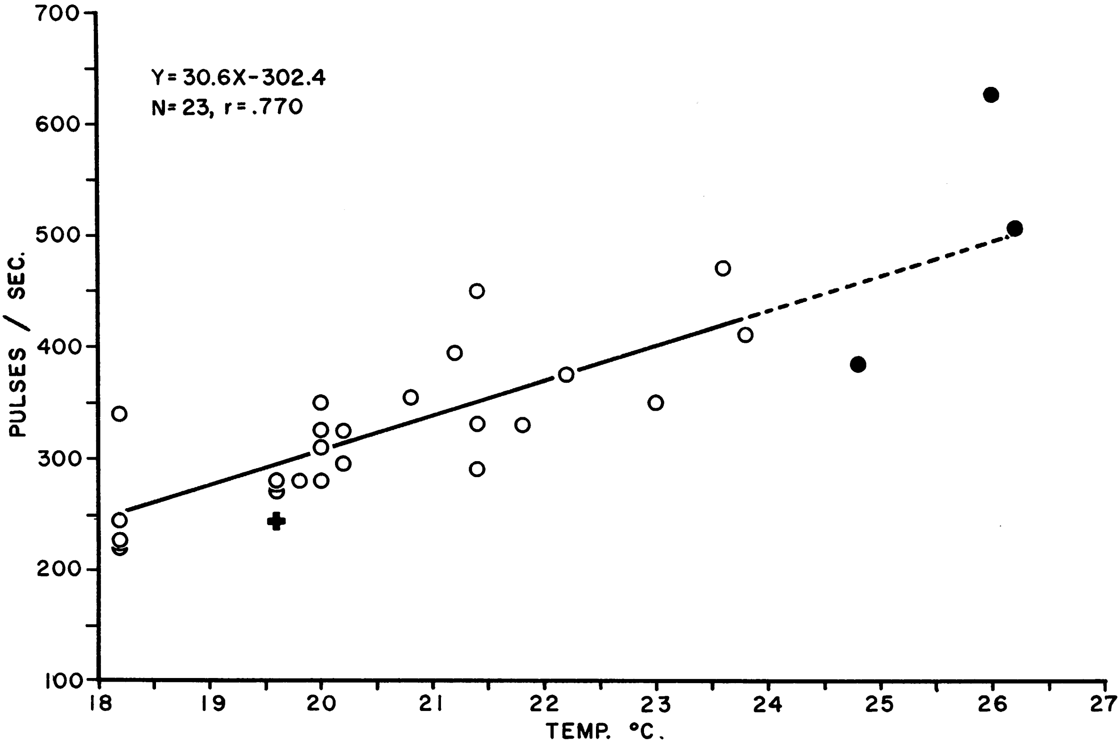

FIG. 38. Relationship between call pulse rate and temperature in *Cophixalus ornatus*. See figure 37 for details.

tatively in most major features. The average note repetition rate of 17.2 per minute (table 18, fig. 40) was the highest recorded among 25 *ornatus*; the individual notes were longer than recorded for other *ornatus* (fig. 37); and the rate at which notes were pulsed was lower than average for the temperature, though slightly above the minimum otherwise recorded (fig. 38). (Pulse rate is rather variable and the slightly lower rate may not be significantly different.) Only the dominant frequency seemed unchanged (fig. 39). In uttering more frequent notes of longer duration while maintaining the dominant frequency within the normal range, the male may provide an enhanced signal to the female, probably facilitating her tracking.

EGGS: Keith McDonald found a clutch of 22 eggs "coiled in a clump . . . under some moss in ferns" on October 6, 1980, together with a male frog of adult size (20.6 mm SV; QNPWS N28733). The ova of the preserved eggs, which show no gross evidence of development, measure about 2.5 mm. The outer jelly coat measures about 4.3 mm; no other jelly layers are seen. The eggs appear to have been arranged in two strings of 11 each, with the capsules of eggs within each string abutting but with the strings joined by mucilaginous cords at each end.

TEMPERATURE TOLERANCE: Brattstrom (1970, pp. 78, 80, table 4) studied *Cophixalus ornatus* from the lowland population at Lacey's Creek (voucher specimens in AMNH, locality "El Arish" as published). He found that all animals held at 4°C died within 24 hours, and half the animals held at 10°C died within ten days. Those that survived acclimation at 10°C had a Critical Thermal Maximum of 31.1°C, whereas frogs acclimated to 30°C had a CTM of 33.3°C. The span of temperatures tolerated is rather low, as is the CTM. The sample comes from the lowest elevation within the species' range. It would be of interest to see if frogs from higher elevations are more tolerant of low tempera-

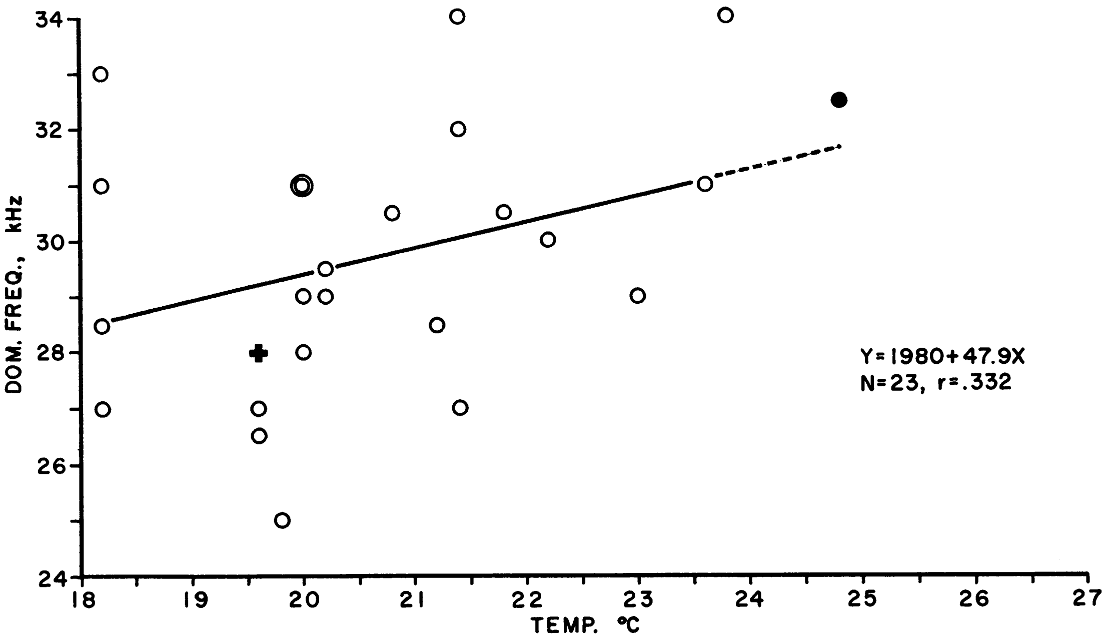

FIG. 39. Relationship between call dominant frequency and temperature in *Cophixalus ornatus*. See figure 37 for details.

tures. It has been shown that frogs from high elevations can tolerate coastal conditions. William Hosmer (personal commun.) released adult male *ornatus* from Mt. Lewis in a garden at sea level near Cairns, and individuals survived for more than a year (one is depicted in fig. 35C).

CALL

The call is a short "beep" lasting about 0.2–0.5 seconds, too rapidly pulsed to be heard as a buzz and not finely enough tuned to be called a peep or whistle (fig. 67, table 18). Notes are uttered at an average of about 11 or 12 per minute, generally with an ill-defined dominant frequency lying between 2500 and 3400 Hz. *Cophixalus ornatus* is the only Australian microhylid for which I have a sufficiently large sample of calls that some details of variation can be investigated. Because of the observed differences between highland and lowland frogs, it is desirable to segregate these samples for comparison of vocalizations. The lowland sample of recordings of only three individuals has too little variation in body size (17.3–18.0 mm SV) and recording temperature (24.8–26.2°C) for meaningful regression analysis, but the individual statistics can be related to trends observed in the larger and more diverse highlands sample (N = 23; 18.9–25.9 mm SV; 18.2–23.8°C; see table 18 for individual body lengths, temperatures, and average call data).

NOTE DURATION: The lengths of call notes decrease significantly with increasing temperature, averaging about 0.46 seconds at 18.2°C and 0.32 seconds at 23.8°C in the highlands sample (fig. 37). Average call lengths of the three lowland frogs (ca. 0.20–0.25 sec) are shorter than any recorded for highland individuals, and the three records fall below the extrapolated regression line for the highlands sample. Considering the variation shown by the latter frogs, however, I do not attribute significance to the shortness of the lowland calls other than as a reflection of the high temperature of the callers.

PULSE RATE: The pulsed nature of the call of *ornatus* is evident in wide-band spectrograms of calls given at low temperatures (fig. 67A) and in the harmonic patterns of narrow-band spectrograms (fig. 67B–F; see Watkins, 1967). Pulse rate is strongly influenced by

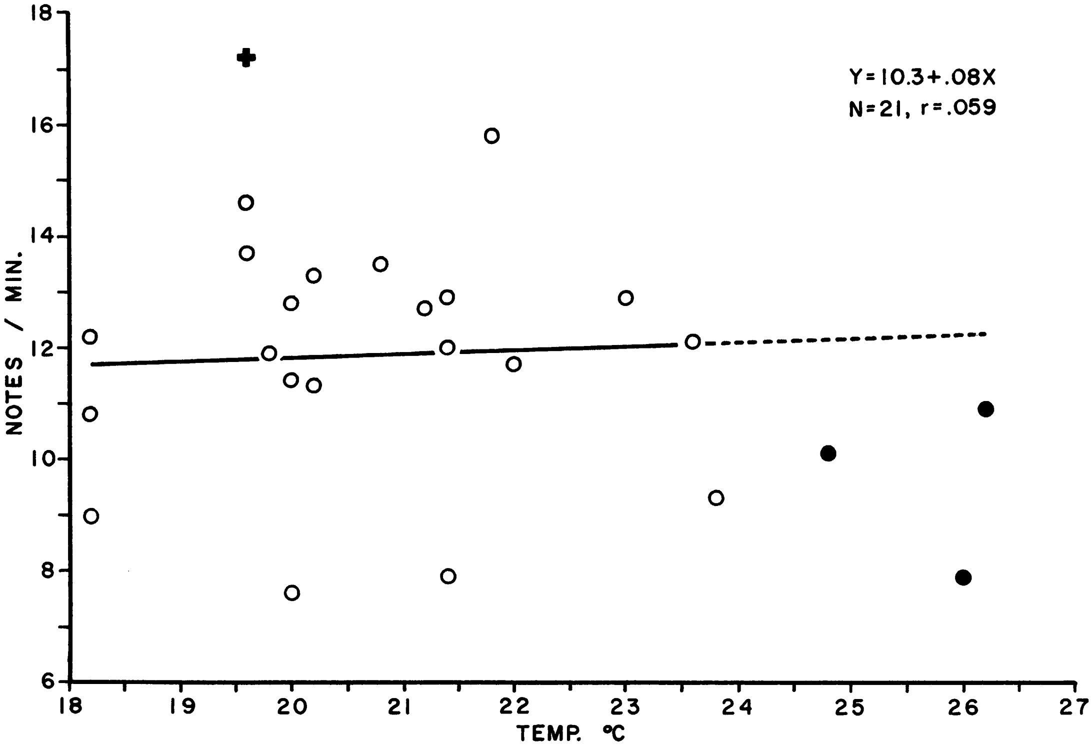

FIG. 40. Relationship between call notes per minute and temperature in *Cophixalus ornatus*. See figure 37 for details.

temperature, increasing from an average of 250 Hz at 18.2°C to 425 Hz at 23.8°C (fig. 38). Pulse rates of the three lowland frogs are diverse, but bracket the extrapolated regression line for the highlands sample; therefore no difference is indicated.

DOMINANT FREQUENCY: In spectrograms of some calls (fig. 67B) the dominant frequency is unambiguous, but in others with frequency modulation (fig. 67C–F) it changes during the course of the note. In such cases I measured the dominant frequency at the midpoint of the note. Where there was a sharp change at about midpoint (e.g., fig. 67F) it was not possible to assign a specific dominant frequency without being too arbitrary, and in others no one of two or more harmonics was clearly dominant.

Dominant frequency has only a low and statistically not significant positive correlation with temperature (fig. 39; $t = 1.611$, probability that $r = 0$ is >0.1). There is, however a strong negative correlation of dominant frequency and body size: $Hz = 5115 - 96.8SV$, $r = -0.880$, $N = 20$). This correlation notwithstanding, the range of variation is sufficiently wide that lowland and highland frogs are not separated (fig. 39).

RATE OF CALLING: Calling is essentially continuous, in the sense that there do not appear to be bouts of calling separated by long silences, but the rate at which notes are uttered is variable and not influenced by temperature. An average of about 12 notes per minute is maintained by highland frogs throughout the range of temperatures investigated (fig. 40). Neither is there an influence of body size on call rate: notes per minute = $5.7 + 0.260SV$, $r = 0.328$, $N = 21$; probability that $r = 0$ is >0.1. Call rate may be influenced by courting behavior, however (see Habitat and Habits).

FREQUENCY MODULATION: In addition to the variations in rates, duration, and frequency discussed above, the call of *ornatus* shows variation in the amount and pattern

TABLE 18
Call Statistics for *Cophixalus ornatus*

Museum Number	Tape No.	SV, mm	Temp., °C	Note Duration, sec Mean (Range)	Pulses per sec	Notes per min	Frequency, Hz	Number of Calls
AMNH 111408[a]	227	20.0	18.2	0.457 (0.45–0.47)	245	–	3300	3
AMNH 111406[a]	227	21.0	18.2	0.494 (0.47–0.51)	220	10.8	3100	5
AMNH 111407	227	21.4	18.2	0.470 (0.45–0.48)	225	12.2	2850	10
QNPWS N28767[b]	239	25.0	18.2	0.328 (0.31–0.34)	340	9.0	2700	10
AMNH 111418[c]	229	23.9	19.6	0.486 (0.47–0.50)	270	14.6	2700	10
QNPWS N28743[d]	239	25.9	19.6	0.484 (0.45–0.50)	280	13.7	2650	10
No spec.[c,e]	229	–	19.6	0.552 (0.53–0.57)	245	17.2	2800	10
QNPWS N28744[d]	239	25.0	19.8	0.415 (0.41–0.42)	280	11.9	2500	10
AMNH 111412[f]	228	21.9	20.0	0.406 (0.39–0.43)	310	11.4	3100	10
AMNH 111417[c]	229	22.0	20.0	0.345 (0.35–0.41)	280	7.6	2900	10
AMNH 111414[g]	228	24.1	20.0	0.453 (0.44–0.47)	350	12.8	2800	10
No spec.[a]	239	–	20.0	0.389 (0.37–0.41)	325	–	3100	10
AMNH 111420[h]	230	21.3	20.2	0.472 (0.46–0.49)	295	11.3	2900	10
AMNH 111421[h]	230	22.2	20.2	0.403 (0.38–0.41)	325	13.3	2950	10
AMNH 111411[f]	228	22.6	20.8	0.415 (0.41–0.42)	355	13.5	3050	6
No spec.[i]	239	–	21.2	0.368 (0.35–0.38)	395	12.7	2850	10
AMNH 111410[f]	228	18.9	21.4	0.370 (0.36–0.38)	330	12.9	3400	6
QNPWS N14235[a]	239	–	21.4	0.405 (0.40–0.42)	290	7.9	3200	10
AMNH 111409[f]	228	25.2	21.4	0.378 (0.36–0.39)	450	12.0	2700	6
QNPWS N14294[j]	239	21.5	21.8	0.329 (0.30–0.34)	330	15.8	3050	10
AMNH 111413[k]	228	22.6	22.2	0.360 (0.32–0.38)	375	11.7	3000	10
AMNH 111416[l]	229	22.4	23.0	0.373 (0.36–0.39)	350	12.9	2900	10
AMNH 111415[m]	228	21.5	23.6	0.273 (0.26–0.28)	470	12.1	3100	10
No spec.[m]	239	–	23.8	0.324 (0.29–0.34)	410	9.3	3400	10
AMNH 111423[n]	230	17.3	24.8	0.248 (0.24–0.26)	385	10.1	3250	10
QNPWS N28797[o]	241	18.0	26.0	0.196 (0.18–0.21)	625	7.9	–	10
QNPWS N28796[o]	241	17.3	26.2	0.218 (0.20–0.23)	505	10.9	–	10

[a] Paluma and vicinity.
[b] Centre Peak, Mt. Bellenden Ker.
[c] Mt. Lewis.
[d] South Bell Peak.
[e] Was courting a female; see text.
[f] Majors Mountain.
[g] Millaa Millaa.
[h] Tinaroo Dam vicinity.
[i] Gadgarra State Forest.
[j] The Crater National Park.
[k] Millaa Millaa Falls.
[l] Kuranda vicinity.
[m] Palmerston National Park.
[n] South Mission Beach vicinity.
[o] Dingo Pocket, WNW of Tully.

of frequency modulation within individual notes. Variation among five individuals is shown in figure 67, which illustrates calls with little or no modulation, slight and abrupt drops in frequency, and a drop followed by a rise in frequency. An individual may utter successive notes with virtually identical modulation, or may vary the modulation in no obvious pattern.

REMARKS

Parker (1934, p. 173) identified as *Cophixalus ornatus* a specimen, MSNG 29138, from Moroka, east of Port Moresby in Central Province, Papua New Guinea. This specimen is one of the syntypes of *Sphenophryne loriae* Boulenger (1898). The syntype series included specimens of at least four species referable to the genera *Cophixalus* and *Oreophryne* (Parker, 1934). I examined the specimen in question briefly in 1968. On a morphological basis, and in the context of knowledge of Australo-Papuan microhylids at the time Parker wrote, its association with *ornatus* was reasonable. Its size (SV 18.4 mm) is within the range for *ornatus*; like that species it has well-developed digital discs, larger on the fingers, and the EN and IN measurements are in the *ornatus* range. I do not know the sex nor do I have other pertinent measurements.

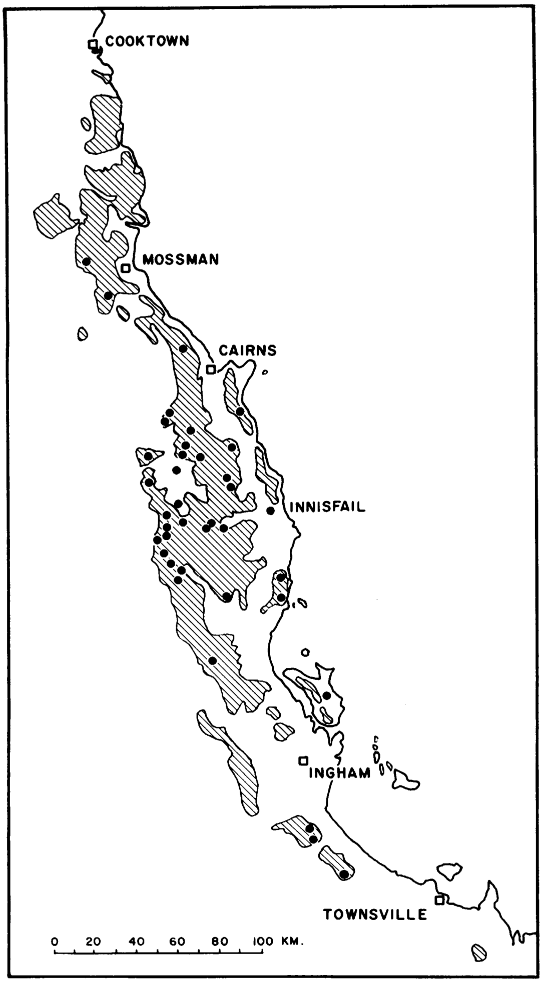

FIG. 41. Distribution of *Cophixalus ornatus*. The species probably inhabits all major areas of rainforest (shaded) between the extreme northern and southern localities plotted.

In the light of present knowledge of Papuan *Cophixalus*, the association of this specimen with a species otherwise known 800 km away across the Coral Sea is much less tenable. The characters shared with *ornatus* are common to many species of *Cophixalus* in New Guinea, including a presumably undescribed one that I have collected near Moroka and elsewhere with a call quite different from that of *ornatus*. I conclude that there is no firm evidence for the presence of *C. ornatus* in New Guinea.

DISTRIBUTION

Cophixalus ornatus is the most widely ranging species of its genus in Australia, found from Mt. Spurgeon (east of Mossman) south to the isolated blocks of rainforest in the Mt. Spec–Paluma region (northwest of Townsville), and from the coast in the vicinity of Tully and Innisfail to the western edge of the Atherton Tableland (fig. 41). It occupies the whole range of elevations available in north Queensland, from virtually sea level near South Mission Beach to the summit of Mt. Bellenden Ker at 1520 m, and is the only Australian microhylid yet found on a coastal island (Hinchinbrook). The absence of the species from collections made on the Mt. Windsor Tableland and on Thornton Peak suggests that Mt. Spurgeon may approximate the true northern range limit. The past distribution in coastal lowlands now cleared of rainforest is quite unknown. At present it is known only from several collections made in the area of Mission Beach and South Mission Beach, and from a specimen found "in a patch of rainforest within the town limits of Innisfail" in 1960 (Dr. Daniel Wilhoft, personal commun.).

LOCALITY RECORDS AND SPECIMENS EXAMINED: All localities are in Queensland: Mt. Spurgeon (MCZ 18374); Mt. Lewis (AMNH 111417–111419; AM R87977; QM J27307, J27320, J39145; QNPWS N14303, N14359, N14360); Black Mountain Road, 1 km E, 3 km N Kuranda, 350 m (AMNH 111416); Black Mountain Road, Kuranda (QM J28748); Kuranda (AM R64822, R64823; FMNH 29033; MCZ 4257–4259); Kuranda State Forest (AM R64822, R64823); 25 miles [40 km] inland from Cairns (AM R222, holotype); Cairns (AM R30296–30298); Cairns District (AM R62655–62657); Tinaroo Creek (SAMA 12317–12321); 35 km SE Mareeba on Tinaroo Creek Road (AM R53879–53811); 7 km N, 4 km E Tinaroo Dam, 1080 m (AMNH 111420–111422); 1–7 km N Tinaroo Lake Road on Forest Road B (AM R87952–87970); Severin Boar Pocket, ca. 13 km E, 1 km S Tinaroo Dam (QNPWS A28 + 1 untagged); South Bell Peak, Melbourn Thompson Range, 860 m (QNPWS N28743, N28744); Baldy Mountain Road, SW of Atherton (QM J39150, J39152, J39153, J39155, J39158); Lake Barrine (AM R29514–29516); Lake Eacham, 760 m (QNPWS N14278, N14279, N14288); Gadgarra State Forest (QNPWS, 10 uncatalogued); Mt. Bellenden Ker, Centre Peak, 1520 m (QNPWS N28767); Malanda (MCZ 17805, syntype of *Phrynixalus reginae*); just before Crater National Park on road from Atherton (QM J29527); Mt. Hypipamee (The Crater) (AM R18297, R18298; QNPWS A287, N14294 + 4 untagged); Longland's Gap, 4 km S, 1 km E of The Crater (QNPWS A443, A444); Boonjee, 6.5 km ESE Lamin's Hill, 650 m (QNPWS N14066, N14067); Russell River (Fry, 1912, p. 93); Mt. Bartle Frere, ca. 1000 m (AM R94434); Mt. Bartle Frere, 1280 m (AMNH 67400); Millaa Millaa, 850 m (AMNH 111414; MCZ 18366, 18367); Millaa Millaa Falls, 850 m (AMNH 111413); 2.5 km NW Palmerston Highway via Theresa Creek Road (AM R87975); Mt. Fischer, 1220 m (QM J31184, J31185, J31252–31258, J31260–31270; QNPWS N28187–28190); Massey Creek, Palmerston Highway (AM R87974); 8.4 km toward Millaa Millaa from turnoff to Atherton on Ravenshoe Road (QM J29677–29679, J29685); Maalan State Forest (QM J31145–31156); 12.5 km S, 13 km E Millaa Millaa, 460 m (AMNH 111415); Henrietta Creek, Palmerston National Park (QNPWS N14240–14242, N14249–14251, N14253, N14254); Palmerston National Park, Forestry camp area 904 (AMNH 111450); Palmerston National Park Headquarters (QNPWS N28733–28735); Palmerston Highway (no specific locality, QM J32062); Palmerston Highway, 34 km W Innisfail (QM J29725–29727); Charmillan Creek, 11.6 km S Kennedy Highway, Tully Falls Road (AM R94444–94447; QM J34427–34432); Vine Creek, ca. 8 km SE Ravenshoe (AM R10964, R96331–96342; FMNH 97088 [42 specimens], 82971–82973; MCZ 18368–18370); N side Major's Mountain, 4.5 km E, 3 km S Ravenshoe, 950 m (AMNH 111409–111412; QM J31061, J31065, J31086–31090, J31104, J31106, J31111, J31121–31127, J31129, J31130; QNPWS N28132, N28133, N28148–28150, N28162, N28172, N28173); 20.5 and 21.1 km S Kennedy Highway at Ravenshoe on Tully Falls Road (AM R87971–87973); Tully Falls area (QM J32118); 6 km N Koombaloomba Township (AMNH 65449); Koombaloomba Creek, 48 km SE Ravenshoe (AMNH 65437–65448); Innisfail (MVZ 77566); Dingo Pocket Road, 2 km N, 11 km W Tully (QNPWS N28796, N28797); Lacey's Creek, 4 km W, 2 km N Mission Beach (AMNH 85273–85291; QM J24813; QNPWS N14127); 16 km ENE Tully, about 3 km N of Tully–South Mission Beach Road (DU 10260, 10261); 2.5 km W, 3 km N South Mission Beach, 0.2 km N Stony Creek Bridge, <20 m (AMNH 111423, 111424; AM R87949–87951); South Mission Beach (DU 10247–10250); Smoko Creek at Kirrima State Forest Road (AM R87945–87948); Kirrima Range, via Kennedy, 700 m (QM J39162–39165); Mt. Bowen, Hinchinbrook Island (QM J26118); Birthday Falls, NE of Paluma (DU 10403–10407); Paluma (QM J26306, J26545–26549, J29669, J32063, J32070, J32154; QNPWS N14216–14222, N14224; DU 10018–10020); Paluma Ridge (MCZ 28408); Paluma Dam Road (QNPWS N14236, N14237); 3 km W Paluma, 880 m (AMNH 111406–111408); 3 km E, 8 km S Mt. Halifax, Paluma Range (K. McDonald, *in litt.*); 1 km E, 11 km S Mt. Halifax, Paluma Range (K. McDonald, *in litt.*).

Cophixalus peninsularis, new species

Figure 42

HOLOTYPE: QM J42061 (formerly QNPWS N14709), collected by J. W. Winter and R. G. Atherton at Rocky Scrub, 29 km northeast of Coen (13°44′30″, 143°21′30″), elevation 520 to 540 m, Cape York Peninsula, Queensland, on May 18, 1978.

PARATYPE: QM J42062 (formerly QNPWS N14710) with the same data as the holotype.

ETYMOLOGY: The specific name is chosen in reference to the species' occurrence on the Cape York Peninsula.

DIAGNOSIS: The following combination of characters distinguishes *Cophixalus peninsularis* from its Australian congeners: body size moderate, adult males 17–18 mm SV, females unknown; EN/IN low, less than 0.7; finger and toe discs moderately enlarged, discs on third finger and fourth toe equally broad. The call is a series of clicks, but has not been recorded and analyzed. The low EN/IN value is shared with only a few individuals of two

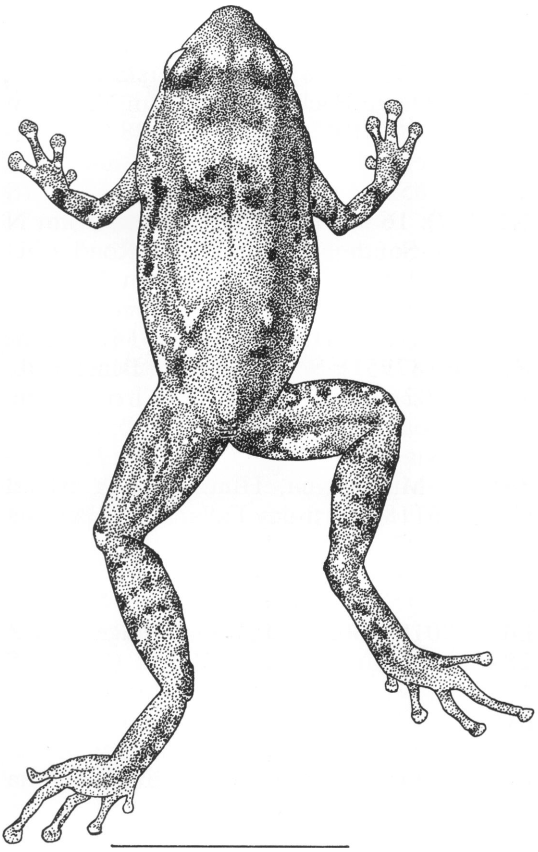

FIG. 42. *Cophixalus peninsularis,* QM J42061 (holotype); scale line spans 10 mm.

other species of *Cophixalus* in Australia; see the following section on comparisons.

DESCRIPTION OF HOLOTYPE: Adult male (calling when captured) with the following measurements and proportions: SV 18.1, TL 7.6, HW 7.2, EYE 2.5, EN 1.2, IN 1.8, third finger disc 0.8 (penultimate phalange 0.4), fourth toe disc 0.8 (0.45), HAND 3.6, FOOT 7.3; TL/SV 0.419, HW/SV 0.398, EYE/SV 0.138, EN/IN 0.667, EN/SV 0.066, IN/SV 0.099, third finger disc/SV 0.044, fourth toe disc/SV 0.044, HAND/SV 0.199, FOOT/SV 0.403.

Head scarcely narrower than body, legs moderate in length. Snout bluntly pointed seen from above, sharply rounded and projecting in profile; canthus rostralis rounded, loreal region vertical, flat; nostrils lateral, closer to tip of snout than to eye, internarial distance greater than eye-naris distance. Eye moderately large, lateral, slightly longer than snout; corneal outline projects beyond lower jaw margin; interorbital distance greater than width of upper eyelid. Relative lengths of fingers 3>4>2>1, first very short, much less than half length of second, but tip slightly flattened and disclike; second to fourth fingers with well-developed grooved discs, that of the third twice width of penultimate phalange and equal in width to disc of fourth toe; subarticular and metacarpal elevations scarcely evident. Toes unwebbed, relative lengths 4>3>5>2>1, first less than half length of second with slightly expanded disc; second to fifth toes with grooved, expanded discs, that of fourth almost twice width of penultimate phalange; subarticular tubercles low, rounded, inconspicuous; inner metatarsal tubercle elongate, similarly inconspicuous; no outer metatarsal elevation. Skin of dorsal and ventral surfaces smooth except for slight trace of scapular and postocular folds.

The dorsal ground color is brown, with the eyelids, snout, and side of the face darker brown and light flecks below the eye. There are indistinct dark brown markings in the scapular region and on the side of the body posterior to the arm, and a faint lumbar ocellus. The dorsal surfaces of the hind legs are brown with ill-defined darker spots and narrow crossbars. The groin region is mottled and the anterior surface of the thigh dark brown with conspicuous light spots. The underside of the thigh is pigmented much like the anterior surface, whereas the posterior of the thigh and underside of the shank bear equally contrasting but less regular markings. The chin and chest are dark brown with small, irregular light spots. The abdomen is much paler but similarly patterned.

VARIATION IN THE TYPE SERIES: With the species represented by only two adult male specimens, little can be said of variation. The paratype has the following measurements and proportions: SV 17.3, TL 6.9, HW 6.6, EYE 2.4, EN 1.2, IN 1.8, third finger disc 0.8 (penultimate phalange 0.5), fourth toe disc 0.8 (0.45), HAND 3.25, FOOT 6.3; TL/SV 0.399, HW/SV 0.381, EYE/SV 0.139, EN/IN 0.667, EN/SV 0.069, IN/SV 0.104, third finger disc/SV 0.046, fourth toe disc/SV 0.046, HAND/SV 0.188, foot/SV 0.364.

The paratype is much like the holotype in color and pattern. The abdomen is darker in the paratype, so there is less contrast between the chin and belly regions, and light spotting on the thighs and lower legs is less conspicuous.

Comparisons with Other Species

Cophixalus peninsularis is known to be sympatric with only one other *Cophixalus*—*C. crepitans.* The latter is a much smaller species, the maximum size among 17 adult males being only 14 mm SV, and also differs in its much longer hind legs—minimum TL/SV 0.466 compared to a maximum of 0.419 in *peninsularis.* The two largest *crepitans,* about 14 mm SV, have longer legs than the smaller of the two *peninsularis* at 17.3 mm SV.

Among allopatric *Cophixalus* there is none with which *peninsularis* can easily be confused. The EN/IN ratio of *peninsularis* (unusually low because of its widely spaced nostrils) is lower than recorded for adults of any Australian *Cophixalus* except *neglectus* and *crepitans.* In having well-developed discs of approximately equal size on fingers and toes, *peninsularis* differs from the smaller species *infacetus, bombiens, hosmeri,* and *exiguus.* Broader finger discs distinguish *ornatus* and *saxatilis* as does their larger size, except for the lowland population of *ornatus. Cophixalus neglectus* differs from *C. peninsularis* in many ways, among which are its larger size, short hind legs, and small finger discs. *Cophixalus concinnus* and *C. peninsularis* are much alike in size, development of digital discs, and leg length. The much lower EN/IN value of *peninsularis* (maximum 0.667) should distinguish it from *concinnus* (minimum 0.757). The morphological relationship of *C. mcdonaldi* to *C. peninsularis* parallels that of *concinnus* to *peninsularis.* In addition, *peninsularis* differs from these two species in having smaller hands.

Habitat and Habits

The types were taken at the same time and place as *Cophixalus crepitans*; see the account of that species for the habitat. The collectors' notes record that the frogs were found on low vegetation by the edge of a creek.

Call

No recording has been made. The collectors noted "similar call to other 2.5 second clicking microhylids [*C. crepitans*], except it is deeper in tone."

Remarks

Although I am not entirely comfortable describing this species from only two specimens, neither of them in the best of condition, I think it best to bring it to light in the context of this monograph rather than await the possible acquisition of more and better material. The diagnostic features noted are likely to stand up, and the fact that the collectors observed the call to differ from that of the sympatric species is significant.

Distribution

Cophixalus peninsularis is known only from the type locality in the McIlwraith Range northeast of Coen on the eastern side of the Cape York Peninsula (fig. 27).

Cophixalus saxatilis Zweifel and Parker
Figure 43

Cophixalus saxatilis Zweifel and Parker, 1977, p. 2 (type locality, "Black Mountain, 13 miles south and 2 miles west of Cooktown, Queensland, Australia"; holotype, MCZ 90205, collected by Fred Parker on February 22, 1971).

Type Locality: On the Helenvale Quadrangle, sheet 7966 of the 1:100,000 series of Australian topographic maps, the name Black Mountain is associated with a peak at grid coordinates 097199. The type locality is on the western slope of a peak 2 km north of Black Mountain, east-southeast (across Black Gap) of Mt. Simon (fig. 44; also Zweifel and Parker, 1977, fig. 7).

Diagnosis: *Cophixalus saxatilis* differs from all other Australian congeners in its combination of large size (adult males 29–35 mm SV, females 39–46 mm) and truncate digital discs with the third finger disc larger than that on the fourth toe.

Description

Morphology: In a sample of eight females dissected, one at 26.9 mm SV appears to be

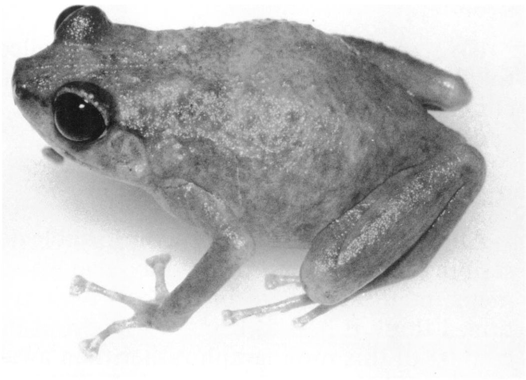

FIG. 43. *Cophixalus saxatilis,* AMNH 111428, Black Gap; adult female, SV 46.5 mm.

immature, whereas seven ranging from 39.2 to 46.5 mm are mature. Seven males 29.5 to 34.9 mm SV are mature—the largest was calling when captured, and the others have vocal slits. The minimum sizes at maturity are not established for either males or females.

Head narrower than body. Snout bluntly rounded, almost truncate seen from above, vertical and slightly rounded in profile; canthus rounded; loreal region steeply sloping, flat to shallowly concave; nostrils much closer to tip of snout than to eye, internarial distance greater than eye-naris distance. Eyes large, corneal outline visible, but not broadly so, from beneath; interorbital distance greater than width of upper eyelid. Tympanum obscure, its diameter less than half that of eye. Relative lengths of fingers 3>4>2>1, the first at least half that of the second; all fingers with enlarged, truncate discs with terminal grooves, disc of first finger much the smallest; subarticular tubercles rounded, moderately prominent; low, rounded inner and outer metacarpal elevations present. Relative lengths of toes 4>3>5>2>1, the first equal to or greater than half that of the second; all toes with enlarged, truncate discs with terminal grooves, disc on fifth toe smallest; discs smaller than those on fingers; subarticular tubercles rounded, moderately prominent; a low, elongate inner metatarsal tubercle but no outer. Preserved specimens smooth dorsally and ventrally, but slight wartiness evident in life (fig. 43).

COLOR AND PATTERN: Preserved adult specimens are pale yellowish tan to light brown with dark markings obscure to virtually absent. The side of the head is generally darker than the top but does not give a distinct face-mask effect, and dark pigment in this region may be concentrated in a canthal line. Some specimens show a white line along the edge of the upper eyelid and there may be a dark postorbital streak. A scapular W-shaped mark may be dimly indicated. Ventral surfaces are pale, virtually unmarked or with the chin dusted with brown, more concentrated around the jaw margin and speckled with white. Juveniles tend to be more heavily marked dorsally, with distinct lumbar ocelli (see Zweifel and Parker, 1977, fig. 4).

Living frogs seen at night were conspicuous for their pale yellow dorsal color and black eyes. The palest individuals are yellow with virtually no pattern and an orange wash in the groin and on the posterior of the thighs (fig. 43). In a darker phase the dorsum is greenish gray with darker gray mottling, a faint scapular W-mark, and indistinct lumbar ocellus. Canthal and postorbital dark markings are evident. The throat is yellow, sometimes with gray mottling. The abdomen may be nearly unpigmented, with the liver showing as a dark shadow, or may be pale yellow. The undersides of the hind legs are yellow to pale orange. The iris is black with sparse silver speckles. The margins of upper and lower eyelids are pale, almost white.

VARIATION IN PROPORTIONS: Proportions of adults are summarized in tables 9–11. In view of the restricted range of *saxatilis,* nothing can be said of geographic variation.

Cophixalus saxatilis is by far the longest legged of the larger Australian *Cophixalus,* and is comparable only to *ornatus* in its relatively large hands and finger discs. Regression coefficients for tibia length and foot length are greater than 0.9, and for hand length and third finger disc width are greater than 1.0. This indicates that these measurements increase in approximately a 1:1 ratio with body size or even increase relatively greater than body size, in contrast to most Australian *Cophixalus* in which the relative proportions decrease significantly with growth. The features involved—leg length, foot and hand size, disc size—are all concerned with locomotion

FIG. 44. Habitat of *Cophixalus saxatilis* at Black Gap.

and undoubtedly reflect the jumping and scansorial abilities these frogs demonstrate so well.

COMPARISONS WITH OTHER SPECIES

No other microhylid is sympatric with *Cophixalus saxatilis,* so far as is known. Only *C. ornatus* among allopatric species has similar finger and toe discs and approaches the minimum adult size of *saxatilis.* See the diagnosis of *ornatus* for comparisons.

HABITAT AND HABITS

The habitat of *Cophixalus saxatilis* is unique for Australasian microhylids (Anon., 1974; Zweifel and Parker, 1977). The Black Trevethan Range is composed of a jumble of granite boulders and in the vicinity of the type locality rises from a base level of about 90 m to a little over 425 m on Black Mountain. The range has a northwest-southeast trend over a distance of about 7 km, and is essentially a spur projecting from uplands associated with Big Tableland on the southeast. Black lichen coats the exposed surfaces of the boulders, many of which are as large as 10 m in diameter. This gigantic rock pile offers almost no foothold for other vegetation, so except for occasional trees the slopes are barren (fig. 44; see also Anon., 1974, fig. 1; Zweifel and Parker, 1977, fig. 10). The size of the boulders is such that their interstices provide a mazelike complex of passageways into the mountain large enough for a person to enter and follow, with difficulty, for varying distances. Access for smaller animals is virtually infinite. Humidity at the time of our visit in January was oppressively high and probably remains so the year round, at least deep within the jumble.

Vegetation within Black Gap and surrounding the range is mapped as medium and low woodlands (Tracey and Webb, 1975). About 5 km to the southeast, rainforest vegetation (mesophyll vine forest) occurs.

When William Hosmer, Keith McDonald, and I visited Black Gap in partly sunny weather on January 22, we could hear numerous *C. saxatilis* calling from deep within

TABLE 19
Call Statistics for *Cophixalus saxatilis*

Museum Number	Tape No.	SV, mm	Temp., °C	Call Duration, sec Mean (Range)	Pulses per Call Mean (Range)	Pulses per sec Mean (Range)	Frequency, Hz	Number of Calls
AMNH 111425[a]	229	34.9	25.6	2.97 (2.87–3.05)	25.4 (25–26)	8.24 (8.0–8.4)	1300	10
No spec.[a]	239	—	—	2.26 (2.08–2.38)	17.7 (14–20)	7.14 (6.2–7.7)	1500	10[c]
No spec.[b]	248	—	—	3.17 (2.55–3.48)	22.1 (18–24)	6.67 (6.4–6.9)	—	11

[a] Black Gap.
[b] Black Mtn.
[c] N = 15 for notes per call.

the jumble. Returning that night, we found the number of frogs calling greatly diminished, suggesting that their calling activity is somewhat keyed to "twilight" conditions deep within the crevices during daylight hours. The frogs are active at night, however, and can be found in crevices or more exposed on boulders or on trees or fallen logs beside a stream. The frog I tape recorded was calling at night from deep within a horizontal crevice not much higher than the frog's body.

Cophixalus saxatilis is not the only species unique to the Black Trevethan Range: a gecko, *Nactus galgajuga* (Ingram, 1978) and a skink, *Carlia scirtetis* Ingram and Covacevich (1980) are also known only from there. The only species of frog other than *C. saxatilis* as yet found within the boulder habitat is *Litoria genimaculata* (*L. serrata sensu* Cogger et al., 1983), which William Hosmer (personal commun.) has collected along a small stream. We found the snakes *Boiga irregularis* and *Liasis childreni,* both potential predators on *saxatilis,* within the boulder area.

CALL

The call of *Cophixalus saxatilis* is a series of clicks uttered over a period of about 2 to 3 seconds (fig. 65D, table 19). Among three individuals recorded the mean number of clicks per call ranges from about 18 to 25 and the mean number of clicks per second from 6.67 to 8.24. Each pulse (click) extends on the audiospectrogram over a broad range of frequencies, as a white noise click should, though there is evidence of a concentration of energy in the region of 1300–1500 Hz. One frog called at the mean rate of one call started every 8.3 seconds (range 5–18) over a period of about 2 minutes. This appeared to be a steady-state rate that was established after the frog had been disturbed and then resumed calling at a lesser rate, giving calls shorter than average. Data are not adequate to determine any influence of body size or temperature on the call.

REMARKS

Almost nothing is known of the natural history of *Cophixalus saxatilis.* Anyone who wishes to study the species should go prepared as for caving, in order safely to follow the animals down into the labyrinth of the Black Trevethan Range.

It would be of interest to determine the extent of the species' geographic range, especially to the southeast where the Black Trevethan Range merges into the rainforested Big Tableland. Two microhylids—*Cophixalus exiguus* and *Sphenophryne fryi*—occur there.

DISTRIBUTION

All records for this species are in the immediate vicinity of Black Gap, where the Cooktown Road passes through the Black Trevethan Range about 22 km south and 3.5 km west of Cooktown (fig. 25).

LOCALITY RECORDS AND SPECIMENS EXAMINED: All localities are in Queensland: Black Mountain (AMNH 88238–88240; MCZ 87514, 87515 [foregoing are paratypes], 90205 [holotype]; AM R53981, R53982 [paratypes]; Black Gap (AMNH 111425–111430; AM R97586, R97587; QNPWS N28773, N28774); 20 km S Cooktown (QM J27150).

MORPHOLOGY

OSTEOLOGY

I have examined osteological features that seemed to hold promise for elucidating systematic relationships. The material available is inadequate for investigating variation, and this should be kept in mind even where not specifically mentioned in the discussions. I have examined adult specimens cleared and stained for cartilage and bone of each of the following species (except where indicated, there was only one specimen): *Cophixalus bombiens, C. concinnus, C. crepitans, C. hosmeri, C. infacetus, C. mcdonaldi, C. neglectus, C. ornatus* (2 highland, 1 lowland), *C. saxatilis*; *Sphenophryne fryi* (1 additional pectoral girdle examined), *S. gracilipes* (specimen from Papua New Guinea), *S. pluvialis* (1 additional pectoral girdle examined), *S. robusta.* A specimen of *C. exiguus* is stained for bone only. *Cophixalus peninsularis* and *Sphenophryne adelphe* were unrepresented in this study, although some years before I examined a cleared and stained specimen of the latter species, verifying that it has the typical *Sphenophryne* pectoral girdle.

Except for brief statements concerning the presence or absence of the clavicle (pertinent to generic diagnosis), published information on the skeletal morphology of Australian microhylids has been limited to that presented by Fry (1912) in his original report on microhylids in Australia. He gave a detailed description of the skull and pectoral girdle of "*Austrochaperina robusta.*" Unfortunately, it is uncertain whether his series of specimens included only *S. robusta* or both that species and *S. fryi* (see species account of *S. robusta*), so one cannot be sure which species he described.

I make frequent reference to Trueb's (1973) very useful summary of salientian osteology, and record instances where new information on the genyophrynine microhylids calls for revision of some of her generalizations.

SKULL

The skulls of Australian *Cophixalus* and *Sphenophryne* agree or differ only slightly in most features of their morphology (figs. 45, 46). They are toothless, with well-developed and well-ossified nasal and frontoparietal bones. The maxillae show the eleutherognathine condition typical of the Genyophryninae, with short facial processes that scarcely overlap the premaxillae. The quadratojugal articulates with the maxilla in all specimens examined. There is no dermal ornamentation of the skull such as is seen in at least one genyophrynine genus (*Genyophryne*) and in some asterophryines. The zygomatic ramus of the squamosal is variably developed, but the otic ramus is rather small and does not extend far mesially over the crista parotica. The sphenethmoid is well ossified, but the more posterior walls of the braincase are largely membranous. The otoccipital and vomerine regions are discussed separately in following paragraphs.

OTOCCIPITAL REGION: Trueb (1973, p. 88) made the categorical statement that "the prootic and exoccipital . . . are indistinguishably fused in the modern anurans." In adult *Sphenophryne* and *Cophixalus* the otoccipital region may be well ossified, but more often there is an evidently paedomorphic condition with the prootics largely cartilaginous, showing only buried centers of ossification. The exoccipital invariably is well ossified, though it does not always fuse with the frontoparietals. My specimen of *S. gracilipes* (fig. 45B) has the prootics and exoccipitals well fused, and has a heavily calcified juncture of these bones with the frontoparietals. Essentially the same condition obtains in the specimens of *S. fryi* and *S. pluvialis,* but *S. robusta* exhibits the opposite extreme (fig. 45A). In this last specimen prootic ossification centers are visible deep within the cartilaginous matrix, but dorsally the exoccipitals stand alone. This skull of *robusta* contrasts with a description and illustration by Fry (1912) that may, however, have been based on *fryi.* In my specimen of *fryi* the prootic region is thoroughly ossified, with no sutures visible between the prootics and the exoccipitals.

Variation in Australian *Cophixalus* resembles that in *Sphenophryne.* The prootics are ossified and closely associated with the exoccipitals in *C. saxatilis* (fig. 46A), *C. concinnus,* and *C. exiguus.* An intermediate condition is seen in three *C. ornatus* (fig. 46B), *C. bombiens, C. mcdonaldi,* and *C. neglec-*

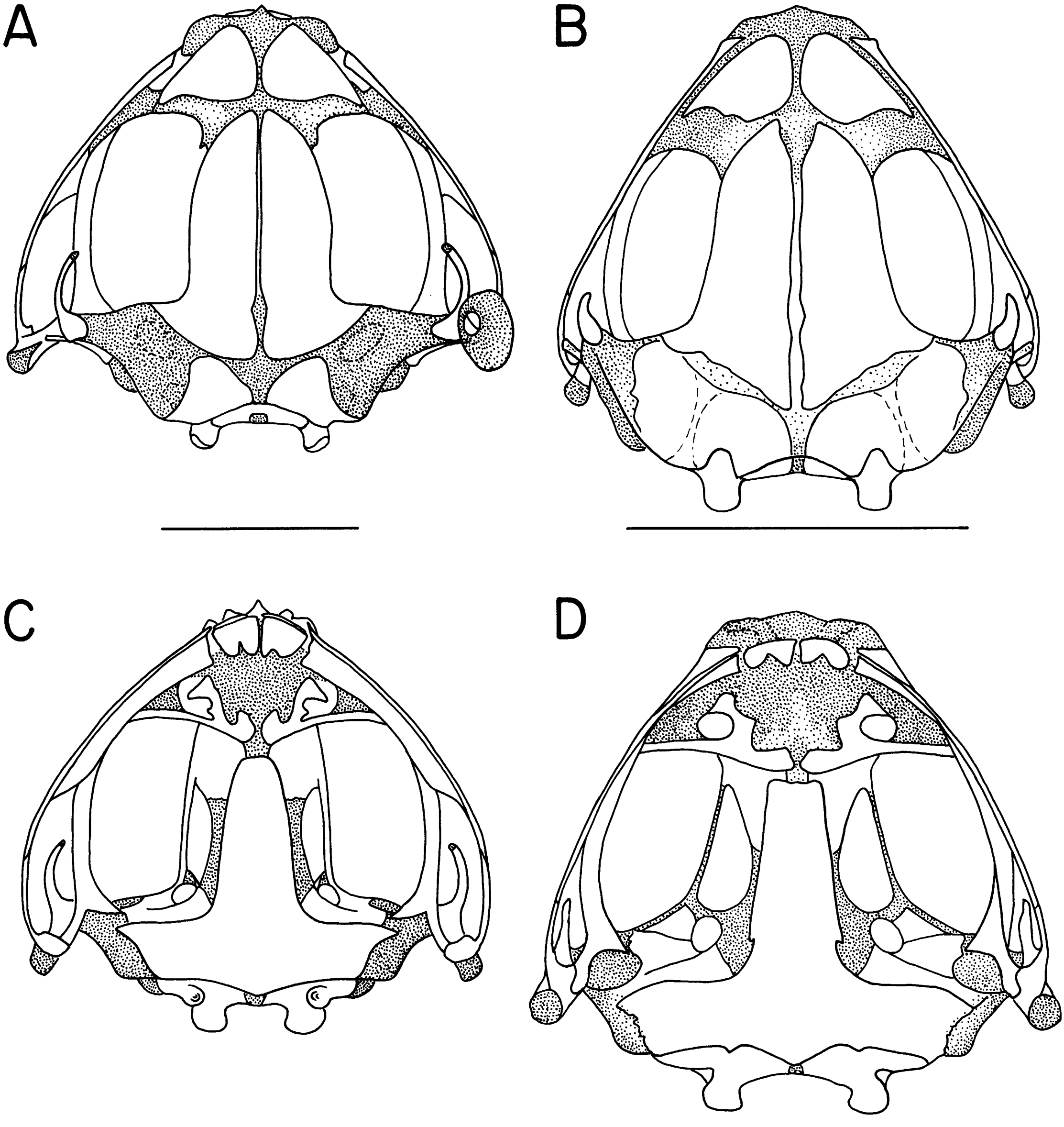

FIG. 45. Skulls of *Sphenophryne*. **A,** *S. robusta,* AMNH 111476; **B,** *S. gracilipes,* AMNH 90407; **C** and **D,** same skulls from beneath. Stippling indicates cartilage; scale lines span 4 mm.

tus, whereas *C. hosmeri* and *C. infacetus* resemble *Sphenophryne robusta* in that ossification of the prootic as seen from above is restricted to buried nubbins.

The extent to which individual variation influences the state of ossification of the otoccipital region remains to be determined, as does the extent of ontogenetic change (all specimens cited are adults). It is noteworthy that the degree of ossification does not necessarily correlate with adult size: the smallest *Sphenophryne* is well ossified, as are both large (*saxatilis*) and small (*exiguus*) *Cophixalus.* Within New Guinean species of *Cophixalus* and *Sphenophryne,* where in some instances I have several cleared and stained individuals of a species, there is individual variation among adults of similar size ex-

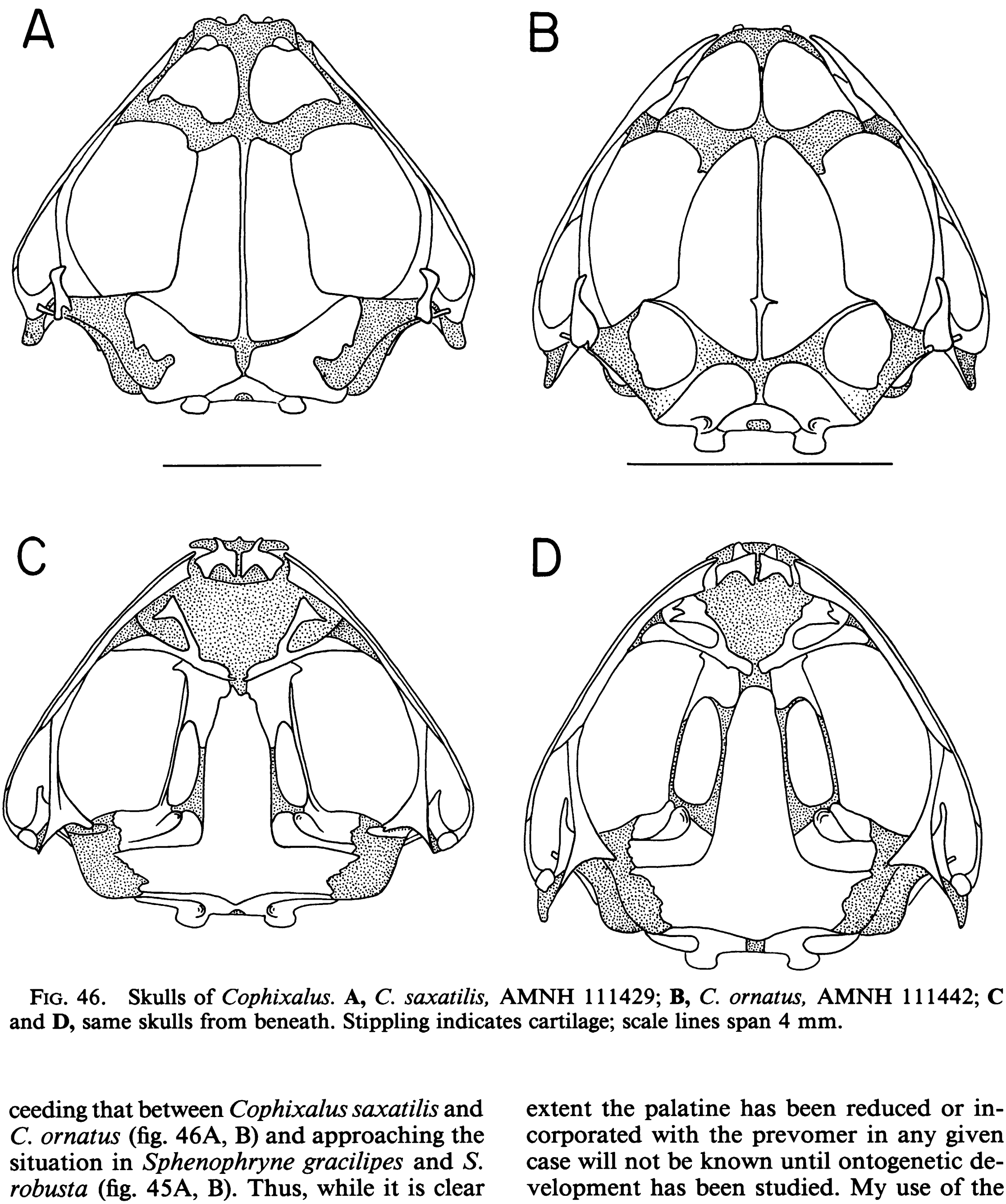

FIG. 46. Skulls of *Cophixalus*. **A,** *C. saxatilis,* AMNH 111429; **B,** *C. ornatus,* AMNH 111442; **C** and **D,** same skulls from beneath. Stippling indicates cartilage; scale lines span 4 mm.

ceeding that between *Cophixalus saxatilis* and *C. ornatus* (fig. 46A, B) and approaching the situation in *Sphenophryne gracilipes* and *S. robusta* (fig. 45A, B). Thus, while it is clear that *Cophixalus* and *Sphenophryne* tend to a paedomorphic condition of the otoccipital region, especially with respect to the lateral prootic area, seeming interspecific differences must be interpreted with caution.

PREVOMER: As Trueb pointed out (1973, p. 82), the bones of the anterior palatal region are complex in the Microhylidae, and to what extent the palatine has been reduced or incorporated with the prevomer in any given case will not be known until ontogenetic development has been studied. My use of the term prevomer is a convenience, and does not imply any knowledge of the fate of the palatine in the Australian species.

The prevomers of Australian *Cophixalus* and *Sphenophryne* are similar in general form, with a well-developed posterior transverse arm (prevomer plus palatine?) arising from a variably expanded area at the midline of the

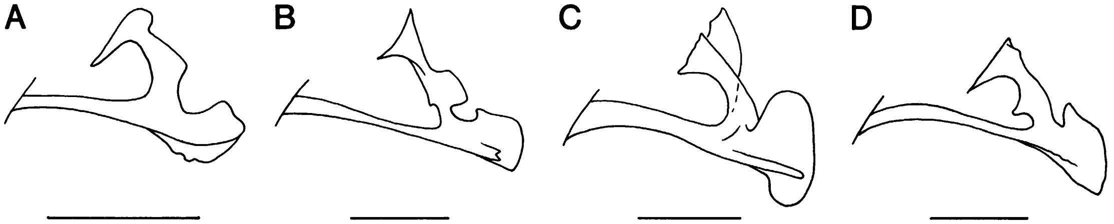

FIG. 47. Right prevomerine bones of *Sphenophryne* in ventral view. **A,** *S. gracilipes,* AMNH 90407; **B,** *S. pluvialis,* AMNH 111497; **C,** *S. fryi,* AMNH 111454; **D,** *S. robusta,* AMNH 111476. Scale lines span 1 mm.

palate, and an anterior arm that passes mesial to and then anterior to the internal naris (figs. 47, 48). Parker (1934, pp. 3–4) regarded this sort of prevomer as primitive. The part anterior to the naris is dilated and warped in various ways not readily depicted in line drawings, and slight differences in the orientation of the specimens can alter the apparent outlines. These considerations and the likelihood of individual variation lead me to attach no taxonomic significance to the variation seen in this anterior arm.

Australian *Cophixalus* and *Sphenophryne* differ in the lateral extent of the transverse arm. In *Sphenophryne* (fig. 47) this arm reaches to the maxilla, or close enough that its end is well hidden beneath the maxillary shelf. In seven of the nine *Cophixalus* the bony arm terminates short of the maxillary shelf and is joined to the maxilla by cartilage. In the remaining two *Cophixalus* the arm reaches the shelf but still is tied to the maxilla by cartilage (fig. 48). I assume that the condition in *Cophixalus* is paedomorphic.

PREMAXILLA: This bone is of interest because of its use in generic diagnoses; see the foregoing diagnosis of *Cophixalus.* In its typical condition in *Cophixalus,* seen in all Australian species except *C. concinnus,* the alary process is slender in relation to the width of the base of the bone (fig. 49A). *Cophixalus concinnus* differs in that the process is relatively broader and not so distinct basally (fig. 49B), approaching the condition in *Copiula. Sphenophryne* tends to an intermediate morphology (fig. 49C).

Another peculiarity of *Cophixalus concinnus* is the presence of toothlike serrations on the premaxilla and maxilla. My specimen of *C. exiguus* has a single such point on each premaxilla as well as some serration on the maxilla, but I can see no such structures on the remaining Australian *Cophixalus* or on *Sphenophryne.* The exact nature of the serrations is difficult to discern in these tiny frogs. They do not appear to be well-formed teeth, but whether they represent vestigial teeth (hence, a primitive character) or are a novel, apomorphic development I cannot say. Similar structures in the large Papuan species *C. riparius* appear more toothlike, leading me to favor the first explanation.

HYOID AND PECTORAL REGIONS

HYOID APPARATUS: Trewavas (1933, p. 519) considered the Microhylidae "well characterized by the structure of the hyolaryngeal apparatus" (especially if *Breviceps* and *Hemisus,* the latter now referred to the Ranidae, were excluded). Hyoids of the Australian species agree in all important particulars with the more diverse group studied by Trewavas, including thickening of the median part of the hyoid plate. A variable degree of calcification accompanies this thickening. To what extent differences among my four specimens of *Sphenophryne* reflect individual variation is unknown. The shape of the alary process shows the greatest variation (fig. 50A–D). I have examined the hyoids of 11 specimens of 9 species of Australian *Cophixalus*: *bombiens, concinnus, crepitans, hosmeri, infacetus, mcdonaldi, neglectus, ornatus* (3 specimens), and *saxatilis.* They are a much more uniform group even than *Sphenophryne*—so much so that one illustration will serve (fig. 50E). The hyoid seems to offer no features useful in diagnosing these genera and, in the near absence of information on individual

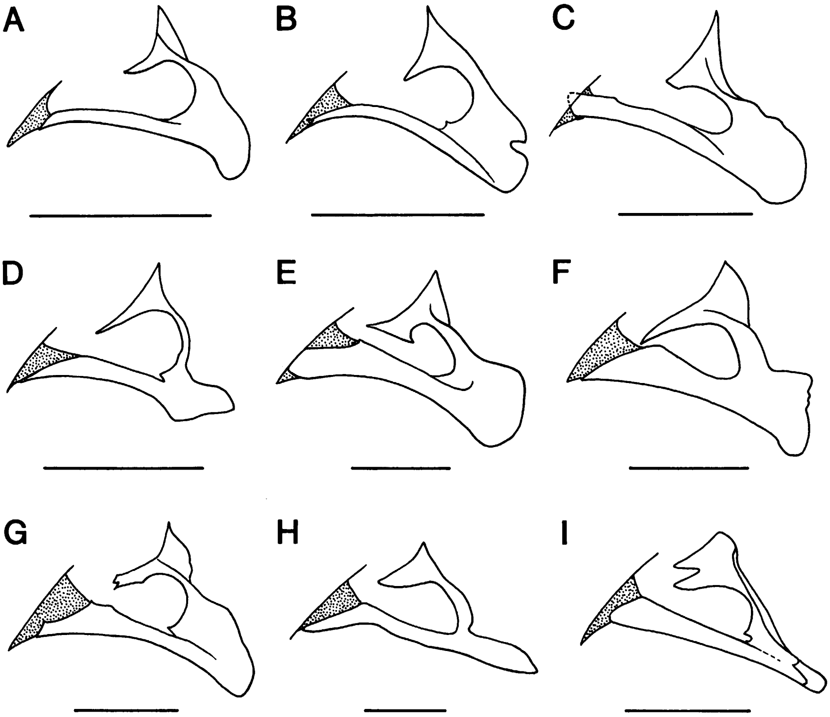

FIG. 48. Right prevomerine bones of *Cophixalus* in ventral view. **A,** *C. bombiens,* AMNH 111437; **B,** *C. hosmeri,* AMNH 111443; **C,** *C. exiguus,* AMNH 81310; **D,** *C. infacetus,* AMNH 111449; **E,** *C. concinnus,* AMNH 111386; **F,** *C. neglectus,* AMNH 111402; **G,** *C. mcdonaldi,* AMNH 111485; **H,** *C. saxatilis,* AMNH 111429; **I,** *C. ornatus,* AMNH 111422. Stippled areas indicate cartilage; diagonal line at left of each figure marks edge of maxillary shelf; scale lines span 1 mm.

variation, nothing of use on the specific level either.

PECTORAL GIRDLE: The nature of the pectoral girdle is the chief feature distinguishing *Sphenophryne* from *Cophixalus.* The former possesses a fuller (more primitive) complement of ventral elements, with procoracoids present and long, gently curved clavicles extending from the scapula almost to the midline of the girdle (fig. 51C, D). *Cophixalus* completely lacks both these elements (fig. 51A, B). The clavicle and coracoid in *Sphenophryne* and the coracoid alone in *Cophixalus* are the only true bony elements present in the ventral parts of the pectoral girdles of these genera. The sternum is cartilaginous, though the mesosternal region may be calcified. Some *Cophixalus* show a small, cartilaginous protrusion on the anterior ventral midline of the girdle, possibly a vestige of the omosternum or of the procoracoid. In two specimens of *Sphenophryne pluvialis* as well as one each of *S. fryi, S. gracilipes,* and *S. robusta,* there is a deep notch where the procoracoids meet on the midline (fig. 51D). One specimen of *S. fryi,* however, lacks such a notch (fig. 51C).

VERTEBRAL COLUMN

PRESACRAL VERTEBRAE: Trueb (1973, table 2-2) indicates that the nonimbricate condition is lacking in the Microhylidae, but all Australian *Cophixalus* and *Sphenophryne* examined (14 species, 16 specimens) have nonimbricate vertebrae with gaps dorsally between the zygapophyseal articulations that approximate those illustrated by Trueb (1973, fig. 2-10a) for the "hypothetical primitive . . . nonimbricate" condition. The same situation obtains in several New Guinean *Cophixalus* and *Sphenophryne,* whereas among astero-

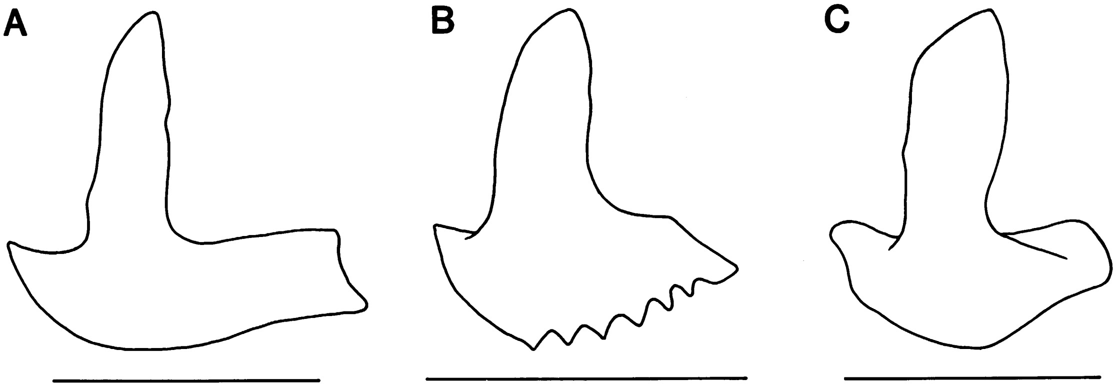

FIG. 49. Left premaxillae of *Cophixalus* and *Sphenophryne* in anterior view. **A,** *C. saxatilis,* AMNH 111429; **B,** *C. concinnus,* AMNH 111386; **C,** *S. robusta,* AMNH 111476. Scale lines span 1 mm.

phryine genera there are both strongly imbricate and nonimbricate species. Specimens of three genera of microhylids from outside the Australo-Papuan region—*Gastrophryne, Kalophrynus,* and *Kaloula*—have imbricate vertebrae.

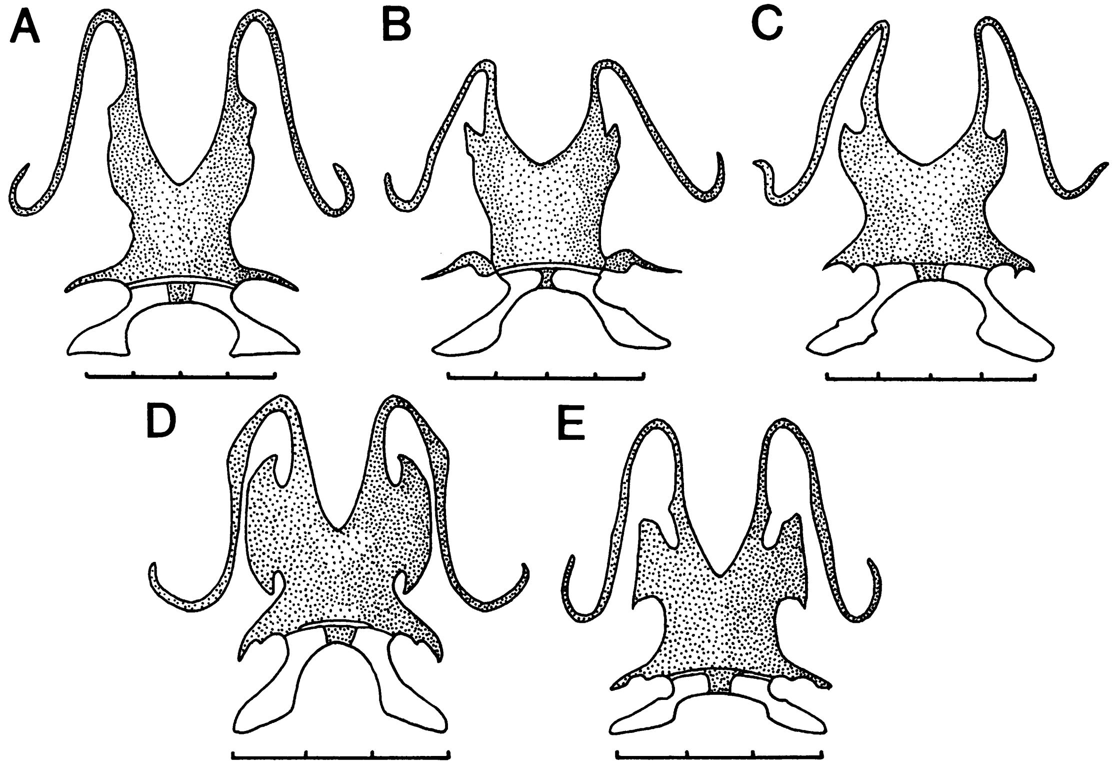

FIG. 50. Hyoids of *Sphenophryne* and *Cophixalus* in ventral view. **A,** *S. robusta,* AMNH 111476; **B,** *S. fryi,* AMNH 111454; **C,** *S. pluvialis,* AMNH 111497; **D,** *S. gracilipes,* AMNH 90407; **E,** *C. ornatus,* AMNH 111450. Stippling indicates cartilage, lightly stippled areas in A–D show calcification. Proportions of bony posteromedial processes, which pass into the plane of the drawing, are distorted by foreshortening. Scale lines marked in mm.

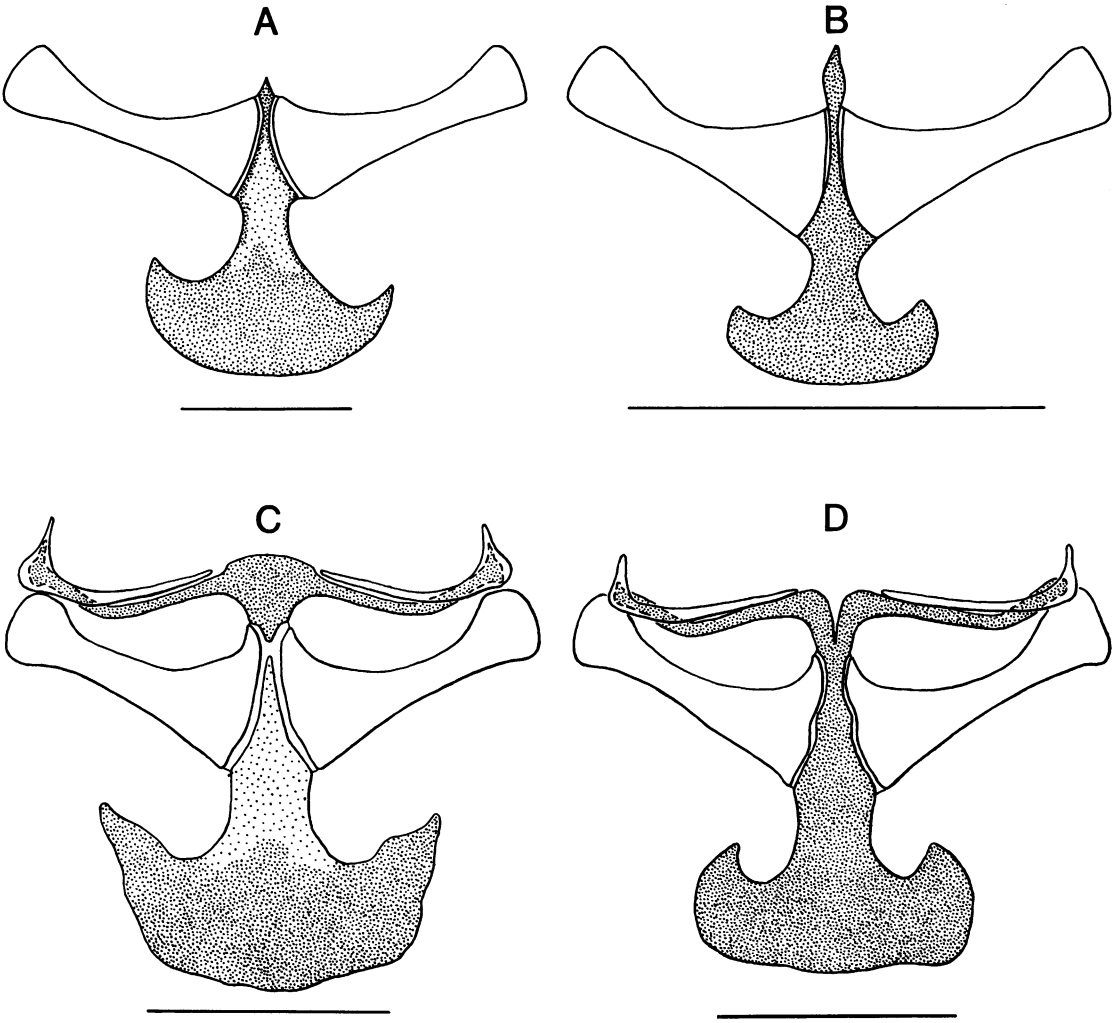

FIG. 51. Ventral elements of pectoral girdles of *Cophixalus* and *Sphenophryne*. **A,** *C. saxatilis,* AMNH 111429; **B,** *C. hosmeri,* AMNH 111443; **C,** *S. fryi,* AM R87921; **D,** *S. pluvialis,* AM R58279. Dense stippling indicates cartilage, sparse stippling calcified cartilage, clear areas bone. Scale lines span 3 mm.

Vertebrae 2 through 8 bear transverse processes with proportions similar to those illustrated by Trueb (1973, fig. 10-2b). The processes of vertebra 3 have the widest span, closely approached by vertebrae 2 and 4, with the more posterior vertebral processes being both shorter and more slender. The ratio of the span on vertebra 3 to that on vertebra 8 ranges from 1.27 in *C. neglectus* (posterior span relatively great) to 1.79 in *C. hosmeri.* The Australian *Sphenophryne* fall within this range too, as do most of the New Guinean *Cophixalus* and *Sphenophryne* examined.

The angle at which the posterior transverse processes project from the vertebral column varies greatly, ranging from 90° in *C. neglectus* (fig. 52E) to 54° (angled sharply forward, fig. 52A) in *S. gracilipes.* Australian *Cophixalus* and *Sphenophryne* appear to differ in this character, with *Sphenophryne* ranging from 54 to 69° (four species) and *Cophixalus* from 68 to 90°. The situation in New Guin-

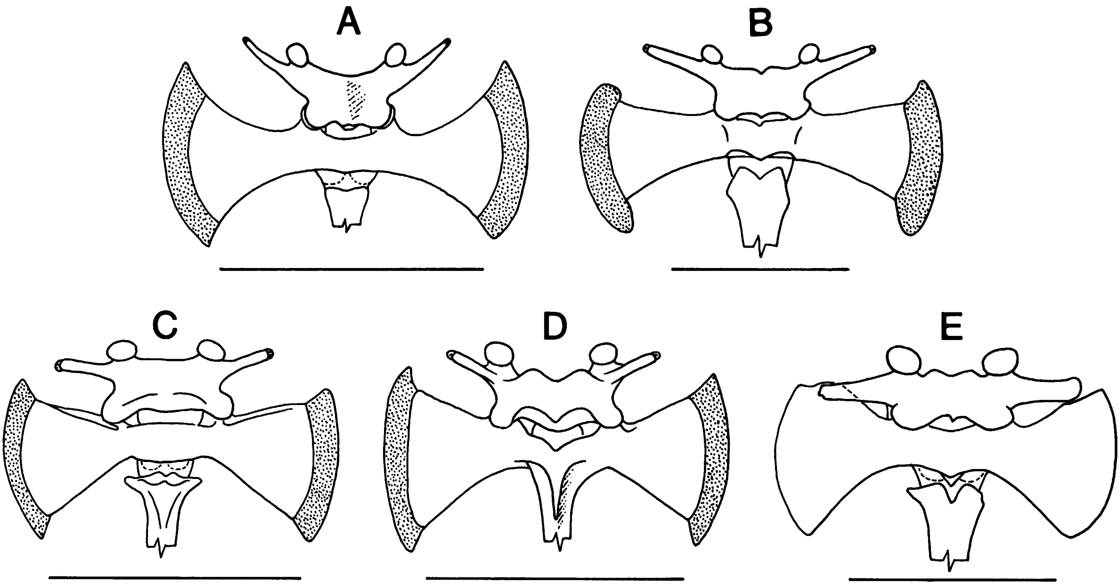

FIG. 52. Bones of sacral region of *Sphenophryne* and *Cophixalus* in dorsal view: vertebra 8, vertebra 9 (sacral), and base of coccyx. **A,** *S. gracilipes,* AMNH 90407; **B,** *S. robusta,* AMNH 111476; **C,** *C. ornatus,* AMNH 85091 (lowland population); **D,** *C. ornatus,* AMNH 111450 (highland population); **E,** *C. neglectus,* AMNH 111402. Stippling indicates cartilage, not stained well enough on E to be delimited. Scale lines span 3 mm.

ean specimens of these genera is similar, with the break at about 70°. This statement excludes, however, specimens of the distinctive *Cophixalus variegatus* group, which have angles more like those of *Sphenophryne.* In view of the notorious variability of vertebral characters, too much emphasis should not be placed on these apparent generic differences, but the character will merit attention when a more comprehensive survey of the extra-Australian species can be made.

SACRAL VERTEBRAE: The sacral diapophyses of *Cophixalus* and *Sphenophryne* are moderately expanded (fig. 52). Expressed as the ratio of greatest expansion (parallel to the vertebral axis) to the distance from vertebral axis to tip, figures range from 0.631 to 0.809 in *Sphenophryne* and from 0.644 to 0.911 in *Cophixalus.* Thus, there is broad overlap between the generic ranges. Almost certainly there are consistent differences between species, but the significance of similarities and differences is questionable. For example, the two species with relatively most expanded

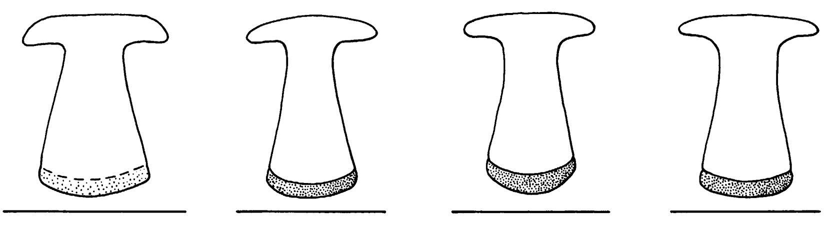

FIG. 53. Terminal phalanges of third fingers of *Sphenophryne.* **A,** *S. gracilipes,* AMNH 90407; **B,** *S. fryi,* AMNH 111454; **C,** *S. pluvialis,* AMNH 111497; **D,** *S. robusta,* AMNH 111476. Stippled areas indicate cartilage; scale lines span 0.3 mm.

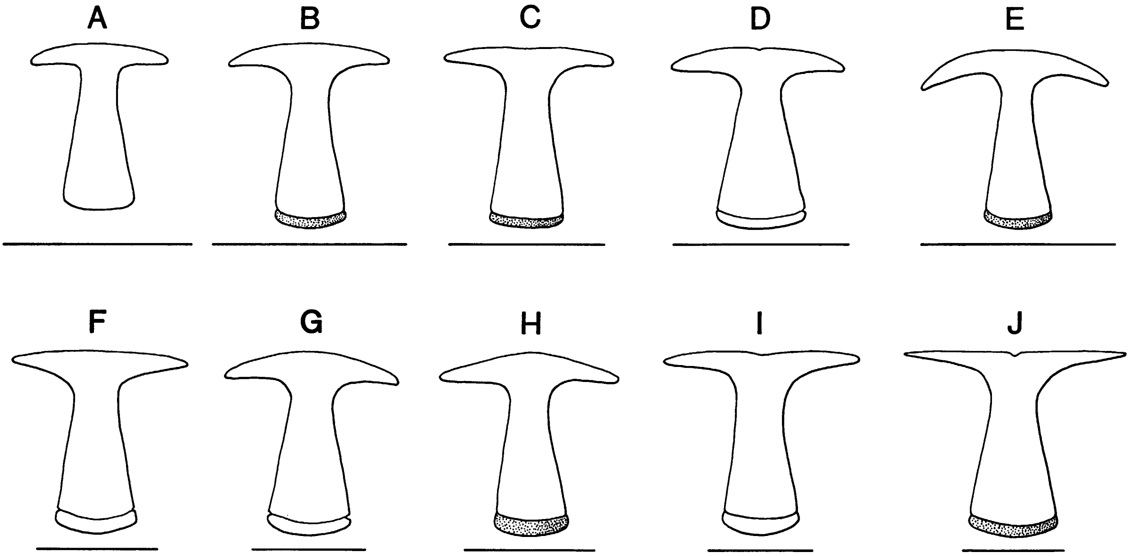

FIG. 54. Terminal phalanges of third fingers of *Cophixalus*. **A,** *C. bombiens*, AMNH 111437; **B,** *C. hosmeri*, AMNH 111443; **C,** *C. exiguus*, AMNH 81310; **D,** *C. infacetus*, AMNH 111449; **E,** *C. crepitans*, AMNH 116917; **F,** *C. concinnus*, AMNH 111386; **G,** *C. mcdonaldi*, AMNH 111485; **H,** *C. neglectus*, AMNH 111402; **I,** *C. saxatilis*, AMNH 111429; **J,** *C. ornatus*, AMNH 111422. Stippled areas indicate cartilage; scale lines span 0.3 mm.

diapophyses, *C. saxatilis* (0.911) and *C. neglectus* (0.909), differ markedly in habits and in other aspects of their morphology.

A specimen of the lowland population of *Cophixalus ornatus* (AMNH 85287) examined by X-ray photography has a normally expanded sacral diapophysis on the right side and a narrow diapophysis characteristic of more anterior vertebrae on the left. A supernumerary (tenth) vertebra has a typical sacral diapophysis on the left and a nubbin on the right. This is the only such gross anomaly noted among 45 skeletons of *ornatus* (42 seen in X-ray).

COCCYX: Trueb (1973, table 2-2) indicated that coccygeal transverse processes are not found in the Microhylidae and stated (1973, p. 107) that they "seem to be absent among more advanced families." Similar to the case with the nonimbricate presacral vertebrae, *Cophixalus* and some *Sphenophryne* exhibit a more primitive condition. All species of Australian *Cophixalus* of which I have skeletal specimens (12 specimens of 10 species, 1 species unrepresented) show at least slight development of vestigial transverse processes. The minimum development is exemplified by *C. neglectus* (fig. 52E) and the average by lowland *C. ornatus* (fig. 52C). Australian *Sphenophryne* show less development of these processes, with one species (*S. gracilipes*, fig. 52A) lacking them and three others with minimal development (e.g., *S. robusta*, fig. 52B).

Among 42 specimens of *Cophixalus ornatus* seen in X-ray, only one appeared to lack diapophyses altogether, and the majority had at least the degree of development shown in figure 52C. In another respect, *ornatus* presents a special case. The cleared and stained specimen from the otherwise somewhat distinctive coastal lowland population (see species account) has an average degree of development of these processes (fig. 52C), but in the two specimens from inland populations at higher elevations the coccygeal transverse processes are incorporated into a fusion of the coccyx with the sacral vertebra (fig. 52D). I examined X-ray photographs of 26 specimens of the lowland population and 16 upland frogs, but was unable by this means to determine whether fusion existed. I find no examples of such fusion in skeletal specimens of other Australian *Cophixalus* nor in 33 specimens representing ten typical species of *Cophixalus* from New Guinea. Fusion occurs in some species of the *Cophixalus variegatus* species group of New Guinea, but a variety of other morphological attributes makes it unlikely that this implies a special relationship with *C. ornatus.*

The majority of specimens of typical New Guinean *Cophixalus* have at least stubs of coccygeal diapophyses, and individual variation is apparent. For example, four of five specimens of *C. parkeri* lack projections, whereas the fifth has a unilateral one. Six of seven specimens of *C. cryptotympanum* have at least short diapophyses but the seventh has none. Members of the *variegatus* group all have diapophyses often incorporated in sacral fusion. Specimens of New Guinean *Sphenophryne* present a picture similar to that of Australian ones, with coccygeal diapophyses small or lacking. Individual variation is evident here, too, where short series of single species are available.

APPENDAGES

I have made little study of the appendicular skeleton other than to measure and compare the terminal phalanges. The tips of the ultimate phalanges of both hands and feet of all Australian *Cophixalus* and *Sphenophryne* typically bear prominent processes, T-shaped when seen from above or below, and if well developed, slightly decurved seen end on. The only exceptions occur in those *Cophixalus* that have the first finger greatly reduced in size. On this finger, processes may be nearly absent, represented only by minute bumps. (The first finger, even when reduced, still retains the typical two phalanges.)

The phalanges of the third fingers exemplify the degree of development seen in the several species. The relative expansion may be expressed as the ratio of the width of the T to the length of the phalange. *Sphenophryne* shows relatively little expansion—in all four species the width of the T is less than the length of the bone, ranging from 70 to 80 percent (fig. 53). *Cophixalus* consistently has a greater degree of expansion, ranging from a low of 83 percent in *C. bombiens* to a mean of 115 percent in three *C. ornatus* (range 110–120%, fig. 54).

Another way of considering the shapes of these phalanges is to compare the width of the T to a standard measurement of body size, snout-vent length. Such a comparison suggests that the small species *S. gracilipes* has virtually the same proportion of digital expansion as do the larger species of *Sphenophryne.* Among *Cophixalus* species, those of larger body size have relatively greater expansion of the T. The exception is *C. ornatus,* which has much greater expansion than other species of comparable size and equals or exceeds the much larger *C. saxatilis.* The closely related matter of expansion of digital discs is taken up in more detail in the analysis of body proportions.

SUMMARY

The skeletons of Australian *Sphenophryne* and *Cophixalus* are closely similar in most respects, the only trenchant difference being the relatively primitive condition of the pectoral girdle of *Sphenophryne,* which possesses well-developed clavicles and procoracoids, structures absent in *Cophixalus.* The prevomer of *Sphenophryne* is more thoroughly ossified laterally than that of *Cophixalus,* which has a cartilaginous, presumably derived and paedomorphic, distal portion. The terminal phalanges, T-shaped in both genera, are more broadly so in *Cophixalus*; the polarity of this character on the generic level is not determined. *Cophixalus* has at least vestigial transverse processes on the coccyx, possibly the primitive condition, whereas such diapophyses are absent or scarcely developed in *Sphenophryne.* Interspecific differentiation in skeletal characters of *Cophixalus* and *Sphenophryne* is too poorly documented to justify the use of such characters in inferring relationships.

Paedomorphy is a theme that runs through the skeletons of both genera. The prootic region of the skull is often much less well ossified than is typical in frogs, including other microhylids, and the lesser development of the prevomer of *Cophixalus* may also be an example of paedomorphy. The nonimbricate condition of the vertebrae in both genera is clearly paedomorphic, judged from the imbricate vertebrae of other microhylids.

MYOLOGY

A survey of the myology of the Australian microhylids is not within the intended scope of this work. However, a note by Burton (1984) on the throat musculature of *Cophixalus* and *Sphenophryne* calls attention to a useful character for distinguishing between these genera and so requires discussion here.

Burton examined the superficial throat musculature of specimens of several species of the two genera, including the Australian *C. neglectus, C. ornatus, S. fryi,* and *S. robusta,*[8] and found a consistent intergeneric difference in the supplementary slip of the M. intermandibularis (fig. 55). He characterized the difference with the following couplet (Burton, 1984, p. 206):

Supplementary slip of M. intermandibularis narrow, arising from either a posterior tendon or from dentary, and oriented parallel to the mandible .... *Cophixalus*
Supplementary slip of M. intermandibularis broad, arising from ventral fascia of angulosplenial, and oriented medially and only slightly anteriorly .... *Sphenophryne*

I have examined the throat musculature of nine of the eleven Australian *Cophixalus* and of four of the five *Sphenophryne* (in addition to several Papuan species) and can confirm that they correspond to Burton's description. The condition he illustrated for *Cophixalus ornatus* (1984, fig. 1A), with the supplementary slip widely separated from the M. intermandibularis (a condition I confirm in my specimen), is perhaps extreme. In other species of *Cophixalus* I examined the two may be much more closely associated. In *C. saxatilis* (fig. 55A) I could not clearly separate the two muscles posteriorly, though anteriorly the fiber directions are clearly different. I also did not find the M. intermandibularis and M. interhyoideus readily separable in *C. saxatilis.* My specimens of *Sphenophryne* (e.g., fig. 55B) agree well with Burton's characterization of the genus.

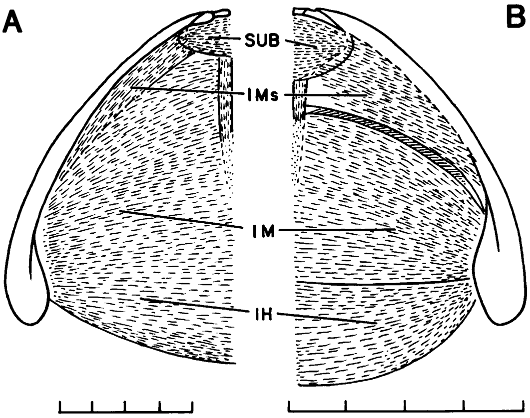

FIG. 55. Superficial throat musculature of *Cophixalus* and *Sphenophryne*. **A,** *C. saxatilis,* AMNH 111430; **B,** *S. robusta,* AMNH 88235. SUB, M. submentalis; IMs, supplementary slip of M. intermandibularis; IM, M. intermandibularis; IH, M. interhyoideus. Scale lines marked in mm.

ONTOGENETIC TRENDS, ECOLOGICAL AND SYSTEMATIC IMPLICATIONS

My purpose is to determine how some aspects of the gross morphology of Australian microhylids may correlate with habits and habitat, and to see if ontogenetic trends can be helpful in understanding adaptations and interspecific relationships. I have concentrated on the body parts routinely measured for systematic descriptions: tibia length, hand length, foot length, head width, orbit length, eye-naris distance, internarial span, length of first finger, and widths of terminal discs of third finger and fourth toe. Ratios of sizes of body parts to body length have some utility (as seen in the species diagnoses), but cannot readily take into account changes that accompany growth. Therefore, where material was adequate I calculated regression statistics for one or more samples of each species for most measurements listed. A power curve of the form $Y = \alpha X^{\beta}$ almost invariably provides a better fit to the data than does a rectilinear

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[8] From information furnished by Dr. Burton (in litt.), it appears probable that the specimen of "*S. fryi*" he examined is more likely *S. robusta,* while his "*S. robusta*" is properly identified and his specimens of "*S.* sp. nov." are *S. fryi.* The specimens of *Cophixalus ateles* probably are *C. shellyi.*

TABLE 20
Regression Statistics for Thirteen Samples of the Genus *Cophixalus*[a]

Sample	TL/SV				HW/SV				HAND/SV				FOOT/SV				EYE/SV			
	α	β	r	n	α	β	r	n	α	β	r	n	α	β	r	n	α	β	r	n
C. bombiens	.861	.734	.951	40	.615	.803	.952	40	.304	.861	.944	40	.605	.867	.949	40	.257	.733	.935	40
C. concinnus[b]	1.038	.686	.921	18	.228	1.130	.985	15	.244	.979	.989	12	.811	.773	.960	12	.144	.974	.954	17
C. concinnus[c]	.844	.753	.929	46	.401	.992	.945	46	.253	.959	.925	46	.865	.746	.910	46	.297	.707	.905	45
C. crepitans	.588	.935	.799	18	.668	.762	.649	14	.333	.829	.690	17	.905	.731	.730	18	.318	.690	.720	17
C. exiguus	1.120	.668	.902	35	.591	.858	.916	25	.328	.857	.909	26	.822	.772	.897	26	.210	.841	.924	41
C. hosmeri	1.190	.585	.844	42	.811	.725	.872	42	.327	.835	.874	42	1.024	.639	.822	42	.296	.697	.890	42
C. infacetus	1.009	.723	.837	22	.288	1.103	.897	22	.480	.710	.876	22	.908	.734	.828	21	.263	.735	.857	22
C. mcdonaldi	.919	.740	.967	22	.535	.906	.919	22	.367	.837	.941	22	.811	.788	.939	22	.175	.877	.944	22
C. neglectus[d]	.674	.793	.961	31	.665	.821	.942	33	.363	.827	.953	30	.699	.800	.946	29	.325	.666	.938	31
C. neglectus[e]	.713	.796	.954	25	.585	.877	.987	26	.387	.839	.910	23	.637	.866	.923	23	.362	.637	.941	26
C. ornatus[f]	.628	.867	.978	37	.631	.825	.919	35	.247	1.019	.971	36	.467	.962	.983	36	.282	.724	.944	37
C. ornatus[g]	.516	.957	.954	31	.579	.851	.920	29	.159	1.159	.954	30	.398	1.012	.946	30	.207	.826	.906	25
C. saxatilis	.652	.915	.993	14	.372	1.008	.994	19	.228	1.031	.997	13	.593	.912	.996	13	.227	.829	.994	19

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

[b] Thornton Peak.

[c] Mt. Lewis.

[d] Mt. Bellenden Ker.

[e] Mt. Bartle Frere.

[f] Upland sample.

[g] Lowland sample.

TABLE 21
Regression Statistics for Thirteen Samples of the Genus *Cophixalus*[a]

Sample	EN/SV				IN/SV				Third Finger Disc/SV				Fourth Toe Disc/SV			
	α	β	r	n	α	β	r	n	α	β	r	n	α	β	r	n
C. bombiens	.197	.636	.915	40	.257	.647	.909	40	.023	1.150	.873	40	.036	1.082	.870	40
C. concinnus[b]	.103	.906	.960	17	.263	.638	.839	17	.008	1.546	.916	16	.066	.845	.908	16
C. concinnus[c]	.118	.850	.877	46	.179	.756	.899	46	.020	1.206	.754	45	.043	.982	.693	44
C. crepitans	.205	.626	.596	16	.408	.482	.563	17	.031	1.127	.522	15	.057	.906	.337	17
C. exiguus	.129	.815	.889	40	.182	.756	.920	41	.045	.898	.667	41	.052	.931	.818	41
C. hosmeri	.189	.640	.749	42	.254	.630	.861	42	.046	.911	.716	41	.070	.809	.726	40
C. infacetus	.189	.694	.833	22	.158	.844	.919	21	.010	1.568	.808	20	.020	1.333	.766	20
C. mcdonaldi	.195	.704	.887	22	.204	.747	.913	22	.039	.984	.905	22	.050	.924	.884	22
C. neglectus[d]	.158	.715	.939	31	.241	.683	.913	31	.026	1.107	.951	30	.048	.942	.921	30
C. neglectus[e]	.185	.684	.931	24	.229	.723	.945	24	.053	.893	.868	22	.080	.796	.831	22
C. ornatus[f]	.136	.828	.953	37	.170	.784	.965	36	.023	1.295	.935	37	.042	1.018	.920	57
C. ornatus[g]	.115	.882	.861	25	.194	.744	.911	25	.016	1.418	.900	31	.035	1.078	.898	30
C. saxatilis	.145	.896	.945	19	.145	.876	.996	19	.038	1.128	.988	19	.045	.985	.947	18

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

[b] Thornton Peak.

[c] Mt. Lewis.

[d] Mt. Bellenden Ker.

[e] Mt. Bartle Frere.

[f] Upland sample.

[g] Lowland sample.

equation; therefore graphic comparisons are presented as power curves. Smith (1980) and Harvey (1982) have discussed the use of the power function in studies of allometry. My usage is in line with Harvey's arguments. Least squares regression coefficients, sample sizes, and r values are given in tables 20, 21, 23, and 24.

Figures 56, 57, 60, and 61 summarize the growth trends for *Cophixalus* and *Sphenophryne.* I present the curves alone and not the original data points for the sake of improving legibility. In viewing the curves it should be appreciated that even where lines are well separated there may be considerable overlap in ranges of data among species. In several instances where geographic variation is apparent there are lines for two samples of a species. The curves for *Cophixalus* are truncated at 29 mm SV and for *Sphenophryne* at 30 mm SV to present them at a favorable scale. One species, *Cophixalus saxatilis,* greatly exceeds 29 mm but for purposes of interspecific comparisons the curves presented are adequate. The largest *Sphenophryne* is less than 35 mm, and most specimens fall within the range plotted.

GENUS *COPHIXALUS*

MORPHOLOGICAL VARIATION

There are only two specimens of *Cophixalus peninsularis,* so this species is omitted from the regression lines though not from discussion. The size range in the sample of *C. crepitans,* 11.6–14.1 mm, is so short that the curves may not give reliable estimates of growth trends. The elevations of the curves on the Y axes, however, still provide an idea of relative sizes of body parts in comparison with other species.

BODY SIZE: Because females are not known for all species, male body size is the best criterion for comparing species. Maximum male snout-vent lengths for Australian *Cophixalus* range from 14 to 35 mm (rounded to nearest mm), which is equivalent to a weight difference of almost tenfold. There are five conspicuously small species, with maximum lengths of 14–16 mm: *bombiens, crepitans, exiguus, hosmeri,* and *infacetus.* A less compact group includes *peninsularis* (18 mm), lowland *ornatus* (19 mm), *concinnus* (20–22 mm in different populations), *mcdonaldi* and *neglectus* (23 mm), and upland *ornatus* (27 mm). With its length of 35 mm, *saxatilis* stands alone. The only species for which the data are clearly inadequate is *peninsularis,* with only two specimens. Additional specimens may add a millimeter or so to this species, increasing the distinctiveness of the middle-size group.

Body size is the only morphological feature (aside from vocal sac apparatus and reproductive organs) in which Australian *Cophixalus* show sexual dimorphism. In all species for which there are data (thus excluding *peninsularis*) females mature at and attain slightly larger size than do males. The difference ranges from the largest male being 10 percent smaller than the largest female in *ornatus* (both lowland and highland populations) to a differential of 24 percent in *saxatilis,* with a mean of 15.8 percent. There is considerable overlap in the size ranges of mature males and females where large samples are available, so this is probably the case in all species.

HEAD WIDTH: No clear groups of species appear in these curves (fig. 56A). *Cophixalus concinnus* has the broadest head and two tiny species, *bombiens* and *crepitans,* the narrowest. The steepness of the curve for *concinnus* may be slightly exaggerated, as the largest specimen in the topotypic sample plotted appears flattened and the HW measurement may be too great. Two other geographic samples of *concinnus* (not plotted) have curves virtually identical to that of *mcdonaldi,* and the curves for *infacetus* and *concinnus* are colinear over their mutual extent. Geographic variation is apparent in the two samples of *neglectus,* whereas upland and lowland *ornatus* are not differentiated.

ORBIT LENGTH: Eye size also shows no clearcut groups of species (fig. 56B). Topotypic *concinnus* and *saxatilis* have the largest eyes, and the two specimens of *peninsularis* fall on the *saxatilis* line. These stand somewhat apart from *mcdonaldi, ornatus,* and *neglectus* (the last has the smallest eyes of the large species), but the picture among these larger species is confused by relatively small eyes in the other two samples of *concinnus* (not plotted), whose regression lines bracket those of *mcdonaldi* and *ornatus.* Among the small species, *exiguus* appears to have the

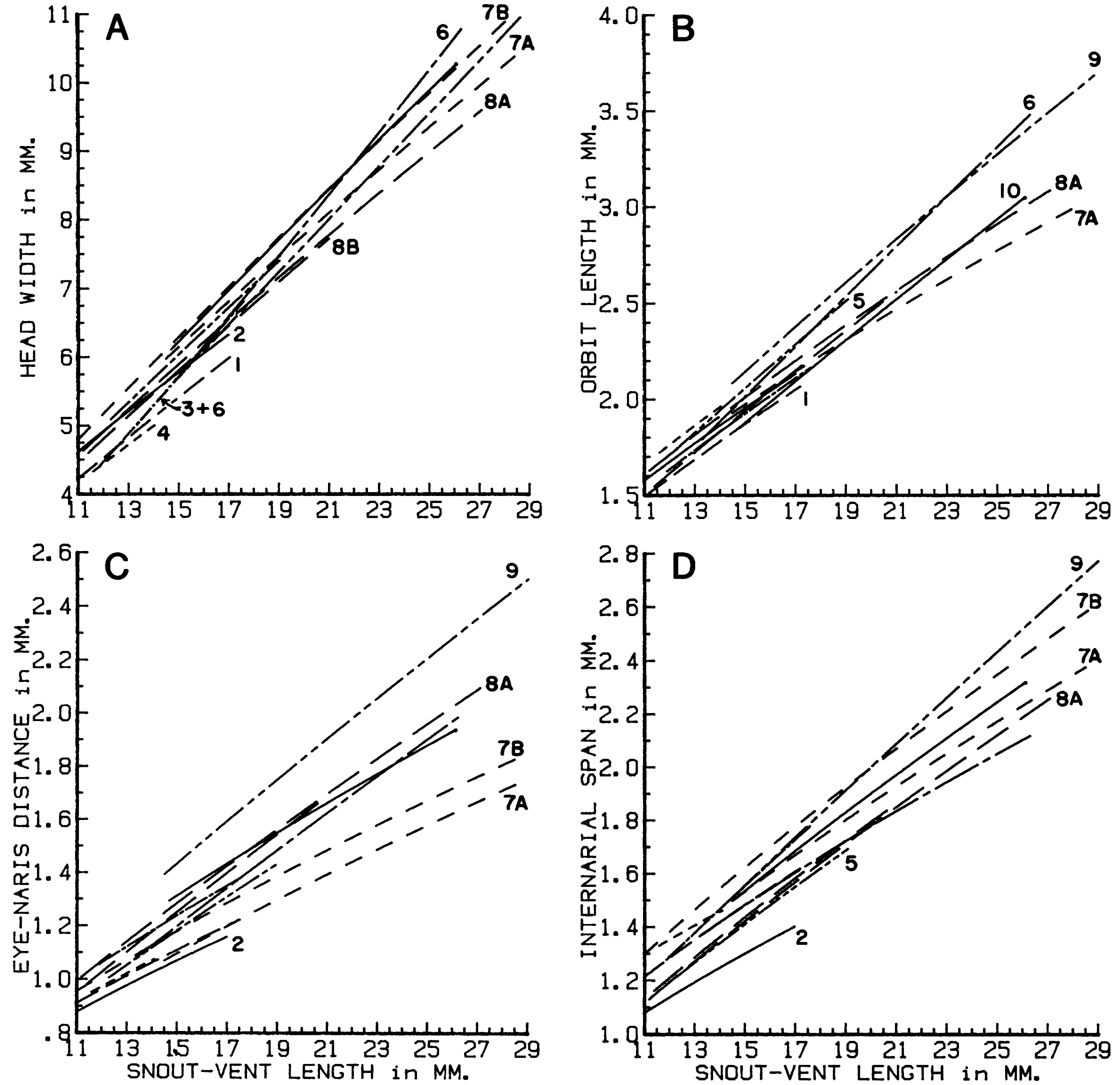

FIG. 56. Regression of body measurements on snout-vent length in ten species of *Cophixalus*. Lines are identified by numbers and patterns; in some instances two samples of a species are plotted. **1**, *C. bombiens*, Mt. Windsor Tableland; **2**, *C. hosmeri*, Mt. Lewis; **3**, *C. infacetus*, Palmerston vicinity; **4**, *C. crepitans*, McIlwraith Range; **5**, *C. exiguus*, Mt. Hartley vicinity; **6**, *C. concinnus*, Thornton Peak; **7**, *C. neglectus*, Mt. Bellenden Ker (7A) and Mt. Bartle Frere (7B); **8**, *C. ornatus*, highland (8A) and lowland (8B); **9**, *C. saxatilis*, Black Gap; **10**, *C. mcdonaldi*, Mt. Elliot. See tables 20 and 21 for regression coefficients, correlation coefficients, and sample sizes.

largest eyes and *bombiens* the smallest, but differences are slight.

EYE-NARIS DISTANCE: *Cophixalus saxatilis* stands apart from the other species in its relatively great eye-naris distance (fig. 56C). An intermediate group of large species comprises *ornatus*, *concinnus*, and *mcdonaldi*, whereas *neglectus* exhibits geographic variation but has the shortest eye-naris distance. Among the small species, *hosmeri*, *bombiens*, and *crepitans* follow trends close to that of *neglectus* from Mt. Bellenden Ker, whereas *exiguus* and *infacetus* are more closely associated with the intermediate group of larger

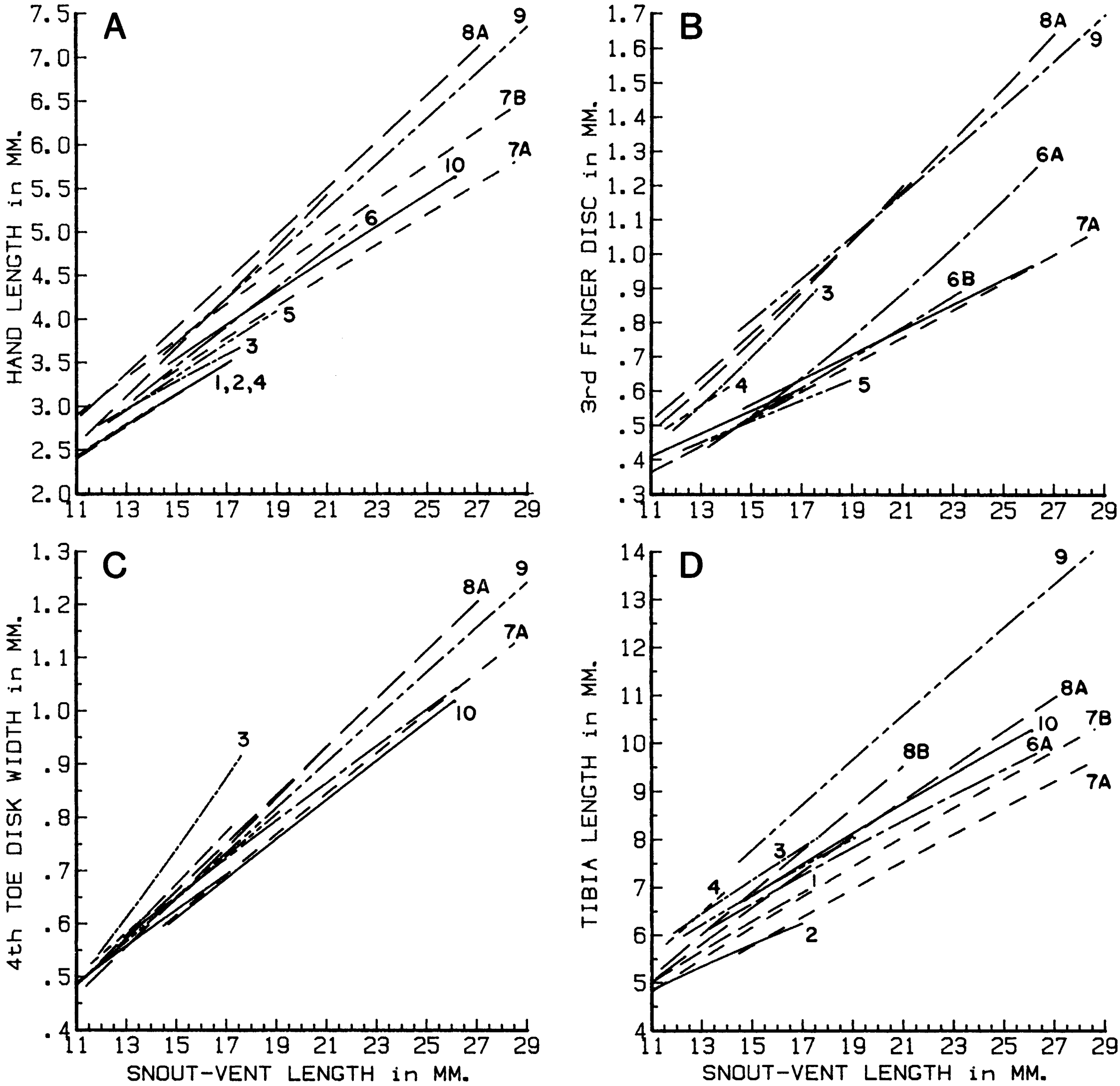

FIG. 57. Regression of body measurements on snout-vent length in ten species of *Cophixalus.* Lines are identified by numbers and patterns; in some instances two samples of a species are plotted. **1,** *C. bombiens,* Mt. Windsor Tableland; **2,** *C. hosmeri,* Mt. Lewis; **3,** *C. infacetus,* Palmerston vicinity; **4,** *C. crepitans,* McIlwraith Range; **5,** *C. exiguus,* Mt. Hartley vicinity; **6,** *C. concinnus,* Thornton Peak (6A) and Mt. Lewis (6B, finger discs only); **7,** *C. neglectus,* Mt. Bellenden Ker (7A, all graphs) and Mt. Bartle Frere (7B, hand and TL only); **8,** *C. ornatus,* highland (8A) and lowland (8B); **9,** *C. saxatilis,* Black Gap; **10,** *C. mcdonaldi,* Mt. Elliot. See tables 20 and 21 for regression coefficients, correlation coefficients, and sample sizes.

species. The two specimens of *peninsularis* (not plotted) have very short EN measurements, comparable to those of *hosmeri.*

INTERNARIAL SPAN: Regression lines are rather evenly dispersed (fig. 56D). *Cophixalus saxatilis* has the greatest internarial span among the large species, *concinnus* the smallest, and *neglectus* shows geographic variation. The small species group shows similar dispersion: *infacetus* is nearly colinear with the large *saxatilis* (*peninsularis* closely agrees with these two), *bombiens* is colinear with *concinnus,* and *exiguus* is close to *ornatus.* Only *hosmeri,* with its very narrowly spaced nostrils, stands apart from the crowd.

HAND LENGTH: The large species fall into two distinct groups (fig. 57A): in *ornatus* and *saxatilis* the hands attain a large size and increase in size relative to body size through ontogeny, whereas *concinnus, mcdonaldi,* and *neglectus* have distinctly less rapid relative growth of the hands. The small species, including *peninsularis,* have markedly smaller hands. Only *exiguus* attains the minimum hand size of the smallest of the larger species (*neglectus* from Mt. Bellenden Ker). The regression lines for *bombiens, crepitans,* and *hosmeri* are superimposed, and the two data points for *peninsularis* fall on and below these lines.

DISC OF THIRD FINGER: *Cophixalus saxatilis, C. ornatus* (both large-bodied and small-bodied populations), and *C. infacetus* have large discs that exhibit high positive allometry (fig. 57B). These contrast with *neglectus, mcdonaldi,* nontopotypic *concinnus, exiguus, hosmeri,* and *bombiens,* all of which have initially smaller discs with negative or less positive allometry. Topotypic *C. concinnus* has relatively small discs initially, but exhibits a high positive allometry and thus as an adult has an intermediate disc size. The remaining two species are ambiguous because of small sample size: *crepitans* has relatively large discs but the indicated growth trend does not follow that of species with large discs; *peninsularis* (two adult specimens only) falls between the species with large discs and topotypic *concinnus.* I tentatively group these two species with topotypic *concinnus.*

DISC OF FOURTH TOE: Toe discs are more nearly uniform interspecifically than are finger discs (fig. 57C). Discs are somewhat larger in *saxatilis* and *ornatus* than in *neglectus, concinnus,* and *mcdonaldi,* but the differences are slight compared to those among finger discs. For the most part the regression lines for the smaller species fall within the same general range as those of the larger ones. The most conspicuous exception is *infacetus,* whose toe discs are broader on the average than those of any other *Cophixalus* at the same body size.

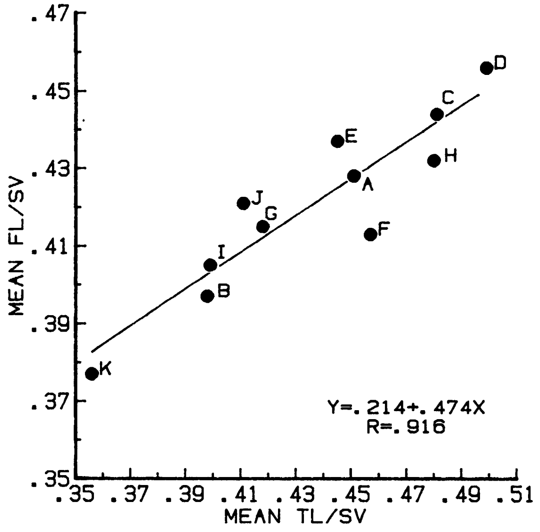

FIG. 58. Relationship between foot length and tibia length, each expressed as the ratio with snout-vent length in adult *Cophixalus,* showing the close correspondence between relative tibia and foot lengths. **A,** *C. bombiens*; **B,** *C. hosmeri*; **C,** *C. infacetus*; **D,** *C. crepitans*; **E,** *C. exiguus*; **F,** *C. ornatus* (lowland); **G,** *C. ornatus* (highland); **H,** *C. saxatilis*; **I,** *C. concinnus*; **J,** *C. mcdonaldi*; **K,** *C. neglectus* (Mt. Bellenden Ker).

DEVELOPMENT OF FIRST FINGER: I could not adequately quantify the size of the first finger or the degree of development to justify regression analysis, but the differences observable deserve mention. This digit ranges from a mere nubbin in *C. crepitans* (fig. 6F) to a well-developed finger about half the length of the second, bearing a distinct subarticular elevation and a broadened, grooved disc in *C. saxatilis* (fig. 7E). Among the large species, *saxatilis, ornatus,* and *concinnus* have relatively well-developed first fingers with grooved discs, whereas *neglectus* and *mcdonaldi* have shorter fingers with no discs (fig. 5). The smaller species are not quite so diverse (fig. 6). *Cophixalus exiguus,* with a relatively long finger with a grooved, scarcely expanded disc, has the maximum development of these structures. All others apparently lack a terminal groove (it can be difficult to see when poorly developed) and only *peninsularis* has the tip even flattened and disclike.

TIBIA AND FOOT LENGTHS: The lengths of these segments of the leg are highly correlated. This is illustrated in figure 58, where the mean TL/SV and FL/SV ratios are plotted for adults in 11 samples (10 species) of *Cophixalus.* The correlation is independent of adult body size: the smallest and largest species, *crepitans* and *saxatilis,* lie at the upper end of the curve, while other large and small species, *neglectus* and *hosmeri,* are at the lower end. It is evident that tibia length and foot length should not be treated as independent variables. I choose to consider tibia length alone.

No group tendencies are evident in tibia length (fig. 57D). Among the larger species, *saxatilis* has the longest legs and *neglectus* the shortest, with the other large forms occupying mostly the lower half of the intervening range. Among the small species, only *hosmeri,* with its short legs, differs much from the rest.

MORPHOLOGY AND ECOLOGY

The attempt to correlate morphology with habitat selection and habits in *Cophixalus* is hampered by the paucity of field data on most of the species, but some inferences can be drawn. *Cophixalus saxatilis* and *C. ornatus* appear to be the most scansorial species and show some traits presumably related to this way of life. These two stand out from the other large species in the greater size of the finger discs (fig. 57B), the greater length of the hand (fig. 57A), and better development of the first finger (fig. 5). The few available notes on topotypic *C. concinnus* (see species account) indicate climbing habits comparable to those of *ornatus.* Hence, it is somewhat surprising to find that the finger discs and hands are distinctly smaller than those of *ornatus* and *saxatilis* of comparable body size, and the first finger is less well developed. The situation is complicated by apparent geographic variation in finger disc size and by lack of information on the habits of nontopotypic *concinnus,* whose adults average smaller discs than those of even topotypic specimens (fig. 57B).

One of the small species, *C. infacetus,* has relatively large finger discs which within its limited body size range nearly match those of *ornatus* and *saxatilis* in size and equal them in growth rate. Like the other small species, *infacetus* is much less of a climber than are *ornatus* and *saxatilis,* yet it possibly is more inclined this way than are *bombiens* and *hosmeri* that have tiny discs (see species accounts). *Cophixalus infacetus* combines relatively large finger discs with small hand size, showing that these two characters need not vary in tandem. Perhaps the additional refinement of large hand size is important only to scansorial animals of larger body size.

Although the toe discs of *ornatus* and *saxatilis* are larger than those of the other large species, the range in toe disc size (fig. 57C) is much less than is seen in finger discs, suggesting that the latter are more important in climbing activity. Curiously, *infacetus* departs from all other species in its large toe discs.

Just as some characters are associated with scansorial habits, others are common to many ground-dwelling species that spend much of their time in the leaf litter. *Cophixalus neglectus* appears to be one such species. Its digital discs and hands are among the smallest of the large *Cophixalus* and grow at slow rates (fig. 57A, B). Additional characteristics associated with this mode of life include small eyes (fig. 56C) and short legs (fig. 57D). Similarities to *neglectus* in hand length and disc size suggest that *mcdonaldi* may have habits like those of *neglectus,* but nothing pertinent is on record.

So little is known of the habits of the several small species of *Cophixalus* that correlations between habits and morphology are mostly undetected if they indeed exist. Mention is made of the relatively large digital discs of *C. infacetus* and its seemingly greater tendency to scansoriality, but even this suggestion is not adequately documented. The significance of most of the observed interspecific differences in morphology in the animal's way of life is unclear for large and small species alike. Much of the variation could bear little or no relationship to habits. For example, a frog with the very short legs of *Cophixalus hosmeri* may operate as well in the leaf litter as does the longer-legged *C. bombiens* in the same habitat on another mountain nearby. Reasons for some differences should perhaps be sought not in a one-to-one relationship with some feature of the environment, but in developmental pathways constrained by less obvious forces. The

Australian *Cophixalus,* for the most part, operate within a relatively narrow range of habitat (even the scansorial species *ornatus* and *concinnus* inhabit terrestrial shelter when inactive), and their generalized morphologies may require little modification in adapting to slightly different niches.

MORPHOLOGY AND INTERSPECIFIC RELATIONSHIPS

Merely establishing that two or more species resemble one another and attain common aspects of their morphology along similar ontogenetic trajectories is inadequate evidence of their close relationship unless it can be shown that the resemblances are not primitive attributes or are not parallel developments. This, of course, requires that the primitive and derived states be established for the characters considered and that parallelism can be detected—typically unrewarding tasks for students of frogs.

The search for character polarity in *Cophixalus* must take place within the New Guinea fauna, with its greater and more diverse array of species. Seventeen species of *Cophixalus* are known at present in New Guinea (Zweifel and Tyler, 1982, table 1, plus *C. sphagnicola,* Zweifel and Allison, 1982), though the total number of valid species undoubtedly far exceeds this. Two species, *C. darlingtoni* Loveridge and *C. variegatus* (van Kampen) together with several undescribed species form a distinctive group sharing morphological characters derived with respect to those of more typical *Cophixalus.* These species do not figure in the following discussion and probably will be found to merit their own genus. The remaining species assort by size into two groups and one isolated species. Six species have maximum male snout-vent lengths of 15–19 mm, eight species fall into the 22–31-mm range, and one far exceeds the others at 45 mm. The situation is thus similar to that in Australia where there is a group of small species, a somewhat less distinctive group of larger species, and one relative giant. I regard extremely large and small size as representing derived conditions, with primitive male body size roughly in the range of 20–30 mm SV.

Almost all the New Guinean *Cophixalus* are known to be, or can reasonably be assumed to be, scansorial. The exceptions are *C. pansus* and *C. sphagnicola* (Zweifel and Allison, 1982). The first of these is a short-legged, small-eyed terrestrial frog lacking digital discs that lives at high elevations (2800–3800 m). Its form and habitat are so peculiar for *Cophixalus* that it is best considered a highly derived species. *Cophixalus sphagnicola* inhabits terrestrial moss and leaf litter at moderately high elevations (2300–3000 m). It is a small species without digital discs and appears to be most closely related to two scansorial forms that inhabit lower elevations and possess digital discs. I infer that the primitive condition in *Cophixalus* includes scansorial habits and morphology associated with these habits: enlarged digital discs (especially those of the fingers), unreduced first finger, and moderate hand size. For purposes of coding (table 22) I assume that extremes of enlargement or reduction (as traced in the regression lines) represent derived conditions, both in the characters related to scansoriality and in other attributes measured (head width, tibial length, eye size, narial position).

Table 22 presents the character states and their inferred primitive or derived status. Seven of the ten characters vary in both derived directions—enlarged or reduced—in one or another species and none is invariably primitive over the entire range of species. Some derived characters appear in only one species and, while useful in defining species, they provide no information on relationships.

Cophixalus concinnus is the most primitive species: all characters can have the primitive condition, though there are two instances of geographic variation to derived states. The species most different from *concinnus* are *saxatilis* and *bombiens,* each with seven out of ten derived states. The first of these two species presents an exaggeration of the characters of *concinnus*—e.g., larger eyes, longer legs, greater size—whereas *bombiens* shows the opposite extremes of diminution. Most of the remaining species depart from *concinnus* in the same morphological direction as does *bombiens.* Exceptions are *ornatus,* which shares two derived characters with *saxatilis* but has geographic variation in

TABLE 22
Morphological Character States in Australian *Cophixalus*[a]

Species	SV	HW	TL	EYE	EN	IN	HAND	Third finger disc	Fourth toe disc	First finger length
1. *bombiens*	−	−	0	−	−	0	−	−	0	−
2. *hosmeri*	−	0	−	0	−	−	−	−	0	−
3. *infacetus*	−	0	0	0	0	0	−	+	+	−
4. *crepitans*	−	−	0	0	−	0	−	0	0	−
5. *exiguus*	−	0	0	+	0	0	0	−	0	0
6. *concinnus*	0	0	0	+0	0	0	0	−0	0	0
7. *neglectus*	0	0	−0	−	−	0	0	−	0	−
8. *ornatus*	−0	0	0	0	0	0	+	+	0	0
9. *saxatilis*	+	0	+	+	+	+	+	+	0	0
10. *mcdonaldi*	0	0	0	0	0	0	0	−	0	−
peninsularis	0	0	0	0	0	0	−	0	0	−

[a] Character states are coded as follows: 0, primitive state; −, derived by way of reduction (e.g., reduced digit size); +, derived by way of enlargement or elongation (e.g., larger hands). Two states in one cell indicate geographic variation. Numbers in left column correspond with those in figures 56 and 57, *peninsularis* is not in the figures.

body size, and *infacetus* and *exiguus*, which deviate from *concinnus* in different directions in three or more characters each.

My attempts to formulate a hypothesis of interspecific relationships based on the data in table 22 have been unsatisfying. Examination of the table and of figures 56 and 57 will identify some obvious groups of species sharing derived characters. Examples include the five small-bodied species, the two species with large hands, the five species with small hands, and those with either large or small finger discs. But efforts to integrate such groups into a higher degree of ordination produce rather unparsimonious arrangements acceptable only on the assumption of parallel developments in the majority of characters employed.

The diagram of relationships presented here (fig. 59) is only one of many similarly unparsimonious statements constructed. I have not identified a single most parsimonious arrangement, but doubt that it would be any more defensible than this one, which is tenuous at best.

The left-hand group of species is characterized by the unique possession of small hands, a derived character. All except *peninsularis* are of distinctly small size, and that species lies on the borderline between large and small species. These five species also share the derived character of a reduced first finger. The remaining six species are more diverse and do not form a coherent group. The pair *saxatilis* and *ornatus* share the unique derived character of large hands, and their synapomorphy of enlarged finger discs appears only once elsewhere in the diagram, as a parallel development in *infacetus. Cophixalus concinnus,* almost lacking in derived characters, stands alone.

The placement of *mcdonaldi, neglectus,* and *exiguus,* species with no unique shared derived characters, is the principal variable in the several diagrams of relationships I have constructed. Rearrangements of these do not significantly alter parsimony.

It could be argued that *exiguus* might better be grouped with the other small species, but the primitive state of its first finger and hand sizes would confound that arrangement. *Cophixalus ornatus,* with its geographic variation, offers clear evidence of independent derivation of reduced body size, so I think it reasonable to suppose that small size in *exiguus* may be a parallel development to that seen in the other small species. I interpret the small finger discs of *exiguus, mcdonaldi,* and *neglectus* as adaptation to a ground-dwelling existence, or at least a less scansorial habit than the primitive one. This parallels adaptations seen in *hosmeri* and *bombiens.* The

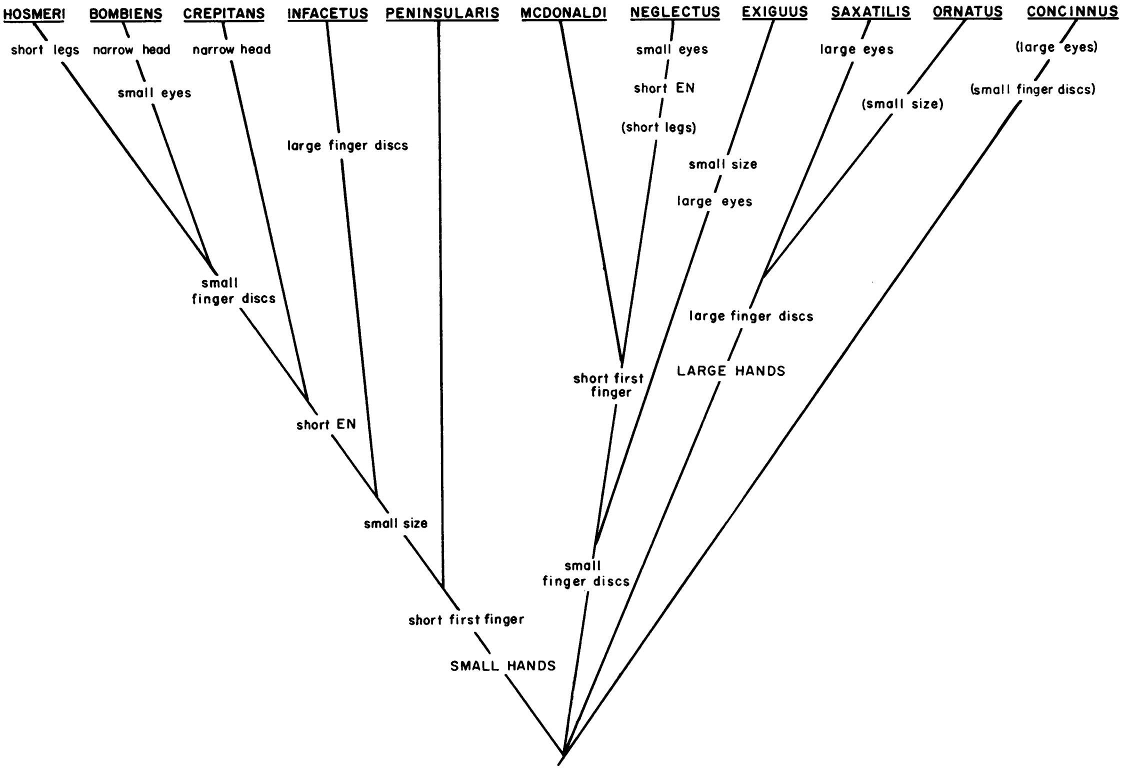

FIG. 59. A hypothesis of interspecific relationships in Australian *Cophixalus*. Capital letters indicate derived character states unique to that branch of the diagram; characters in lower-case letters appear in parallel in more than one place in the diagram; characters within parentheses vary geographically within the species. States unique to a species are not included. See table 22.

geographic variation of disc size in *concinnus* is evidence that change in disc size may have occurred independently in more than one line.

The arrangement presented here rests (as do its numerous conceivable variations) on many possibly insecure assumptions. First among these is that the species form a monophyletic unit and are not derived from two or more lines separately rooted within New Guinean *Cophixalus*. I regard the similarity of advertisement calls as evidence for monophyly (see section on calls), but knowledge of calls and morphology of New Guinean species is inadequate to indicate just where within that assemblage the Australian species may find their closest relatives. Other problems include the unsatisfactory samples of *crepitans* and *peninsularis* and the puzzling geographic variation in *concinnus*.

GENUS *SPHENOPHRYNE*

MORPHOLOGICAL VARIATION

BODY SIZE: The five species assort into two size groups: (1) the small sibling species *adelphe* and *gracilipes*; and (2) the large *pluvialis* and the sibling pair *fryi* and *robusta.* As is the case in *Cophixalus,* Australian *Sphenophryne* are sexually dimorphic in size at maturity and in maximum size, with females being the larger. Largest males are from 5 to 14 percent smaller than the largest females in the five Australian species samples (mean 11.0%), suggestive of slightly less dimorphism than in *Cophixalus* (10–24%, mean 15.8%). New Guinean *S. gracilipes* apparently show more dimorphism than Australian (13% vs. 5%), but this may merely reflect the more adequate New Guinean sample.

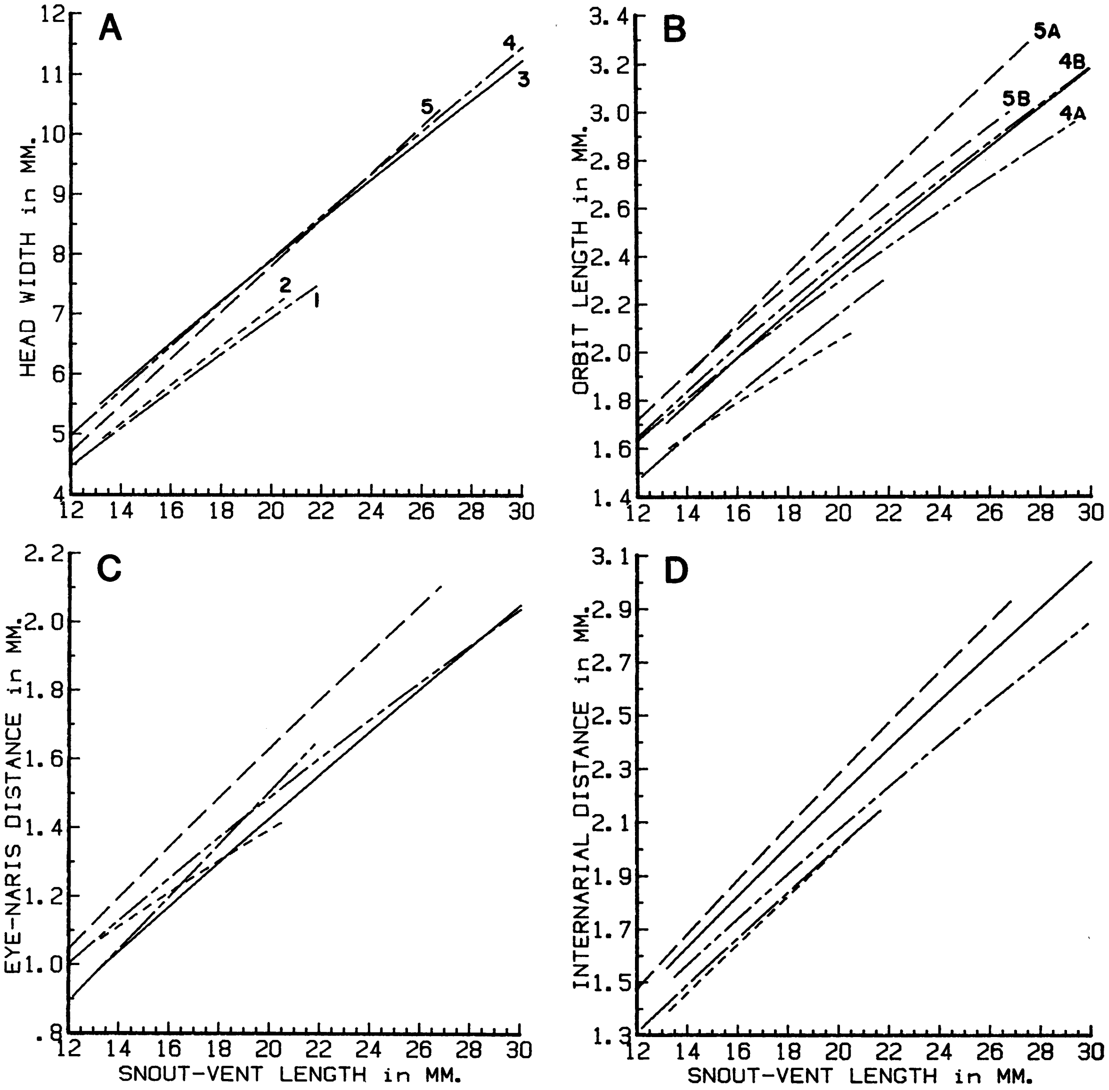

FIG. 60. Regression of body measurements on snout-vent length in five species of *Sphenophryne*. Lines are identified by numbers and patterns; in some instances two samples of a species are plotted. 1, *S. adelphe*, Northern Territory; 2, *S. gracilipes*, Queensland; 3, *S. robusta*, Queensland; 4, *S. fryi*, Mt. Windsor Tableland (4 and 4B), Thornton Peak (4A only); 5, *S. pluvialis*, Kuranda and vicinity (5 and 5B), Thornton Peak (5A only). See tables 23 and 24 for regression coefficients, correlation coefficients, and sample sizes.

Males of *Sphenophryne adelphe* and *S. gracilipes* reach a maximum of 19–20 mm SV, females 21–23 mm. The maxima in the larger three species are: *pluvialis* males 25.7 mm, females 29.3 mm; *robusta* males 26.5 mm, females 32.9 mm (but almost always less than 30 mm); *fryi* males 30.4 mm, females 34.9 mm.

HEAD WIDTH: The small siblings *adelphe* and *gracilipes* have conspicuously narrower heads than do the three larger species (fig. 60A), but within either group the species are virtually identical.

ORBIT LENGTH: Eye size shows both inter- and intraspecific variation (fig. 60B). The eyes are smaller and of similar size in *adelphe* and

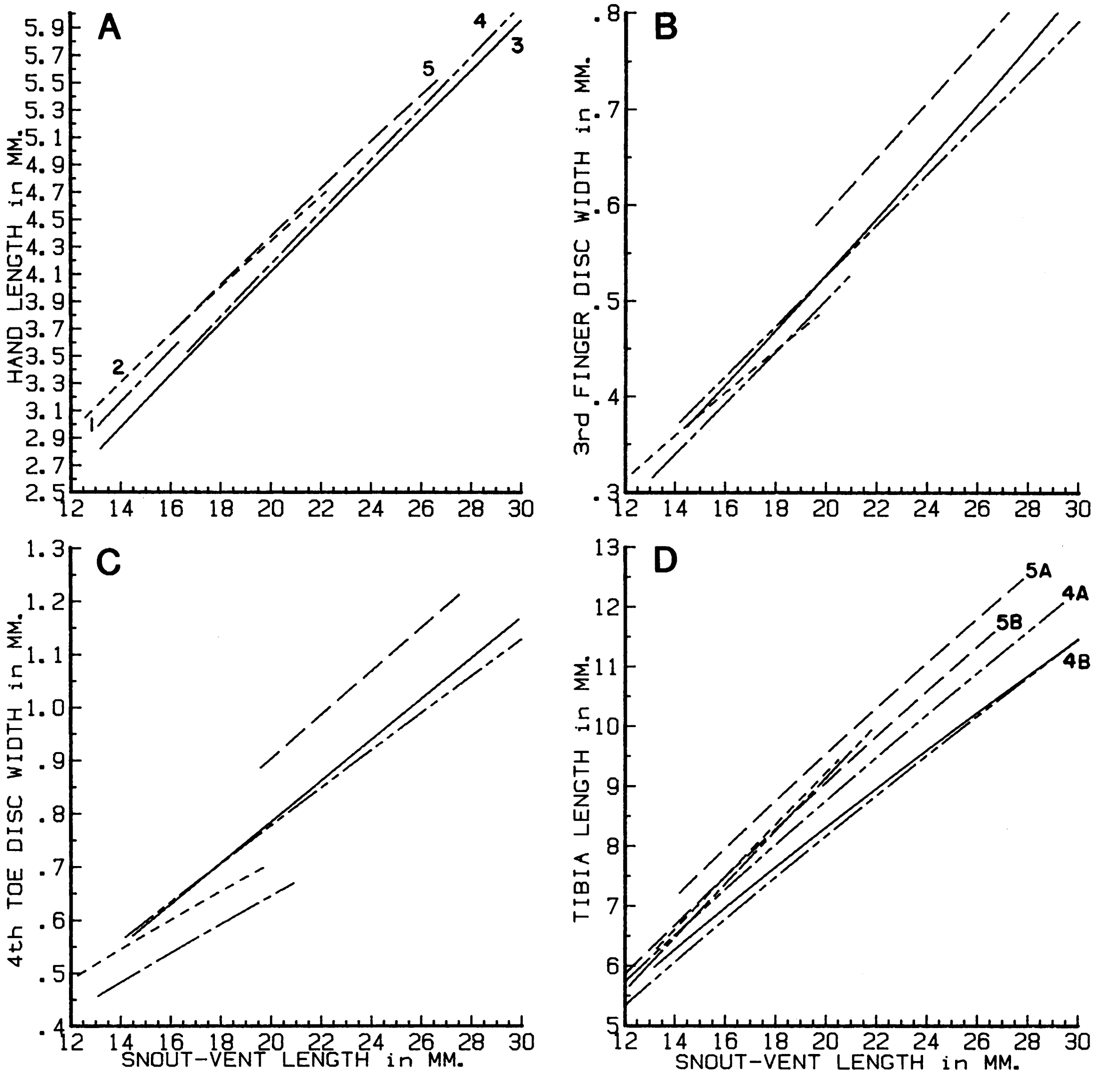

FIG. 61. Regression of body measurements on snout-vent length in five species of *Sphenophryne*. Lines are identified by numbers and patterns; in some instances two samples of a species are plotted. 1, *S. adelphe*, Northern Territory; 2, *S. gracilipes*, Queensland for TL, Papua New Guinea for others; 3, *S. robusta*, Queensland; 4, *S. fryi*, Queensland except 4A (Thornton Peak) and 4B (Mt. Windsor Tableland); 5, *S. pluvialis*, Kuranda vicinity for HAND, Queensland for finger and toe discs, Thornton Peak (5A) and Kuranda vicinity (5B) for TL. See tables 23 and 24 for regression coefficients, correlation coefficients, and sample sizes.

gracilipes. Among the three larger species, *pluvialis* has the largest eyes and shows geographic variation, *robusta* shows no variation of consequence, and *fryi* is variable but in one sample identical to *robusta*.

EYE-NARIS DISTANCE: *Sphenophryne pluvialis* has the largest dimension, but in this character the species do not assort into the size groups seen in head width and orbit length. Eye-naris distances are relatively similar in the remaining four species, with the peculiarity that the slopes of the lines for *adelphe* and *gracilipes* differ (fig. 60C). This is the only character in which such an apparent difference exists between these species.

INTERNARIAL SPAN: Again, *S. pluvialis* has the largest dimensions and the small pair *adelphe* and *gracilipes* the smallest (fig. 60D). This is the only character in which the siblings *fryi* and *robusta* differ consistently.

HAND LENGTH: Regression lines for the five species are nearly identical in slope and similar in elevation (fig. 61A). For example, average hand length at 20 mm SV ranges only from a minimum of 4.1 mm in *robusta* to 4.4 mm in *pluvialis,* with the other species intermediate. In comparison, hand lengths of nine species of *Cophixalus* at the same body size (extrapolating slightly for the smaller ones) would average from about 4.0 to 5.2 mm—four times the range of *Sphenophryne.*

DISC OF THIRD FINGER: The discs are small in all species; only *pluvialis* stands out with its slightly larger discs (fig. 61B).

DISC OF FOURTH TOE: Toe discs are larger than finger discs in these *Sphenophryne* and show some interspecific variation (fig. 61C). *S. pluvialis* again has the larger discs and the small species the relatively (and absolutely) smaller ones. The apparent difference in disc size between *adelphe* and *gracilipes* will require confirmation with a larger sample of *adelphe*—I have measurements of only 12 specimens of *adelphe* for this character.

DEVELOPMENT OF FIRST FINGER: Aside from the slightly larger disc in *S. pluvialis,* the first fingers are similar in all *Sphenophryne* (fig. 4).

TIBIA AND FOOT LENGTHS: As in *Cophixalus,* the species with the longest tibias have the longest feet. *Sphenophryne pluvialis, S. adelphe,* and *S. gracilipes* have the longest legs with *pluvialis* showing geographic variation (fig. 61D). The shorter-legged *fryi* also shows geographic variation, with *robusta* closely resembling the shorter legged of the two samples of *fryi.*

MORPHOLOGY AND ECOLOGY

The rather restricted morphological variation summarized above correlates well with the similarity of habits of the species. The three large species appear to be confined strictly to forest floor leaf litter. The two small species also inhabit leaf litter but the males of *gracilipes,* at least, call from more exposed positions up to at least 45 cm above the ground. On the whole, these are rather generalized terrestrial frogs.

TABLE 23
Regression Statistics for Eleven Samples of the Genus *Sphenophryne*[a]

Sample	TL/SV				HW/SV				HAND/SV				FOOT/SV				EYE/SV			
	α	β	r	n	α	β	r	n	α	β	r	n	α	β	r	n	α	β	r	n
S. adelphe	.504	.967	.940	37	.522	.863	.924	37	.338	.847	.792	9	.562	.932	.810	9	.227	.751	.947	37
S. gracilipes[b]	.560	.935	.918	37	.493	.890	.921	37	—	—	—	—	—	—	—	—	.339	.600	.856	36
S. gracilipes[c]	.822	.804	.931	61	.528	.843	.966	73	.440	.764	.886	61	.775	.828	.931	61	.358	.577	.897	39
S. fryi[d]	—	—	—	—	—	—	—	—	.265	.920	.965	16	—	—	—	—	—	—	—	—
S. fryi[e]	.726	.831	.982	31	—	—	—	—	—	—	—	—	—	—	—	—	.313	.664	.968	31
S. fryi[f]	.669	.835	.985	41	.021	1.065	.950	12	—	—	—	—	.623	.861	.984	39	.273	.722	.979	41
S. robusta[g]	.779	.790	.964	50	.588	.867	.973	50	.271	.908	.973	43	.731	.814	.957	48	.242	.757	.958	50
S. robusta[h]	1.046	.696	.867	46	.453	.942	.924	21	—	—	—	—	.846	.772	.898	38	.252	.746	.883	46
S. robusta[i]	.863	.756	.939	33	.516	.918	.945	32	.301	.877	.927	24	.852	.753	.924	29	.247	.747	.952	34
S. pluvialis[e]	.837	.812	.985	33	.367	1.016	.989	33	—	—	—	—	—	—	—	—	.223	.811	.966	33
S. pluvialis[j]	.734	.839	.975	45	.396	.995	.980	45	.390	.807	.930	13	1.158	.693	.884	13	.284	.721	.962	45

[a] Power curves of the form $Y = \alpha X^{\beta}$.
[b] Queensland.
[c] Papua New Guinea.
[d] Pooled sample.
[e] Thornton Peak.
[f] Mt. Windsor Tableland.
[g] Pooled sample.
[h] Lamins Hill and Boonjee.
[i] Mt. Spec vicinity.
[j] Kuranda and south.

TABLE 24
Regression Statistics for Twelve Samples of the Genus *Sphenophryne*[a]

Sample	EN/SV				IN/SV				Third Finger Disc/SV				Fourth Toe Disc/SV			
	α	β	r	n	α	β	r	n	α	β	r	n	α	β	r	n
S. adelphe	.070	1.024	.886	37	.164	.836	.937	37	.019	1.092	.877	12	.056	.816	.636	12
S. gracilipes[b]	.208	.635	.876	36	.140	.888	.941	36	—	—	—	—	—	—	—	—
S. gracilipes[c]	.232	.606	.925	39	.260	.665	.939	39	.035	.882	.869	21	.080	.727	.749	21
S. fryi[d]	—	—	—	—	.195	.789	.980	57	.026	1.004	.956	25	.050	.916	.952	25
S. fryi[e]	.145	.783	.973	31	.207	.768	.985	31	.021	1.065	.950	12	.054	.905	.984	12
S. fryi[f]	.146	.775	.986	41	.277	.666	.977	41	—	—	—	—	—	—	—	—
S. robusta[d]	.098	.894	.966	50	.181	.833	.961	50	.019	1.109	.865	29	.041	.985	.936	29
S. robusta[g]	.110	.858	.914	52	.136	.920	.897	52	—	—	—	—	—	—	—	—
S. robusta[h]	.107	.865	.951	34	.210	.778	.952	34	—	—	—	—	—	—	—	—
S. pluvialis[d]	—	—	—	—	—	—	—	—	.031	.984	.645	37	.057	.922	.654	37
S. pluvialis[e]	.100	.923	.972	33	.181	.850	.979	33	—	—	—	—	—	—	—	—
S. pluvialis[i]	.125	.857	.969	45	.180	.847	.978	45	—	—	—	—	—	—	—	—

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

[b] Queensland.

[c] Papua New Guinea.

[d] Pooled sample.

[e] Thornton Peak.

[f] Mt. Windsor Tableland.

[g] Lamins Hill and Boonjee.

[h] Mt. Spec vicinity.

[i] Kuranda and south.

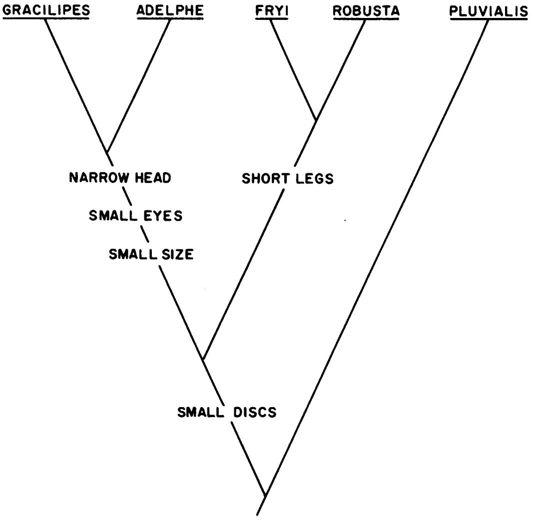

FIG. 62. A hypothesis of interspecific relationships among Australian *Sphenophryne*. Characters given are presumed to be synapomorphies of the species of that branch on which they lie.

MORPHOLOGY AND INTERSPECIFIC RELATIONSHIPS

The relative morphological uniformity of Australian *Sphenophryne* implies a dearth of characters useful in determining interspecific relationships. Primitive states may be estimated with even less confidence than in *Cophixalus*. Again, the larger New Guinean fauna provides the comparison.

Fifteen species of *Sphenophryne* are listed at present for New Guinea, including *gracilipes*, the one species also found in Australia, one species in the Aru Islands, and an undescribed species in New Britain (Zweifel and Tyler, 1982, table 1). Other apparently distinct species await study. The New Guinean *Sphenophryne* are morphologically more diverse than their Australian congeners. The former include a scansorial species with enlarged digital discs, several leaf-litter forms with little or no disc development, terrestrial forms with apparently less cryptic habits than the litter dwellers, and a streamside species with webbed toes. One species is known only from a hatchling and another from a single specimen 16.5 mm in length. Aside from these two and *gracilipes*, the New Guinean *Sphenophryne* are mostly larger than the Australian, with seven species larger than any Australian one, and one giant reaching 60 mm SV.

As defined at present, *Sphenophryne* is not demonstrably a monophyletic group (though there is no reason to question the monophyly of the Australian forms). Not only is there considerable morphological diversity, but the key diagnostic difference from other genera of the subfamily Genyophryninae—possession of an elongate clavicle reaching from the scapula almost to the midline of the girdle—is a primitive state. If the scansorial and riparian extremes seen in the New Guinean species may be taken as derived conditions, then the Australian species fall with the remaining New Guinean forms in a group of forest floor-dwelling species of rather generalized and perhaps primitive morphology.

The assumed synapomorphies of small size, small eyes, and narrow head define the sibling species *adelphe* and *gracilipes* as a monophyletic group (fig. 62), but placement of the other species is less secure. I regard *pluvialis* as the most plesiomorphic Australian *Sphenophryne*. If this is correct, the possession of smaller digital discs distinguishes the branch bearing the other four species, and the synapomorphy of shorter legs characterizes the sibling pair *fryi* and *robusta*. This hypothesis requires testing by use of other characters, perhaps those contained in muscular and biochemical systems.

VOCALIZATIONS

Methods of recording, analyzing, and describing vocalizations are presented in the section on Methods, and descriptions of vocalizations are in the species accounts. The purpose here is to make interspecific and intergeneric comparisons with the purpose of possibly using characteristics of calls in inferring evolutionary relationships. Vocalizations discussed here are the "advertisement" calls (Wells, 1977), commonly but perhaps

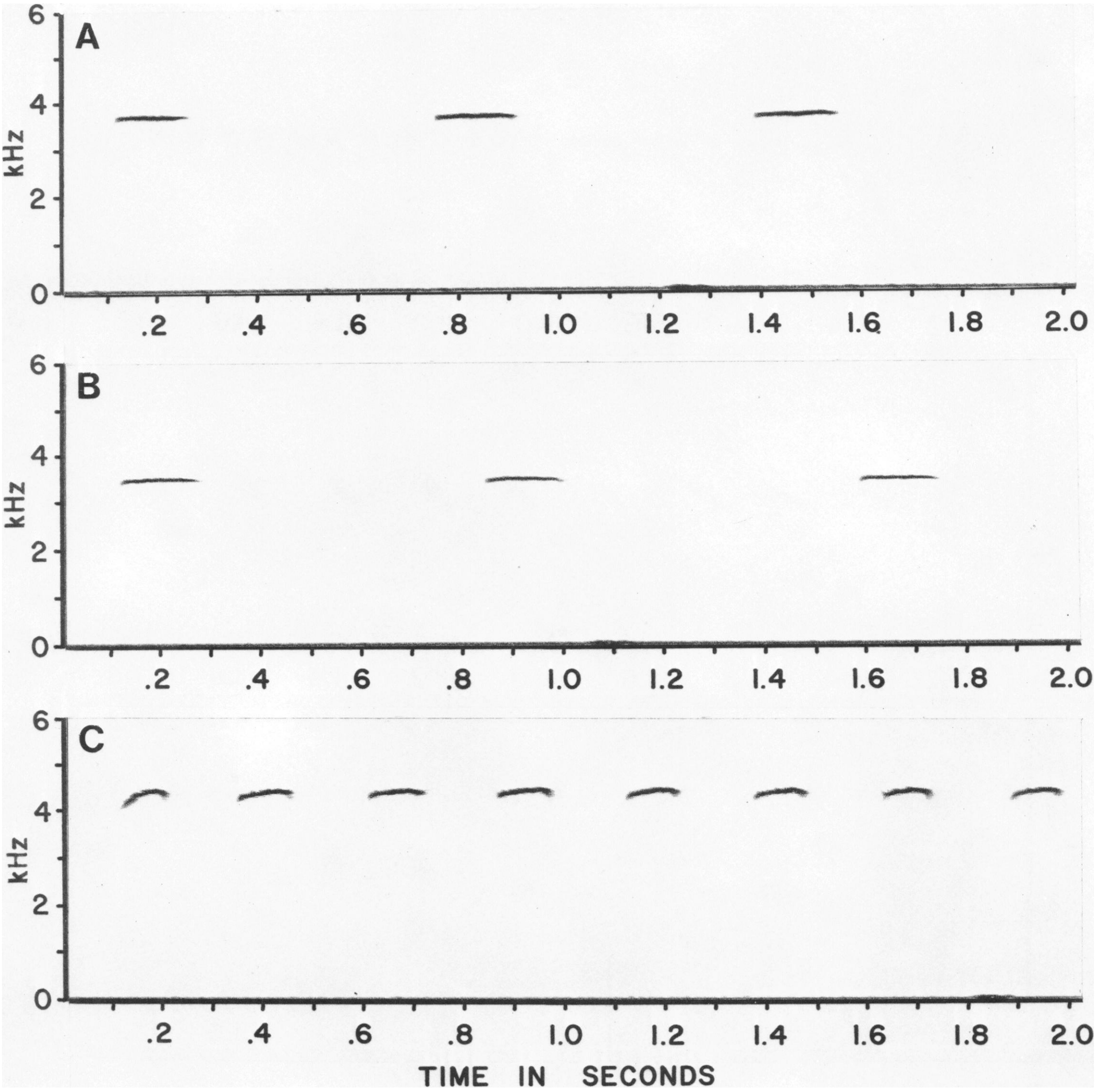

FIG. 63. Audiospectrograms of parts of advertisement calls of *Sphenophryne,* all graphed with 45 Hz filter. **A,** *S. gracilipes,* AMNH 83069, Wipim, Papua New Guinea, air 22.8°C; **B,** *S. gracilipes,* QNPWS N32254, near Coen, Queensland, air 24.0°C; **C,** *S. adelphe,* voucher not identified but possibly holotype, Croaker Island, Northern Territory, no temperature.

too specifically referred to as "mating" calls in much of the literature.

GENUS *SPHENOPHRYNE*: I have recordings of all five Australian species, though for *S. adelphe* I have only brief segments from two individuals. The calls of these species are basically similar (figs. 63, 64) though abundantly distinct. Individual notes are short (0.05–0.15 sec), moderately high pitched (3.5–4.5 kHz), and well tuned (not harsh and unmusical). The chief difference among the calls is the rate at which notes are uttered. This ranges from a low of 1.5 notes per second in *gracilipes* to about 14 per second in *pluvialis.* Notes are grouped into calls averaging from about 1–16 seconds long, though only one species, *gracilipes,* averages more than 5 seconds. Some slight frequency modulation is

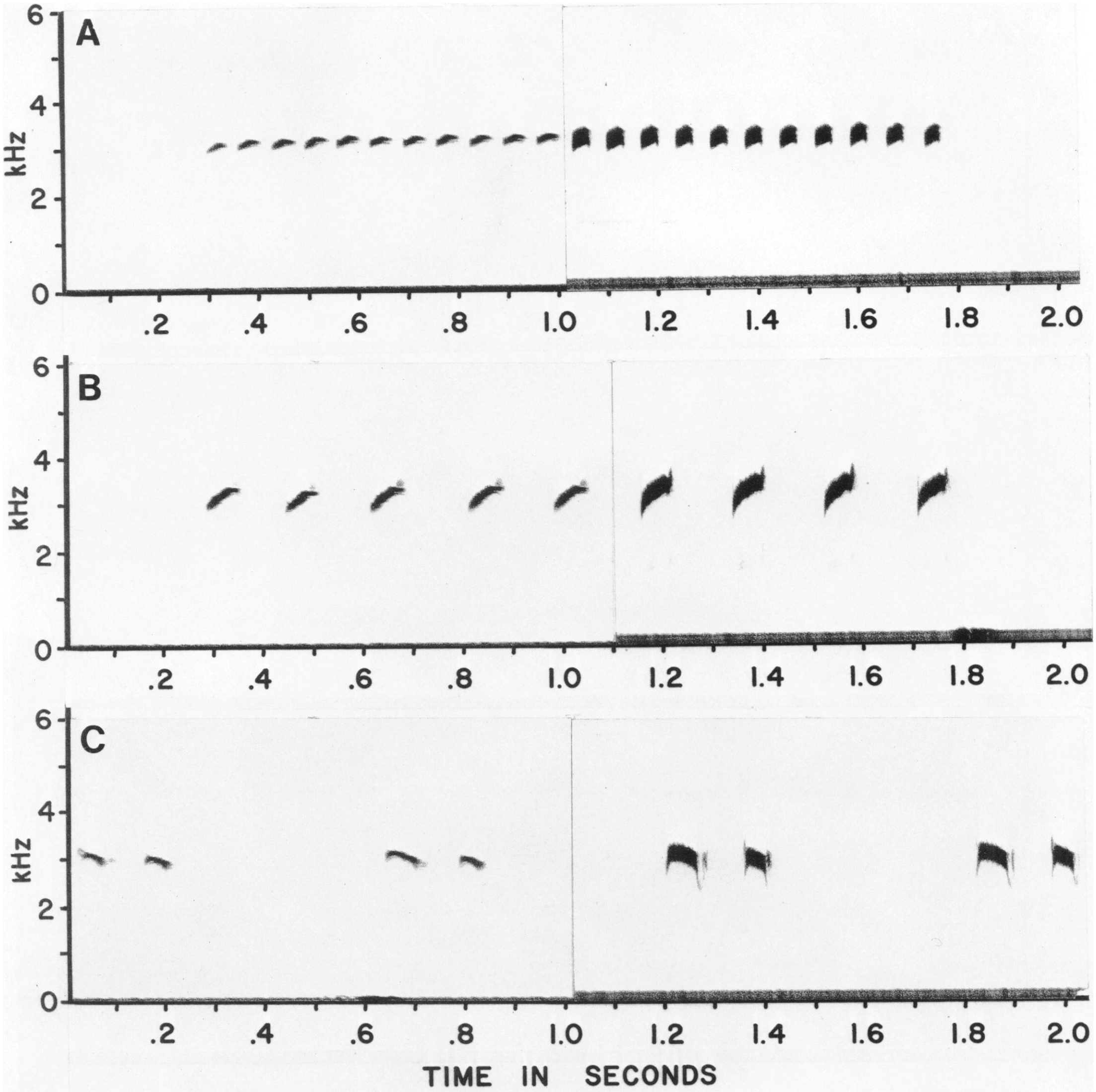

FIG. 64. Audiospectrograms of advertisement calls of *Sphenophryne,* all recorded in Queensland and graphed with 45 Hz filter on left and 300 Hz filter on right. **A,** *S. pluvialis,* AMNH 111466, vicinity of Kuranda, substratum 23.4°C, entire call; **B,** *S. fryi,* AMNH 111452, Mt. Windsor Tableland, substratum 20.6°C, entire call; **C,** *S. robusta,* AMNH 111468, Paluma, substratum 18.4°C, part of call.

evident in most calls. *Sphenophryne robusta* gives notes in couplets whereas the other species space them rather evenly.

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 utterings of *S. robusta,* possibly a derived condition, I see no objective way of arranging the calls on a primitive to derived axis.

Comparison of the calls with those of the more abundant New Guinean species is a logical step, but these are rather poorly known. I have a recording from one species, possibly undescribed, that has a call much like that of the Australian *S. pluvialis.* The only published audiospectrogram for a New Guinean

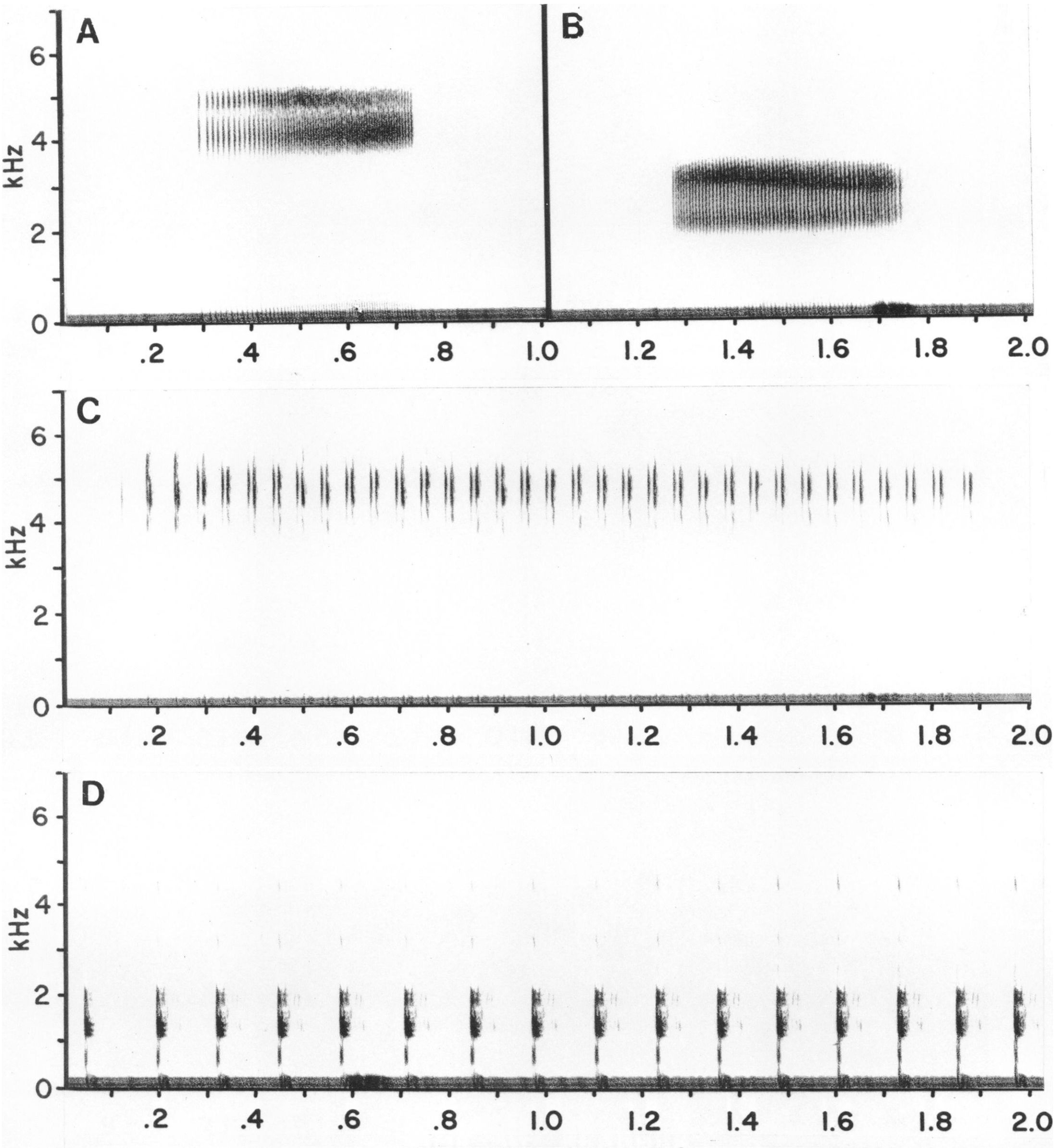

FIG. 65. Audiospectrograms of advertisement calls of *Cophixalus,* all recorded in Queensland and graphed with 300 Hz filter. **A,** *C. bombiens,* AMNH 111433, Mt. Windsor Tableland, substratum 20.6°C; **B,** *C. neglectus,* AMNH 111393, Mt. Bellenden Ker, air 18.2°C; **C,** *C. crepitans,* QM J41648, McIlwraith Range, air 24.4°C; **D,** *C. saxatilis,* AMNH 111425, Black Gap, air 25.6°C, initial part of call only.

species depicts a harsh call likened to the "bark of a dog" (Tyler and Menzies, 1971, p. 83), and thus utterly unlike the Australian calls. Much more information will have to be gathered before vocalizations of New Guinean and Australian species can profitably be compared.

GENUS *COPHIXALUS*: Recordings of calls of 8 of the 11 *Cophixalus* are at hand. Seven species (and probably another, for which only

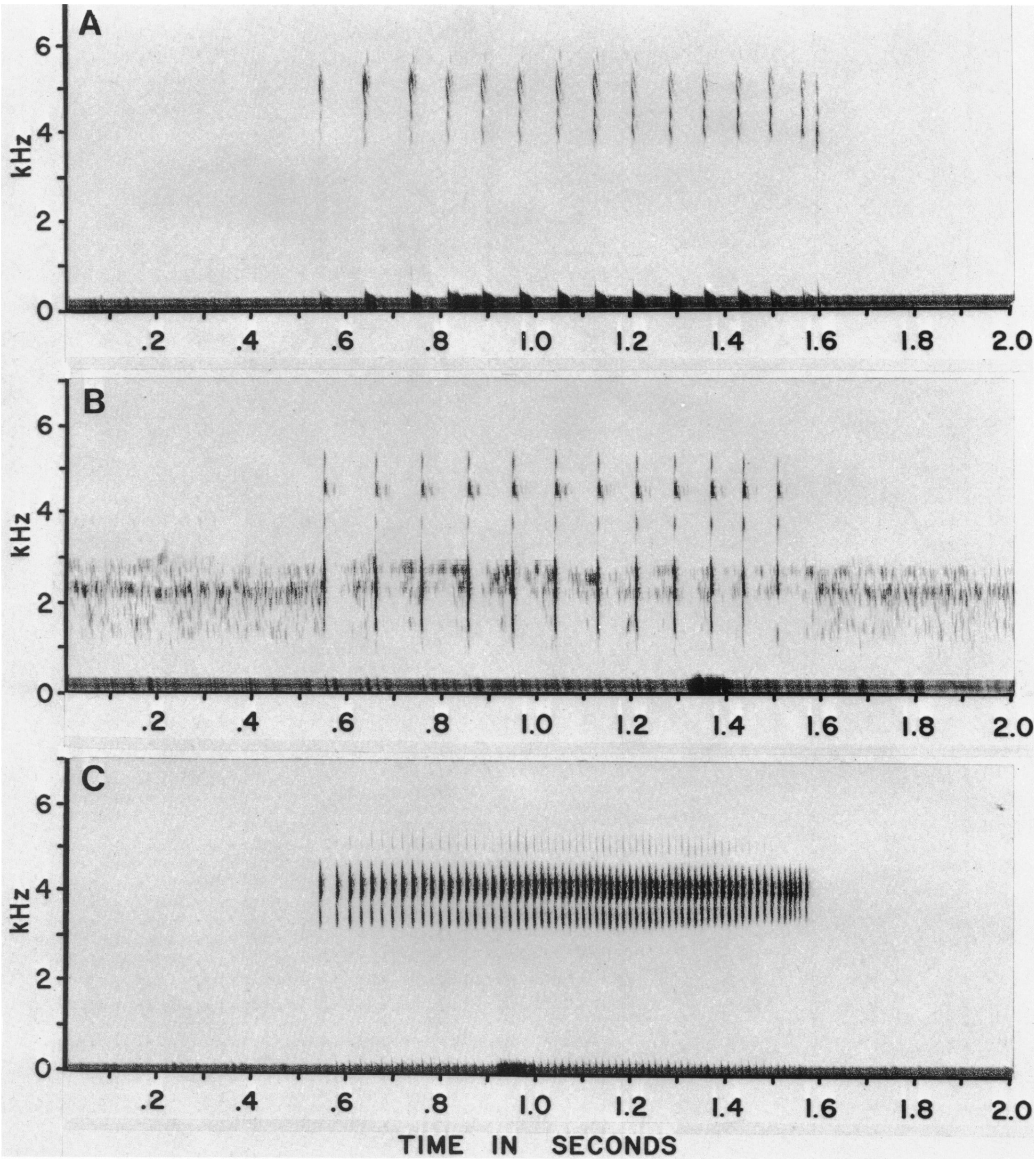

FIG. 66. Audiospectrograms of advertisement calls of *Cophixalus*, all recorded in Queensland and graphed with 300 Hz filter. **A,** *C. hosmeri*, AMNH 111444, Mt. Lewis, air 19.3°C; **B,** *C. concinnus*, AMNH 117290, Mt. Lewis, air 22°C; **C,** *C. infacetus*, QM J42059 (holotype), 12.5 km S, 13 km E Millaa Millaa, air 23.4°C.

a verbal description is available) have calls consisting of trains of sharply defined pulses. In some instances the pulses are so closely spaced as to be heard as a buzz rather than a series of clicks or taps (figs. 65, 66). The eighth species, *C. ornatus* (fig. 67), has a call that sounds quite different from the others and upon gross examination of the audiospectrograms appears quite different. However, it too can be considered as a pulsed call,

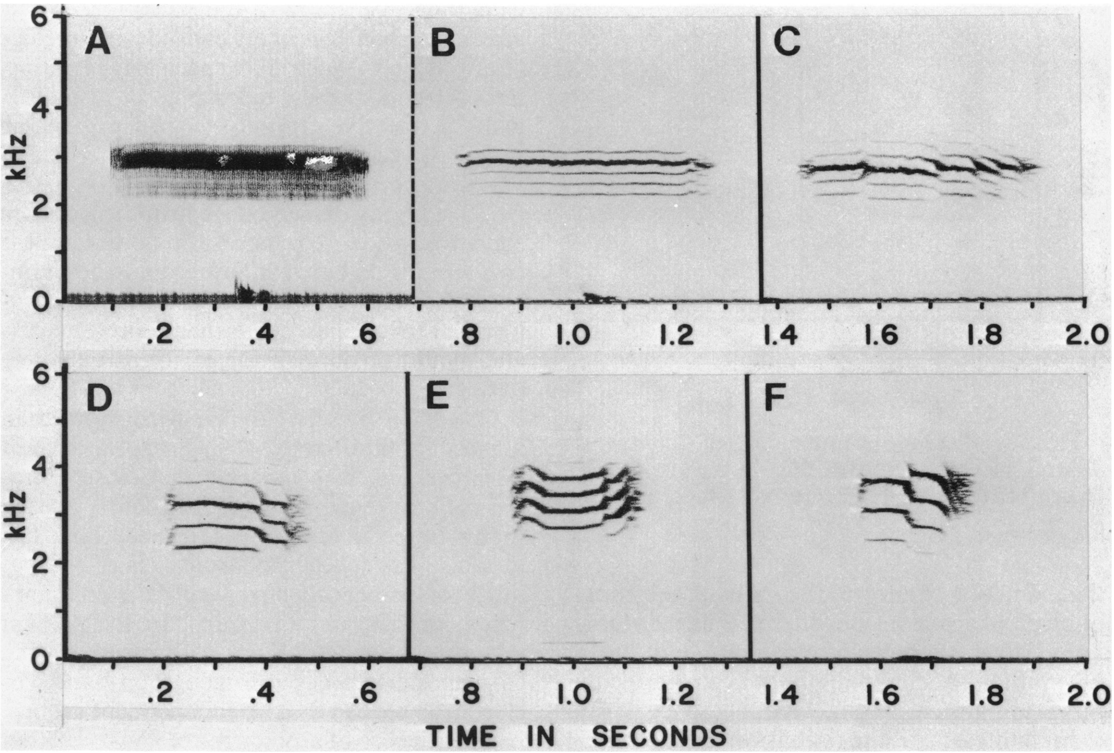

FIG. 67. Advertisement calls of *Cophixalus ornatus* recorded in Queensland. **A,** AMNH 111406, Paluma, air 18.2°C, 300 Hz filter; **B,** same note as A but this and subsequent calls graphed with 45 Hz filter; **C,** AMNH 111420, vicinity of Tinaroo Dam, air 20.2°C; **D,** AMNH 111415, vicinity of Palmerston National Park, air. 23.6°C; **E,** AMNH 111423, vicinity of South Mission Beach, air 24.8°C; **F,** QNPWS N28797, vicinity of Tully, air 26.8°C. Note variation in frequency modulation and in note duration. Calls A–D are from highland populations, E and F from coastal lowlands.

but with the pulse rate greatly exaggerated over the most rapid rate seen in other species (cf. fig. 67A).

As in *Sphenophryne,* the communality of call structure among these species is consistent with a monophyletic origin for Australian *Cophixalus,* especially so when compared to the diversity of calls in New Guinean congeners (see below). I recognize that the Australian call may be a generally primitive type, but it seems more reasonable to suppose a monophyletic origin for the Australian group with subsequent diversification in morphology and calls than to hypothesize independent derivation of two or more Australian lines that inherited and retained highly similar calls.

The problem of making interspecific comparisons of Australian *Cophixalus* is the same as that in *Sphenophryne*: the calls differ mainly in one feature, pulse repetition rate, and I see no reason for considering any particular rate as primitive. Indeed, there is no reason to suppose that evolutionary change in pulse rate is gradual rather than saltatory and, hence, no ground for proposing a linear arrangement of pulse rates as representing an evolutionary progression. Differences in dominant frequencies of calls (fig. 65A, B offers a good example) probably are related to body size and do not provide an independent character. The double-pulsed call of *crepitans* and the extremely high pulse rate of *ornatus* may be considered derived, but these autapomorphies contribute nothing to understanding interspecific relationships. Call parameters show essentially no correlation with relationships as deduced from morphology

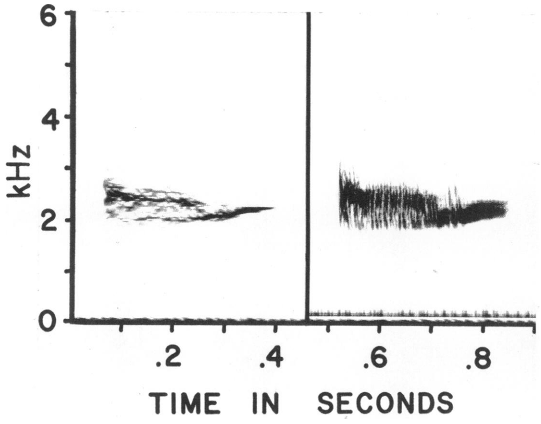

FIG. 68. Possible encounter call of *Cophixalus ornatus* recorded by Glen Ingram on Mt. Lewis, December 6, 1975; 45 Hz filter on left, 300 Hz on right.

(fig. 59). For example, the calls of the morphological sister species *saxatilis* and *ornatus* are at opposite poles of pulse rate, and those of another species pair, *bombiens* and *hosmeri,* are almost as different.

In contrast to the situation in *Sphenophryne,* I have recordings of a good variety (18 species) of New Guinean *Cophixalus,* but this still does nothing to clarify relationships between New Guinean and Australian species. The New Guinean species have an extremely diverse array of calls. Some peep like Australian *S. gracilipes* (Zweifel and Allison, 1982, fig. 7); others have buzzing, chirping, or quacking notes. The two having click-train calls most like those of the Australian mode are among the least likely candidates for close relationship to Australian species. One, a tiny, undescribed species, belongs to an osteologically distinctive group of *Cophixalus* which may deserve generic status. The other is *Cophixalus pansus* (Zweifel and Allison, 1982, fig. 9), a highly derived terrestrial frog of high elevations. A close relationship between these two species or between either and the members of the Australian radiation is most unlikely. The similarities either represent parallel evolution or retention of primitive calling patterns.

CONCLUSIONS: To anyone with more than a passing familiarity with frogs and their vocalizations, it is apparent that closely similar calls have evolved independently a great many times in different families. This homoplasy has made me suspicious of the validity of using call structure as a character when inferring relationships. In the present instance, however, I am impressed by the correspondence between geography and vocalization seen in the two independent groups. In the absence of any morphological or other information to the contrary, I accept the intrageneric similarities of call structure as indicating that the Australian *Sphenophryne* and *Cophixalus* each represent a monophyletic unit with respect to the more numerous and diverse members of these genera in New Guinea. On the interspecific level, calls appear to be of no help in deducing relationships.

ZOOGEOGRAPHY

Microhylids constitute a small proportion of the Australian frog fauna and have figured prominently in few discussions of the biogeography of the region, being mentioned principally in the context of dispersal between Australia and New Guinea.

Savage (1973) considered the Microhylidae as a Gondwanaland element that was present in tropical areas of early Cretaceous Australia. His scenario has Australian microhylids invading New Guinea when that land mass emerged in the Miocene and from there moving northward through the Indonesian region to mainland China. He suggested that with increasing aridity over the Tertiary, "tropical humid conditions and associated frogs were eliminated from northern Australia, probably in early Pliocene, and only later became re-established" (Savage, 1973, p. 439). In his view, "the Australian microhylid . . . fauna is derived completely from New Guinea" (*loc. cit.*). As part of his zoogeographic analysis, Savage reinterpreted the content and status of the subfamilies Asterophryinae and Sphenophryninae (=Genyophryninae), concluding that only one subfamily should be recognized (Asterophryinae) and that it should include the Asian genus *Caluella*. The later decision extended the range of what had been a basically Australo-Papuan group through Indomalaya into southern China.

Tyler (1979a) critically reviewed and rejected Savage's biogeographic and systematic conclusions. He drew upon information (his own and Zweifel, 1971) not available to Savage when his work was written, but also emphasized the unity of the Australo-Papuan species especially with respect to the derived character of direct embryonic development, a feature not found in *Caluella*. Tyler's and Savage's biogeographic views converged in regarding the Australian microhylids as of New Guinean origin, but Tyler favored a Southeast Asian rather than Gondwanan ultimate source for the Australo-Papuan fauna.

I agree with Tyler that the inclusion of *Caluella* in the same subfamily as the Australo-Papuan microhylids is unsupportable. There is nothing in the morphology of *Caluella*—no shared derived character—that convincingly allies this evidently primitive genus with the genyophrynines or with the more derived asterophryines. Savage's systematic arrangement also imposes a biogeographic anomaly in that the most primitive genus of his redefined Asterophryinae is at the farthest-flung fringe of the distribution with the more advanced forms closer to the hypothesized Gondwanan homeland.

The view of extermination of microhylids in Australia prior to reinvasion from New Guinea also is open to question. Australia became progressively more arid through the Tertiary, but recent studies do not affirm the elimination of tropical humid conditions that Savage (1973, p. 439) postulates. Sluiter and Kershaw (1982, p. 220) summarized their conclusions: "There is some evidence of Late Tertiary vegetation trends continuing into the Pleistocene with a further reduction in evergreen rainforest, but it may not have been until the Late Quaternary that there was any major disruption to the established Pliocene vegetation patterns.... most likely as a result of the activities of aboriginal man."

Whether the Australo-Papuan microhylids were derived from a now extinct Australian-Gondwanan line or from Southeast Asian stock (itself possibly Gondwanan, via the drifting Indian continent) will not be determined by concocting further scenarios. An immunological approach that compared South American, Asian, and Australo-Papuan taxa could be enlightening. For example, if the three groups were roughly equally distant from one another immunologically this would favor the hypothesis of each having been derived directly from Gondwanaland. If the Asian and Australo-Papuan groups proved to be much closer to each other than either was to the South American group, the hypothesis of Southeast Asian derivation for the Australo-Papuan fauna would be favored.

The age of the genera of genyophrynine and asterophryine microhylids is an open question. Tyler, Watson, and Martin (1981, p. 1281) stated: "Several New Guinea genera are highly adapted to montane conditions. These montane genera simply cannot be of any greater antiquity than the elevation of the mountains on which they occur; so that, with only one or two notable exceptions..., they evolved no earlier than the mid-Miocene." These statements are based on an erroneous assumption. In fact, all 13 genera of Genyophryninae and Asterophryinae have species that occur at low elevations (less than 100 m), so the possibility that some or all genera were in existence prior to the mid-Miocene collision of plates that gave rise to New Guinea cannot be dismissed. Probably it is some of the species, especially the montane ones, and not the genera of New Guinean (and Australian) microhylids that are no older than mid-Miocene.

Whatever the ultimate source and age of the Australo-Papuan microhylids, there can be no doubt that the Australian forms are a small subset of a basically Papuan fauna. That the forerunners of the present Australian microhylids dispersed from New Guinea to Australia in the Pleistocene is implicit or explicit in the zoogeography of authors who have discussed the subject. Tyler (1972, p. 253) stated that "Representatives of the genera *Sphenophryne, Cophixalus* and *Nyctimystes* [a hylid genus most speciose in New Guinea] entered Australia across an exceptionally moist land communication probably cloaked in rainforest. . . ." Tyler considered this to be part of the earliest of a sequence of faunal exchanges through the region that is now Torres Strait. The Pleistocene was not specifically mentioned, but in reference to Tyler (1972), Tyler, Watson, and Martin (1981, p. 1281) stated "The limited colonization of northern Australia by a few microhylids from New Guinea is postulated by Tyler . . . to be a Pleistocene event."

Savage's (1973, p. 439) statement that microhylids "were eliminated from northern Australia, probably in early Pliocene, and only later became re-established" seems to imply a Pleistocene reinvasion.

An important fact brought out by Kikkawa, Monteith, and Ingram (1981) is the near lack of rainforest species of frogs common to New Guinea and Australia. Thirteen species of frogs are known to occur both in New Guinea and Australia. These are the "bidomicilic" species of Tyler (1972, table 13.1), less *Lechriodus fletcheri* (confined to Australia) but including *Uperoleia lithomoda* and *Ranidella remota,* both of which occur in Australia and in New Guinea (Tyler and Davies, 1984; Tyler, Davies, and Martin, 1981, p. 153). Only one species, the hylid *Litoria genimaculata,* is restricted to rainforest and is found in both areas. It is widespread in New Guinea and lives in northeast Queensland rainforests as far south as the Mt. Spec region. Some species among the 13 (e.g., *Litoria infrafrenata* and *L. nasuta*) occur in rainforest on both sides of Torres Strait, but also live in drier and more seasonal habitats. The clear implication of the dissimilarity of rainforest faunas is that the Torres Strait region—whether above or below sea level during Pleistocene oscillations—has provided minimal opportunity for interchange of species of frogs dependent upon rainforests.

Kikkawa, Monteith, and Ingram (1981, p. 1717) contrasted the distribution exemplified by *Litoria genimaculata* with a "much older rainforest connection between New Guinea and Australia as pointed out by Tyler" with reference to the genera *Cophixalus, Sphenophryne,* and *Nyctimystes.* These authors (1981, p. 1718) suggested that this "earlier connection of rainforest between New Guinea and Cape York Peninsula may have existed in the early Pleistocene or Pliocene."

I see no reason for assuming that the initial vicariant event separating Australian and New Guinean microhylids occurred as recently as the Pleistocene; such an assumption implies that virtually all speciation of Australian microhylids has taken place in Australia in the Pleistocene unless Papuan conspecific populations have been exterminated. Paleobotanical evidence (Sluiter and Kershaw, 1982) and paleoclimatic inferences (Beard, 1977) indicate that habitat suitable for tropical microhylids has existed in Australia since the mid-Tertiary juxtaposition of tectonic plates that initiated the elevation of the New Guinea region. Opportunities for dispersal from either Australia to proto-New Guinea (Savage, 1973) or the other way (Tyler, 1972) date back that far as do the possibilities for vicariant events associated with continued plate movement.

Rainforest regions of Australia suffered climatic vicissitudes during the Pleistocene with rainforest no doubt being fragmented and recombined, eliminated, and reconstituted (Webb and Tracey, 1981, pp. 662–667). When the habitat is subdivided into discrete units there is a temptation, irresistible to some biogeographers, to seek out taxonomic groups with congruent patterns of distribution and to date the speciation events from what can be inferred of the most recent disjunction of the habitats. In the case of the Australian microhylids, this could lead to inferring late Pleistocene—even Quaternary—speciation. For example, the possible sister species *Cophixalus hosmeri* and *C. bombiens* (fig. 59) occur on adjacent, narrowly disjunct forest blocks (fig. 23), ideal grist for the Pleistocene speciation mill. *Cophixalus exiguus* and *C. mcdonaldi* are more isolated from closely related species but could be fit into a scenario of Pleistocene speciation without too much difficulty.

The work of Heyer and Maxson (1982) on neotropical frogs, in which concepts of vicariance and forest refugia figure prominently, provides a welcome cautionary note to those who would accept the correlation of present-day distributions with inferred refugia as evidence of Pleistocene speciation. These authors present biochemical evidence indicating that in many such instances speciation events were much more ancient, mostly pre-Pliocene. Similarly, Maxson and Roberts (1984) use biochemical evidence to refute a hypothesis of multiple Pleistocene dispersal and speciation in the genus *Helioporus* in southern Australia. To me, the paleobotanical evidence and the fact that 15 of 16 Australian species of microhylids do not occur in New Guinea (and the sixteenth is anomalous in being distributed in non-rainforest habitats) implies a long evolutionary history for the group in Australia, certainly predating the Pleistocene. If my inference that Australian *Cophixalus* and *Sphenophryne* are each monophyletic in Australia is correct, then these lines could each derive from a single Tertiary dispersal or vicariance event involving genyophrynine stock evolved in the emerging New Guinea region. Alternatively, they could derive from relicts of a Gondwanan fauna largely exterminated in Australia as tropical rainforest became progressively restricted to the northeastern fringe of the continent.

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