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AND EVOLUTION OF FROGS OF THE
NEOTROPICAL GENERA ATELOPUS,
DENDROPHRYNISCUS,
MELANOPHYRNISCUS,
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By ROY W. McDIARMID

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COMPARATIVE MORPHOLOGY AND EVOLUTION OF
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ABSTRACT: Atelopodid frogs are one of the most interesting and diverse groups of Neotropical Anura. The systematic status and evolutionary history of the genera in this family have been poorly understood. The purpose of this study is to analyze available knowledge of the morphology and biology of these frogs in order to clarify their evolutionary relationships and history. The group includes approximately 50 species in four genera: *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*. Data indicate that *Brachycephalus*, a genus originally included in the family, is not closely related to the four genera. Its relationships will be discussed elsewhere.

Representative specimens of all genera and most species were examined. Information concerning myology, osteology, and reproductive morphology was gathered. All available literature was reviewed and pertinent information was assimilated into this report.

A detailed description of thigh and jaw musculature and osteology of the species is presented. The skulls, pectoral girdles, and hyoid apparatus are described and illustrated. Components of the auditory apparatus, certain aspects of their external morphology, reproductive biology, and ecology are described.

Each genus is defined according to 43 characters. Their geographical distributions are stated briefly and their included and referred species are listed. *Atelopus minutus* Melin and *Atelopus proboscideus* Boulenger are placed in the genus *Dendrophryniscus*. *Atelopus rubriventris* Vellard is placed in the genus *Melanophryniscus*.

The four genera are discussed and their character states compared. *Melanophryniscus* has the greatest number of primitive states and the least number of advanced states and is probably most similar to the ancestral stock. *Atelopus* also has many primitive states but possesses the greatest number of advanced states. *Atelopus* and *Melanophryniscus* were derived from the same lineage, but *Atelopus* has undergone a significant radiation at the species level and has several advancements not found in the other genera. *Dendrophryniscus* was derived from the *Melanophryniscus* line and exhibits parallel evolution in some character states with *Atelopus*. *Oreophrynella* has more advanced character states than either *Melanophryniscus* or *Dendrophryniscus* and only one less than *Atelopus*. However, *Oreophrynella* has the highest number of unique states and the lowest number of primitive states. *Oreophrynella* apparently was derived from the ancestral stock at a different time from the *Melanophryniscus-Atelopus-Dendrophryniscus* line and has subsequently become greatly specialized.

Major evolutionary trends and morphological character shifts apparently are associated with changes in means of locomotion; others are the result of differential metamorphosis. Biological modifications associated with the loss of the middle ear apparatus and the development of aposematic coloration are important. The familial status of the Atelopodidae is discussed and rejected. The genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella* are placed in the family Bufonidae which is redefined.

The ancestral stock from which the four genera were derived probably was present in South America before the beginning of the Cenozoic. The ancestral *Melanophryniscus-Dendrophryniscus-Atelopus* stock probably occurred in a savanna or deciduous forest habitat in southeastern Brazil. *Melanophryniscus* has retained many of the generalized ancestral characteristics and currently is found in the same general type of habitat. *Dendrophryniscus* was derived from the *Melanophryniscus* stock and has adapted to the wet tropical forest of eastern Brazil and the Amazon Basin. *Atelopus* has adapted to a stream-side habitat and moved into montane areas which became available with the uplift of the Andes in Late Cretaceous and Early Tertiary. This new habitat has been successfully exploited by *Atelopus* and has been a major factor contributing to their specific radiation. *Oreophrynella* is a very specialized frog that was derived from an old bufonid stock and subsequently restricted to Mount Roraima, an ancient part of the Guiana Shield.

¹Research Associate, Section of Herpetology, Los Angeles County Museum of Natural History; and Department of Biology, University of South Florida, Tampa.

INTRODUCTION

The South American continent, with its complex physiography and vast areas of tropical, subtropical, and temperate forest, is a center of diversity for anuran amphibians. There are more than 750 species assigned to ten families and approximately 105 genera recorded from the continent. One of the most interesting of the South American groups is the nominal family Atelopodidae which includes about 50 species of frogs that are restricted to Central and South America. Most anuran systematists consider these frogs to be species of *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, *Oreophrynella*, and *Brachycephalus*. At the outset of this study I assumed that these five genera formed a natural group (Atelopodidae). As the study progressed it became more and more apparent that the monotypic genus *Brachycephalus* is not closely related to the other four genera. Therefore, only *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella* are considered here. The status of *Brachycephalus* is discussed elsewhere (McDiarmid, MS).

Within this group there is considerable biological and morphological diversity. Species of *Atelopus*, *Dendrophryniscus* and *Oreophrynella* are primarily tropical forms. One species of *Atelopus* is found at sea level in the warm, wet rain forests of the Chocó in Colombia; another species is adapted to the cold, unforested paramos at over 4000 meters elevation in the Andes. Species of *Melanophryniscus* are primarily subtropical and south temperate in distribution, although one form is known from a locality in the Amazon Basin. While species of *Atelopus*, *Dendrophryniscus*, and *Melanophryniscus* are wide ranging forms, the two species of *Oreophrynella* are restricted to a single mountain massif. Most species are terrestrial as adults, but some may be semifossorial, and one species of *Dendrophryniscus* is arboreal and deposits its eggs in bromeliads. Adults range from 14 mm in males of a small species of *Dendrophryniscus* to nearly 60 mm in females of a large species of *Atelopus*. Individuals of most species are thin and elongate with long, spindly legs; some, however, are short and robust. Many species are brightly colored and have variable markings of red, green, yellow, orange, or black; others may be gray, dull brown, or black. Some forms have smooth skin while others have rugose and warty skin. Some species vocalize; others apparently do not. In some areas these frogs are important components of the fauna; in other areas they are relatively rare. At certain times of the year some species are extremely abun-

dant and may be the dominant vertebrate in the area; at other times, this same species may be nearly impossible to find.

The reproductive biology and life history of only four of the more than 40 species of the genus *Atelopus*, which has the greatest spectrum of adaptive types, are known. Limited information is available on the life histories of two species of *Melanophryniscus* and two species of *Dendrophryniscus*, but nothing is known concerning the reproductive biology of *Oreophrynella*.

The generic relationships and systematic status of these frogs are poorly understood. Since the first species were described in the mid-1800's, they have been variously placed in approximately one-half of the currently recognized anuran families, and three of the four genera have been placed in their own families. In one of the classic works on salientian phylogeny, Noble (1922) placed the genera, together with several genera that now comprise the family Dendrobatidae, the firmisternal members of the Leptodactylidae, and the Rhinodermatidae, in a single family. Most workers, including Noble, agree that the atelopodids are related to the Bufonidae, but no one has demonstrated the nature of this relationship.

It was apparent that this group of frogs provided an ideal opportunity for a study of major patterns of anuran evolution. This opportunity, coupled with my interest in ecology and zoogeography of tropical organisms, was the stimulus for this study. The project is designed to answer the following questions: 1) What types of variation, morphological or otherwise, are characteristic of each genus? 2) What characteristics are most useful in defining the genera from the phylogenetic viewpoint? 3) What types of relationship exist among the generic categories? 4) What are the evolutionary implications of the morphological changes within and among the genera? 5) How do the characteristic features of the genera considered as a unit, compare with other groups of closely related genera? 6) What can be said concerning the patterns of historical development of the genera?

This study describes in detail the osteology of each genus (based on examination of about 70% of the included species) and certain aspects of their myology and reproductive morphology. All known features of behavior, ecology, and natural history are considered. The genera are redefined, and their relationships are elucidated together with associated morphological and evolutionary trends. Finally, this study makes possible the evaluation of the familial status of the Atelopodidae.

HISTORICAL REVIEW

The generic name *Atelopus* was proposed by Duméril and Bibron in 1841 for the species *flavescens*. Two years later Fitzinger (1843) erected the family Atelopoda to include *Atelopus flavescens* and *Rhinoderma darwini*.

During the period from 1834 to 1857, several other generic names were proposed for species related to *A. flavescens*. Wiegmann (1834) described *Phryniscus nigricans* from southern Peru. Duméril and Bibron (1841) made reference to *Phryniscus nigricans* from Montevideo. A careful comparison of the two descriptions indicates that *Phryniscus nigricans* Wiegmann is not the same as *Phryniscus nigricans* of Duméril and Bibron. Nevertheless, most workers have referred to the Montevideo frog as *Phryniscus nigricans*.

Wagler (1828) proposed the name *Chaunus marmoratus*. In 1830 he recognized that *Bufo globulosus* Spix (1824) was the same as his *Chaunus marmoratus*, and therefore, because of priority, he allocated the specific name *globulosus* to the genus *Chaunus*. Tschudi (1838) ignored the priority of Spix's *globulosus* and recognized *Chaunus marmoratus* plus a second species *formosus*. Peters (1873) demonstrated that the type of Spix's *Bufo globulosus* was actually a *Bufo granulosus*. Thus *Chaunus* was established for a species of *Bufo* and became a synonym of *Bufo*. Tschudi's (1838) reference to *Chaunus formosus* apparently was based on specimens in the Paris museum of *Phryniscus nigricans* of Duméril and Bibron. However, as pointed out by Boulenger (1894), the name *Chaunus formosus* is a *nomen nudum*. Fitzinger (1843) considered *Chaunus globulosus* a synonym of *Bufo globulosus*. Günther (1858b), Cope (1867), and Boulenger (1882) assigned *Chaunus formosus* to the synonymy of *Phryniscus nigricans*.

In 1856 Lichtenstein and von Martens described the genus *Phrynidium* and two species, *varium* and *crucigerum*, both from Veragoa (= Veragua). Günther (1858b) considered *Phrynidium* a synonym of *Phryniscus*. Cope (1867) maintained *Phrynidium* for the species *crucigerum*, *varium*, *laevis* and *bibronii* and recognized *Phryniscus* as distinct, including only the species *nigricans*. Boulenger (1882) assigned *Phrynidium* to the synonymy of *Phryniscus*.

Oscar Schmidt (1857) described the genus *Hylaemorphus*, a name originally assigned to two species by Fitzinger, *H. dumerilii* from "New-Granada, Provinz Veragua . . .," and *H. bibronii* from "New-Granada, unweit Panama . . ." In the same paper Schmidt described the genus *Phirix* for the species *pachydermus*, based on a specimen from "Western

von New-Granada, bei Bonaventura. . ." All three were illustrated the next year (Schmidt, 1858). Günther (1858b:43) relegated the name *Hylaemorphus* to the synonymy of *Phryniscus*, apparently on the basis of specimens from the Vienna Museum. In the appendix of the same book Günther (1858b:136) relegated *Hylaemorphus* Fitzinger (in Schmidt) and *Phirix* Schmidt to the synonymy of *Phryniscus*. Cope (1867:196) considered *Phirix* a synonym of *Phrynidium* and listed the species *bibronii*, described as *Hylaemorphus bibronii* Schmidt, as *Phrynidium bibronii* without any mention of *Hylaemorphus* being synonymous with *Phrynidium*. However, on the same page Cope listed *Hylaemorphus* Fitzinger as a synonym of *Phryniscus* Wiegmann. Boulenger (1882) relegated *Hylaemorphus* and *Phirix* to the synonymy of *Phryniscus* where they have remained.

Günther (1858a, b) recognized only two genera of these frogs, *Atelopus* for *flavescens*, and *Phryniscus* for *nigricans*, *laevis*, *cruciger*, *varius*, *olfersii* (referred to *Physalaemus* by Parker, 1927), and *bibronii*. Apparently Günther (1858b) was unaware of Cornalia's description of *Phryniscus ignescens* in 1849. *Phryniscus*, family Phryniscidae, was placed in the section Brachycephalina, while *Atelopus*, family Rhinodermatidae, was placed in the section Bufonina.

Cope (1865) placed *Brachycephalus* and *Atelopus* in the family Engystomidae and had *Phryniscus* in the Bufonidae; both families were in the suborder Bufoniformia. It is not known whether Cope's material of *Phryniscus nigricans* was the same as Wiegmann's or the same as that of Duméril and Bibron. However, in 1867 Cope included all three genera in the family Phryniscidae. Although he cites Wiegmann as the source of the name *Phryniscus*, Cope's material came from Buenos Ayres (sic) and probably was representative of the frogs called *Phryniscus* by Duméril and Bibron. Keferstein (1867, 1868a, b) assigned a Costa Rican frog to *Atelopus varius* rather than *Phryniscus varius* as proposed by Günther. However, Keferstein followed Günther's proposal in that he considered *Atelopus* to be a member of the family Rhinodermatidae.

Mivart (1869) placed *Brachycephalus* and *Phryniscus* in a single family Phryniscidae, a treatment not unlike Günther's classification. However, Mivart placed Günther's Rhinodermatidae, which included *Atelopus flavescens*, in the family Engystomidae and characterized the group as having a perfect ear and thus differing from the Phryniscidae.

Jiménez de la Espada proposed *Dendrophryniscus*

cus brevipollicatus and the family Dendrophryniscidae in 1870. In the description he mentioned its similarities to *Atelopus*, but because of its dilated toe tips, he suggested that its relationships were with Günther's group, the Hylaplesina. He illustrated *Dendrophryniscus brevipollicatus* in 1875. In the same publication Jiménez de la Espada (1875) discussed three species of *Atelopus* as members of the family Rhinodermatidae.

Buchholz and Peters (1875) compared *Atelopus* with *Nectophryne* in their description of *Nectophryne atra*.

Brocchi (1878) suggested that the differences between *Phryniscus* and *Atelopus* were not enough to warrant generic distinction. However, he recognized both *Atelopus* and *Phryniscus* in his 1882-1883 publication.

Boulenger (1882) listed *Brachycephalus* and *Phryniscus* in the family Engystomatidae. *Atelopus* was considered a synonym of *Phryniscus*; the latter contained eleven species. *Dendrophryniscus brevipollicatus* and the leptodactylid *Batrachophryne brachydactylus* were maintained in their own family Dendrophryniscidae.

Cope (1887) continued to recognize the family Phryniscidae and the genus *Atelopus*. Boettger (1892) followed Boulenger and maintained *Phryniscus* in the family Engystomatidae. Günther (1900), however, referred *Atelopus* to the family Brachycephalidae.

In 1894 first Philippi and then Boulenger recognized that *Phryniscus nigricans* Wiegmann was not the same as *Phryniscus nigricans* Duméril and Bibron and that *Phryniscus* Wiegmann was based on a *Bufo*. The next available name for the frogs referred to *Phryniscus* by Duméril and Bibron and others was *Atelopus*. Philippi (1894) selected the specific name *formosus* published by Tschudi in 1838 (in the combination *Chaunus formosus*) to replace *nigricans*. However, as previously indicated, *formosus* is a *nomen nudum*. The only name available, as pointed out by Boulenger (1894) is *Phryniscus stelzneri* Weyenbergh (1875); the species hence was designated *Atelopus stelzneri*.

From about 1900 to the present several additional species of *Atelopus* have been described, most in works by Boulenger (1898, 1902), Werner (1899), Peracca (1904), Ruthven (1916), Dunn (1933), Shreve (1936), Andersson (1945), Taylor (1952), and Rivero (1963).

Boulenger (1895a,b) described *Oreophrynella quelchii* from Mount Roraima in British Guiana. He considered *Oreophrynella* to be closely related to *Atelopus* and placed the genus in the family Engystomatidae. In 1900 Boulenger described a

second species of the genus, *O. macconnelli*, from the same area. Rivero (1961) suggested that *macconnelli* is a subspecies of *O. quelchii*.

Gadow (1901) based his classification on the presence or absence of a tongue and teeth, the condition of the shoulder girdle, and the shape of the sacral diapophyses and the vertebral centra. On this basis, *Phryniscus* (Gadow apparently did not accept the change proposed by Boulenger from *Phryniscus* to *Atelopus*), *Oreophrynella*, and *Brachycephalus* were included in the family Engystomatidae. *Dendrophryniscus* was maintained together with *Batrachophryne* in the subfamily Dendrophryniscinae of the Cystignathidae. One of the major characteristics of the latter family was a cylindrical sacral diapophysis. In this character Gadow followed Jiménez de la Espada's description of *Dendrophryniscus* as having a non-dilated sacral diapophysis.

Barbour and Noble (1920) rejected the family Dendrophryniscidae on the grounds that *Batrachophryne* was related to *Telmatobius* and not to *Dendrophryniscus*. It was not until 1926 that Noble placed *Dendrophryniscus* in the Brachycephalidae.

Nicholls (1916) introduced the structure of the vertebral column into anuran classification. He considered *Atelopus* (two species examined) as a member of the Engystomatidae but pointed out that they retained procoelous vertebrae.

In 1922, Noble used the name Brachycephalidae for frogs having a bufonid type of thigh musculature, procoelous centra, arcifero-firmisternal or firmisternal pectoral girdle, cylindrical or dilated sacral diapophyses, five to eight presacral vertebrae, and terminal phalanges that are never claw shaped. He placed *Sminthillus*, *Geobatrachus*, *Brachycephalus*, *Phyllobates*, *Hyloxalus*, *Dendrobates*, *Atelopus*, and *Rhinoderma* into this family. Noble (1922:39) considered *Atelopus stelzneri* to be a *Bufo*.

In 1926 Noble reviewed the brachycephalid frogs and included *Dendrophryniscus brevipollicatus* in the family. Noble pointed out that the sacral diapophyses are broadly dilated in *Dendrophryniscus*. In this same paper he assigned *A. stelzneri*, earlier considered a *Bufo*, and *A. moreirae* to the genus *Dendrophryniscus*. He defined *Dendrophryniscus* as differing from *Atelopus* only in the partially arciferal pectoral girdle.

According to Noble (1926), the Brachycephalidae consisted of three distinct groups of genera each of which was independently derived from bufonid ancestors. However, because all three arose in the same general region and from the same fam-

ily, he considered them a natural group. The first group included *Atelopus*, *Dendrophryniscus*, *Oreophrynella*, and *Brachycephalus*. The second group included *Hyloxalus* (= *Colostethus*), *Phyllobates*, and *Dendrobates*. The third group included *Sminthillus*, *Rhinoderma*, and *Geobatrachus*.

Davis (1935) questioned Noble's consideration of the Brachycephalidae as a natural, even though composite, family. Davis elevated each of Noble's groups to familial status. He recognized the Atelopodidae (= Brachycephalidae), the Rhinodermatidae, and the Dendrobatidae. In the same paper he placed the Asian *Cacophryne borbonica* in the family Atelopodidae, primarily on the basis of its firmisternal girdle and its lack of a Bidder's organ. However, *Cacophryne* later was shown to have a Bidder's organ (Dubois, 1947; Griffiths, 1954b).

Griffiths (1954b) removed *Cacophryne* from the Atelopodidae and put it in the Bufonidae. He considered the firmisternal condition of the girdle as independently derived from that of a *Pedostibes*-like bufonid ancestor. This treatment had been considered, but rejected earlier by Davis (1935).

In 1959 Griffiths restricted the Atelopodidae to include two genera, *Atelopus* and *Brachycephalus*. He placed *Oreophrynella* and *Dendrophryniscus* (based on *D. stelzneri*) in the Bufonidae. In this same work Griffiths placed the three genera of the family Rhinodermatidae into the family Leptodactylidae and considered the Dendrobatidae a subfamily of the Ranidae. In general, Cochran (1961), Goin and Goin (1962), and Cochran and Goin (1970), have followed Griffiths' classification.

Baldauf (1959) postulated the derivation of the Atelopodidae from a bufonid stock similar to the *B. valliceps*, *marinus*, *debilis*, *punctatus* group or possibly from a *B. quercicus* type.

Gallardo (1961a, b) proposed the genus *Melanophryniscus* to include the species *stelzneri*, *moreirae*, and *tumifrons*, thus restricting *Dendrophryniscus* to a single species, *brevipollicatus*.

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METHODS AND MATERIALS

Specimens used in the osteological analysis were prepared in several ways. Most preparations were made from specimens preserved in 10 per cent formalin and stored in ethyl alcohol. This material was measured, sexed and tagged. The frogs were skinned, eviscerated, and then cleared in a 2 to 4

¹This report is a revised edition of a doctoral dissertation completed at the University of Southern California.

per cent solution of potassium hydroxide, stained with Alizarin Red-S, and stored in glycerine. Some specimens were dehydrated and cleaned using dermestid beetles or cleaned by hand and bleached in sodium hypochlorate solution. Osteological information from additional species not available for direct osteological examination was obtained from X-ray radiographs, mostly stereoscopic. The radiographs were exposed from 20 to 30 seconds at instrument readings of 20 or 25 kilovolts and five DC milliamperes. All radiographs are on file at the Department of Biological Sciences, University of Southern California.

Osteological material was available for every genus. The species included, followed by the numbers of specimens examined, are listed below (N = skeletons or cleared and stained specimens, XN = X-rays): *Atelopus boulengeri* 1; *A. carrikeri* X6; *A. certus* X2; *A. chiriquiensis* 1; *A. cruciger* 1, X15; *A. ebenoides* 1, X5; *A. elegans* 2, X8; *A. exigua* 1; *A. flavescens* 2, X10; *A. glyphus* 1, X1; *A. ignescens* 12, X25; *A. longirostris* 1; *A. oxyrhynchus* 1; *A. pachydermus* 1; *A. spumarius* 1; *A. senex* 2, X15; *A. spurrelli* 2, X10; *A. varius* 13, X11; *A. walkeri* X4; *A. zeteki* 4; *Dendrophryniscus brevipollicatus* 4, X6; *D. minutus* 2, X11; *Melanophryniscus moreirae* 4, X14; *M. rubriventris* 2; *M. stelzneri* 3, X9; *M. tumifrons* 2; *Oreophrynella quelchii* 3, X23. In addition, one or two specimens each of four undescribed species of *Atelopus* were cleared and stained and are included in the analysis. Limited dissections provided some osteological data for *Dendrophryniscus leucomystax* and *D. proboscideus*.

Skeletal material was also available for the following genera: *Bufo*, 8 species; *Brachycephalus*, 1 species; *Ansonia*, 2 species; *Cacophryne*, 1 species; *Crepidophryne*, 1 species; *Rhinoderma*, 1 species; *Dendrobates*, 2 species; *Leptodactylus*, 2 species.

In addition to the above material, other specimens were dissected to study musculature and the hyoid apparatus. When necessary, specimens were stained 48 hours in a 1:8 solution of borax carmine and differentiated in one per cent picric acid alcohol solution. All my osteological material was deposited in the collections of the Los Angeles County Museum of Natural History.

Preserved museum specimens of nearly all the species of *Atelopus* were examined. Some information was added from observations of populations of *Atelopus varius* in Costa Rica and several live specimens of Brazilian *Melanophryniscus moreirae* in the laboratory.

My use of the word atelopodid is in reference

to the genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella* and does not imply a formal taxonomic category. All references to a character or character state of a species or a genus are based on individuals that are considered typical of that taxon and should be read accordingly.

ANALYSIS OF CHARACTERS

The majority of anuran systematists agree that taxonomic categories above the specific level should be based on evolutionary relationships inferred from data on the evolutionarily conservative and relatively stable characters of internal morphology (Brattstrom, 1957), rather than external morphology, coloration and habitus, supplemented with whatever information can be obtained from reproductive ethology, general behavior and ecology, genetic compatibility, and biochemistry. Only a cursory examination of the major schemes of frog classification, including the early ideas of Cope (1864, 1865, 1866) and Boulenger (1882), the major contributions of Noble (1922, 1931), the recent comprehensive work of Griffiths (1963) and the phylogenies presented by Inger (1967) and Kluge and Farris (1969), is needed to comprehend the importance of careful consideration and evaluation of different facets of comparative morphology. The emphasis on internal morphology, especially osteology, is extremely important in other vertebrate groups because of the abundance of fossil material with which modern forms can be compared. With frogs, however, the fossil record has added little to our understanding of phylogenetic relationships of modern groups (Hecht, 1963; Inger, 1967). Blair (1962) and Inger (1967) pointed out some of the problems that face the evolutionary morphologist in dealing with anuran classification. In spite of these drawbacks, it has been amply demonstrated that detailed study of a particular group of related organisms (Ritland, 1955a, b; Wake, 1966; Liem, 1970) or a detailed study of a specific morphological character (Bhaduri, 1953; Orton, 1957; Wake, 1968) or system through a wide spectrum of unrelated organisms (Trewavas, 1933; Dunlap, 1960; Starrett, 1968) adds significantly to our understanding of evolutionary relationships at generic and higher levels.

MYOLOGY

Thigh Musculature

Early works by Duges (1835), DeMan (1874), Perrin (1893), Gaupp (1896), and Nussbaum (1898), though somewhat fragmentary in most cases, set the foundation for comparative study of

the pelvic limb musculature of frogs. Noble (1922) was the first to apply characteristics of the thigh musculature from a comparative aspect in an overall scheme of frog phylogeny. Noble's scheme has been criticized, particularly with reference to his use of the arrangement of the distal tendons of the thigh (Latsky, 1930; Parker, 1940; Colifax, 1956; Griffiths, 1959), but has been followed generally. Griffiths (1963:262) argued against defining major taxonomic groups on the evidence of the thigh complex alone but pointed out the value of these characters in determining directions of evolutionary trends within groups whose relationships are well defined by other characters.

A recent comparative study of pelvic myology (Dunlap, 1960) emphasized the usefulness of characteristics of thigh musculature in evaluating relationships among different groups of frogs. I have followed Dunlap's terminology in this study, although, as pointed out by Noble (1922) and Dunlap (1960), the names are largely derived from mammalian muscles and in many cases homologies are unlikely.

Tensor fasciae latae.—In most frogs, this muscle is wide and thin, originates on the ventro-lateral aspect of the ilium and inserts on the dorsal surface of the cruralis or the latero-dorsal surface of the gluteus magnus. Noble (1922) and Dunlap (1960) indicated that there is a general tendency for this muscle to be better developed in what they considered to be the more primitive frogs.

The position and origin of the tensor fasciae latae follow two basic patterns in the specimens studied (Fig. 1). In most species of *Atelopus* studied, the muscle is straplike, much elongated, and has its origin on the ventro-lateral anterior surface of the ilium below the sacral diapophysis. In *A. flavescens*, *spumarius*, *spurrelli*, and an undescribed species, this muscle arises just posterior to the point of connection between the sacral diapophysis and the ilium. In all forms the muscle is covered along its anterior half by the dorso-lateral extension of the external oblique muscle. The insertion of the tensor is on the cruralis; the tendon of insertion extends distally to fuse with the aponeurosis of the knee. The position of the point of insertion is variable. In some species the muscle inserts at a point between the proximal one-third to one-half of the foreleg; in others the insertion may be along the distal one-half to one-third of the foreleg. Generally, the shorter legged species (e.g., *A. ignescens*, *boulengeri*, *ebenoides*, *pachydermus*) have the insertion closer to the distal end of the foreleg.

The second basic pattern is found in species of *Dendrophryniscus*, *Melanophryniscus*, and *Oreo-*

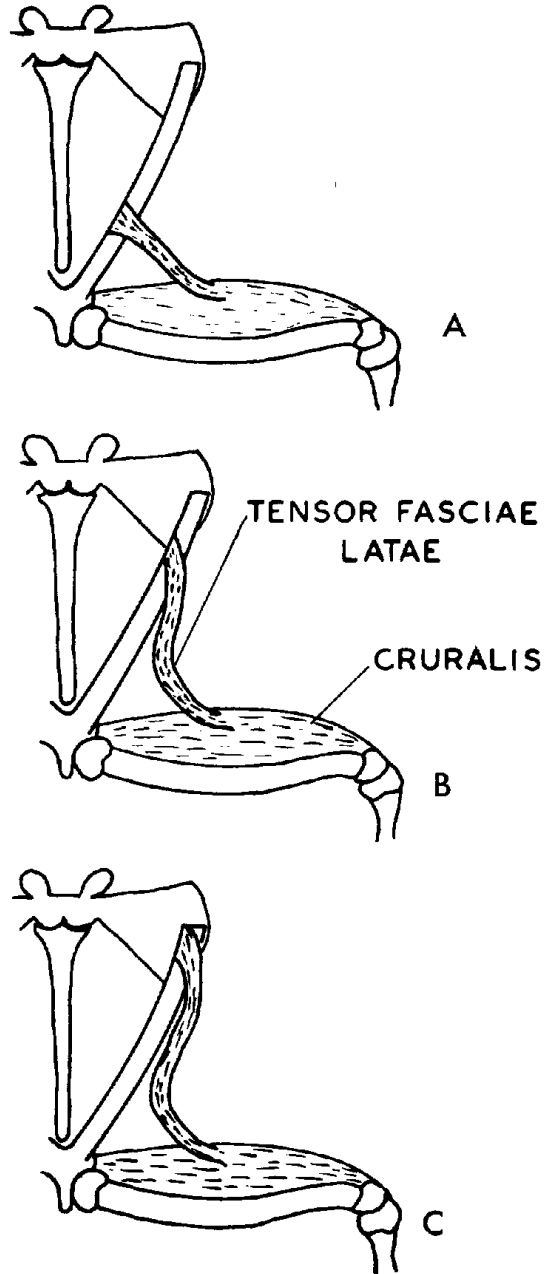


FIGURE 1. Diagrammatic representations of the conditions of the tensor fasciae latae muscle in ventral view. Condition A characteristic of species of *Dendrophryniscus*, *Melanophryniscus*, *Oreophrynella* and *Bufo*. Condition B characteristic of some species of *Atelopus*. Condition C characteristic of most species of *Atelopus*.

phrynella. In specimens of *Melanophryniscus* the muscle is short and broad and originates on the ventral surface of the ilium about one-third the distance from the posterior end. The insertion lies along the lateral surface of the distal half of the cruralis. There is, however, some variation among the species in the width of the tensor muscle at the point of insertion.

The tensor muscle of *Oreophrynella quelchii* is similar to that found in *Melanophryniscus*. The origin is about midway along the ilium, slightly more anterior than in *Melanophryniscus*; the insertion is about midway along the cruralis muscle.

In specimens of *Dendrophryniscus* the origin is on the ventro-lateral surface of the ilium posterior to the midpoint; the insertion is on the cruralis muscle medial to the midpoint. As with some members of the genus *Atelopus*, the longer legged frogs of the genus *Dendrophryniscus* have the insertion nearer the body than do the shorter legged frogs of the genera *Melanophryniscus* and *Oreophrynella*.

Sartorius, semitendinosus, gracilis major and gracilis minor.—These muscles were considered to be of great taxonomic importance (Noble, 1922) not so much because of their individual characteristics, but rather because of their relationship to each other, especially with reference to the disposition of their distal tendons.

The sartorius is a superficial muscle lying across the ventral surface of the thigh. It is thin and narrow in species of *Atelopus* and *Dendrophryniscus*, thin, but broader in *Oreophrynella*, and somewhat thicker and broader in *Melanophryniscus*. It appears that the sartorius in the longer legged frogs (*Atelopus*, *Dendrophryniscus*) is thinner and narrower than in the shorter legged forms (*Melanophryniscus*, *Oreophrynella*).

Primitively, the sartorius and the semitendinosus in most frogs are derived from a common muscle (Noble, 1922; Dunlap, 1960). The semitendinosus is ventrally situated and lies between the gracilis major and the adductor magnus, where it is visible superficially as a thin slip along the distal one-half to two-thirds of its length in all species of *Atelopus*, *Melanophryniscus* and *Oreophrynella*. In *Dendrophryniscus* the semitendinosus muscle lies slightly deeper between the gracilis major and adductor magnus muscles and is not visible superficially.

The distal end of the semitendinosus forms a slender tendon which inserts on the aponeurosis of the knee. This tendon is proportionally longer in *Dendrophryniscus brevipollicatus* than it is in *D. minutus* and species of *Atelopus*, *Melanophryniscus*, and *Oreophrynella*.

The gracilis major and minor muscles are gen-

erally the same in all species studied. The gracilis major has its origin from the postero-ventral edge of the ischial rim of the pelvis and its insertions by one tendon on the aponeurosis of the knee and by a second tendon on the proximal part of the tibia. The gracilis minor has its origin in two heads, one from the ischial region of the pelvis and the other from the skin.

The sartorius inserts, in part, onto the insertion tendon of the semitendinosus via a distal tendon. In all specimens studied the insertion tendon of the semitendinosus passes ventrally and superficially with respect to the insertion tendon of the gracilis major.

Adductor longus and pectineus.—That the adductor longus and pectineus are derivatives of a single muscle mass has been demonstrated unequivocally by Noble (1922) and Dunlap (1960, 1966). The adductor longus arises on the iliac portion of the ventral pelvic rim and inserts on the aponeurosis of the knee. It is visible superficially and lies between the cruralis and the adductor magnus. The pectineus is a short, fan-shaped muscle which inserts along the ventral surface of the femur shaft. It lies beneath the adductor magnus posterior to the cruralis.

Inger (1967, Table 1) reported the presence of the adductor longus muscle in the Atelopodidae. However, the adductor longus muscle is absent from all specimens of *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella* which I examined.

The pectineus is present in all specimens examined. There is considerable variation in the distal extent of the insertion of this muscle. In the long-legged species of *Atelopus* (e.g., *cruciger*, *longirostris*, *oxyrhynchus*, *varius*) the distal end inserts along the proximal one-third to one-half of the femoral shaft. The same condition is found in the long-legged species of *Dendrophryniscus*. However, the short-legged species of *Atelopus* (*ignescens*, *pachydermus*, etc.) and all species of *Melanophryniscus* and *Oreophrynella* have the insertion of the distal end of the pectineus between the distal one-half to three-fourths of the femoral shaft. No attempt was made to categorize this variation other than the apparent correlation between the distal insertion and relative length of the femur.

Jaw Musculature

The first reference to the value of jaw musculature in anuran systematics was made by Griffiths (1954b, 1959) who divided the phaneroglossid anurans into three groups according to the origin of the depressor mandibulae muscle and the angle

which the squamosal-quadrata complex forms with the mandibular arm. Starrett (1960) and Limeses (1965) demonstrated the usefulness of jaw musculature in defining genera and evaluating generic relationships. Recently Starrett (1968) discussed and surveyed the variation in jaw musculature in frogs. The terminology and character state assignments used here generally follow her work.

Depressor mandibulae.—The three groups that Griffiths (1954b) recorded using the disposition of the depressor mandibulae are: (1) originating from the edge of the posterior squamosal arm and the lateral edge of the otic arm; (2) originating from the squamosal, the annulus tympanicus and the dorsal fascia; (3) originating from the dorsal fascia only. Starrett (1968) found much more variation in the origins of the depressor mandibulae than mentioned by Griffiths. Griffiths (1954b:44) stated that the depressor mandibulae has its origin on the supra-otic (*Bufo*idae) and on the latero-otic (*Atelopodidae*) of the squamosal arm. Baldauf (1959:536) demonstrated that the depressor mandibulae muscle may arise from the crista parotica, from the squamosal or from both in species of *Bufo*. On this evidence Baldauf questioned the importance of the origin of the muscle in clarifying bufonid phylogeny.

In all species examined of the four genera, the depressor mandibulae muscle is typical of Griffiths' group one; the muscle has its origin on the squamosal arm and the lateral portion of the prootic, or the crista parotica, inserts on the posterior portion of the mandible, and is referred to as condition SQ. *Atelopus flavescens*, *spumarius*, and an undescribed species and *Dendrophryniscus minutus* have variations of the basic atelopodid pattern. In these three species of *Atelopus* a few fibers of the depressor mandibulae arise on the postero-ventral edge of the annulus tympanicus; this condition is referred to as SQat. In *D. minutus* the depressor mandibulae arises on the anterior projection as well as the posterior arm of the squamosal and on the lateral portion of the prootic; this modified condition is referred to as SQm.

A second characteristic which Griffiths considered in conjunction with the condition of the depressor mandibulae muscle was the angle formed by the connection of the squamosal quadrata complex and the mandible. He indicated that all forms with a depressor mandibulae muscle in condition (1), also have a squamosal angle ranging from 55 to 70 degrees. All other frogs that have a different depressor mandibulae condition have a squamosal angle lower than 50 degrees. He considered the

combination of the group (1) depressor mandibulae muscle and the high value for the squamosal angle as the primitive condition. Starrett (1968) showed that there is much greater variation in the squamosal angle than indicated by Griffiths and rejected the use of this character in discussing relationships because of the wide range of overlap between most higher groups of frogs.

Adductor mandibulae complex.—Starrett (1960, 1968) demonstrated that there are basically three different relationships between the adductor mandibulae muscles and the mandibular branch of the trigeminal nerve (Fig. 2). Some groups of frogs have a single adductor mandibulae muscle, others have two adductor mandibulae muscles, and a few species have none. When present the adductor muscles arise from the anterior arm of the squamosal and insert on the lateral part of the mandible anterior to its articulation with the squamosal. If two muscles are present, the mandibular branch of the trigeminal nerve passes medial to the adductor mandibulae externus superficialis and lateral to the adductor mandibulae posterior subexternus, that is, between the two muscles; this condition is referred to as S and E. In some frogs with one muscle, the mandibular branch of the trigeminal nerve lies across the lateral face of the muscle, so that only the subexternus is present; this condition is designated S. In other frogs with one muscle, the nerve passes medial to the muscle so that only the externus is present; this condition is designated E.

All species of *Atelopus*, *Melanophryniscus*, and *Dendrophryniscus* have the S condition. In *Oreophrynella quelchii* the adductor mandibulae posterior subexternus is absent, and the mandibular branch of the trigeminal nerve passes behind the adductor mandibulae externus superficialis, the E condition.

OSTEOLOGY

Skull

While there are several papers which treat the anuran skull in general, no author has considered the species examined in this study from a comparative aspect. In the classic study by Parker (1882) the skulls of three species of *Atelopus* were described and illustrated. In general Parker's work is adequate in view of the techniques he utilized in preparing specimens. Unfortunately some of his specimens were misidentified. Parker's (1882:233 and Plate 41, figs. 1-5) description and illustrations of *Atelopus cruciger* are based on a male specimen from the "Interior of Brazil." Yet *Atelopus cruciger* occurs only in northern South America. The Catalogue of the Batrachia in the British Museum

(Boulenger 1882: 154) lists no specimens of *A. cruciger* from Brazil. However, four specimens of *A. flavescens* from the "Interior of Brazil" are listed. A comparison of material of both *A. cruciger* and *A. flavescens* with Parker's illustrations

of *A. cruciger* leaves no doubt that he was dealing with a specimen of *A. flavescens* and not *A. cruciger*.

The only other work dealing with the cranial osteology pertinent to this study is that by Badenhorst (1945). She worked with the cranial osteology of *Melanophryniscus moreirae*, relying primarily on sectioning techniques. Laurent (1942) discussed certain aspects of the osteology of *Atelopus varius*. Griffiths (1954b) presented a diagram of the skull of *Atelopus ignescens* in his discussion of the otic element in Amphibia. Several other papers dealing with cranial osteology of bufonid frogs, including those by Parker (1876), Ramaswami (1937), Sedra (1949), Sanders (1953), Baldauf (1959), and Tihen (1962a), were consulted and found useful in interpreting the relationships between the atelopodid genera and genera referred to the Bufonidae.

The cranium can be divided conveniently into two basic components: a dermatocranium, that part of the skull formed from elements of dermal or membrane origin; and a chondrocranium, that part formed from elements of endochondral origin.

Nasal.—The nasal bones in these frogs are subject to considerable interspecific variation. In species of *Atelopus* (Fig. 3) the nasals are broadly triangular in shape and separated on the midline. Dorsally their anterior borders form the anterolateral edge of the skull. In a few species (e.g., *A. longirostris*) the nasals are nearly in contact anteriorly; in most they are separate. The nasals diverge posteriorly on the midline and pass laterally to form an elongate maxillary process. In some species this postero-medial divergence is gradual; in others it forms an obtuse angle just anterior to the prefrontals before passing latero-ventrally into the maxillary process. On the lateral edge anterior to the maxillary process there usually is a septomaxillary process that forms the postero-lateral structure of and gives rigid support to the nasal capsule. The nasals are convex and usually free from the sphenethmoid complex. There is a tendency in some individuals of a few species for the postero-medial edges of the nasal bones to fuse with the underlying chondrocranium.

In *Dendrophryniscus* (Fig. 4) the nasal bones are similar in most characteristics to those described for *Atelopus*. They differ in that they are strongly convex dorsally, nearly in contact anteriorly and do not diverge posteriorly along the median as sharply as in most species of *Atelopus*.

In large adults of *Melanophryniscus* the nasals are fused along the midline (Fig. 5) and, with the exception of *M. rubriventris* and *M. tumifrons*,

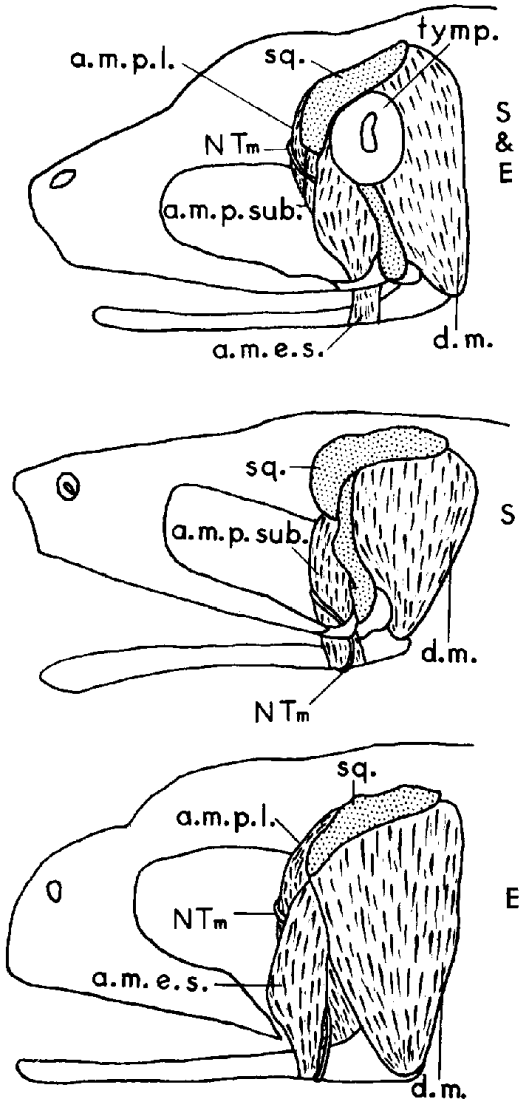


FIGURE 2. Representations of the three different arrangements of the adductor mandibulae muscles. *Upper*—S and E condition typical of *Bufo*; *Middle*—S condition typical of *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*; *Lower*—E condition typical of *Oreophrynella*. a. m. e. s.—adductor mandibulae externus superficialis; a. m. p. l.—adductor mandibulae posterior lateral; a. m. p. sub.—depressor mandibulae; NTm—mandibular branch of trigeminal nerve; sq.—squamosal; t ymp.—annulus tympanicus.

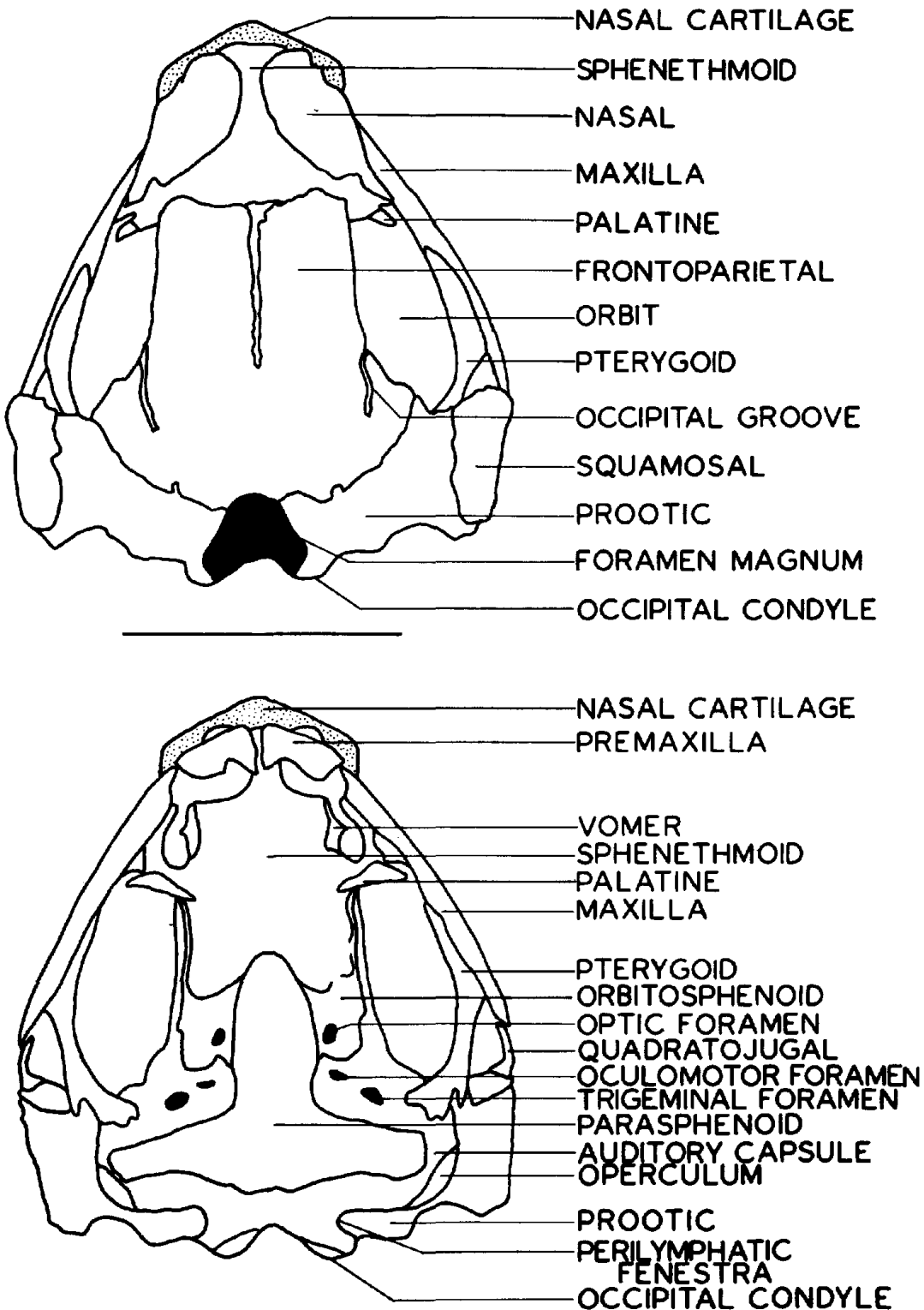


FIGURE 3. Dorsal and ventral views of the skull of *Atelopus varius*, LACM 64437, ♂. Line equals 5 mm.

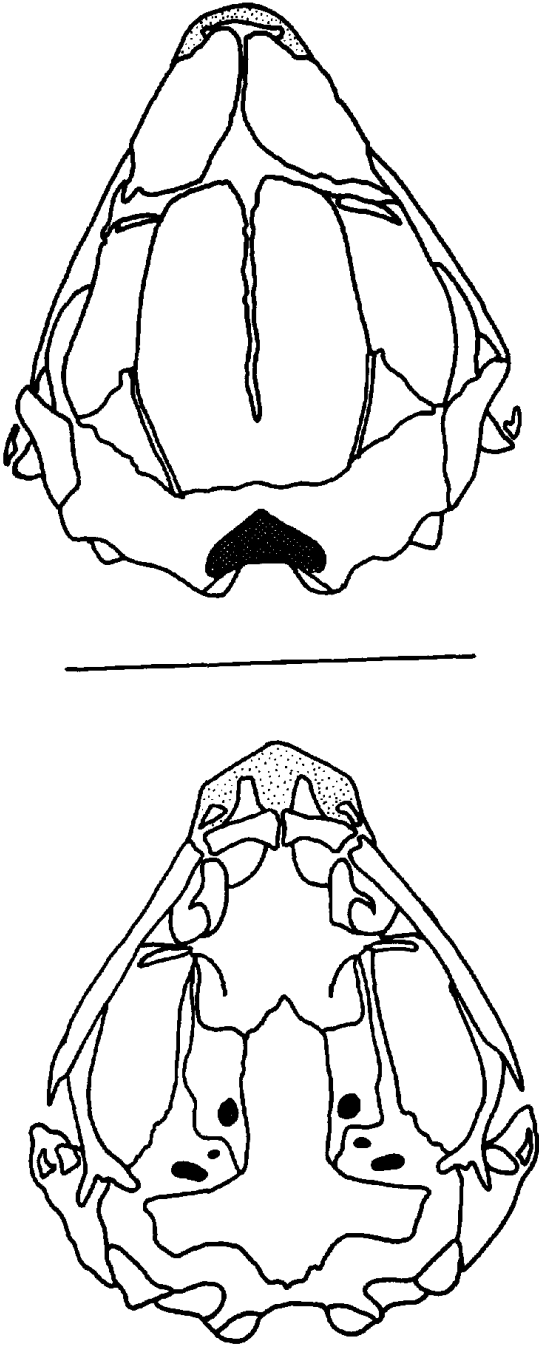


FIGURE 4. Dorsal and ventral views of the skull of *Dendrophryniscus brevipollicatus*, LACM 64438, ♂. Line equals 5 mm.

also with the frontoparietals. Smaller individuals of *M. moreirae* (smaller individuals of other species not available) that exhibit less cranial ossification have the nasals separated, suggesting an ontogenetic trend towards fusion. In addition to the medial fusion, the nasal bones are more convex than in *Atelopus*. In cross section the nasal regions look like two adjacent hills (the nasal bones) that are separated by a shallow valley (the suture zone). Dorsal ornamentation is characteristic of these species. Dorsally the nasals are fused with the sphenethmoid complex but laterally in the maxillary area the two processes are separate. There is no septomaxillary process.

In *Oreophrynella* (Fig. 6) the nasals are generally reduced, widely separated and free from the underlying sphenethmoid complex and the frontoparietals. The maxillary process is present but reduced in length. The overall shape is quadrangular; there is a definite septomaxillary process. The typical convex shape of the nasals is suggested, but there is no indication of any dorsal ornamentation.

Frontoparietal.—The frontoparietal bone covers most of the dorsal surface of the anuran skull. In *Atelopus* it extends from the anterior border of the orbit posteriorly to a point just in front of the foramen magnum and laterally above the auditory capsules (Fig. 3). In some specimens the lateral and posterior margins of the frontoparietal are fused with the underlying chondrocranium. The frontoparietal folds ventrally to form the mid-dorsal wall of the orbit. Each occipital artery lies in a canal near the point at which the frontoparietals pass laterally over the otic capsule on each side. In all species of *Atelopus* examined the occipital grooves are roofed over with bone for at least half of their length. In some, the groove is completely covered, opening only near the anterior end. In one specimen of *A. flavescens* the groove on one side is open along its entire length. Both grooves are open their entire lengths in a specimen of an undescribed but closely related species from French Guiana. These grooves converge slightly and open along the posterior edge of the frontoparietal. Medially the occipital groove delimits the otic portion of the frontoparietal. In most species of *Atelopus* a lateral flange extends out over the orbit at the angle between the main body of the frontoparietal and its otic portion.

Griffiths (1954a) demonstrated that ossification of the frontoparietal element originates in two centers in some amphibians and from a single center in others. Notably, most bufonids have a single center. Griffiths argued that single centers of frontoparietal ossification probably have re-

sulted from the fusion of the center of ossification of the frontal and the center of ossification of the parietal rather than from the loss of either.

Three *Atelopus ignescens*, measuring 12, 18, and 20 mm, were used to determine morphogenesis of the frontoparietal bone. The frontoparietal bone is derived from a single center of ossification on either side of the midline. The two frontoparietal elements have already assumed their general outline in the 12 mm specimen. Between the 12 and 20 mm stages, the elements complete their growth anteriorly. The otic portion, not apparent at the earliest stage, takes on its general appearance lateral to the occipital groove. Beginning posteriorly, the two elements ossify along the midline. The two halves of the frontoparietal have all degrees of medial fusion in individuals of the same or different species. In adults of a single species the frontoparietal elements may be completely separate, or they may be fused along their entire length.

In *Dendrophryniscus* the frontoparietal is essentially the same shape as it is in *Atelopus*. Only in the largest male examined is there any fusion posteriorly between the frontoparietal elements; in all other specimens they are completely separate. The occipital groove is open along its entire length across the frontoparietal (Fig. 4). In the largest individuals the otic portion of the frontoparietal extends laterally nearly to the dorsal section of the squamosal arm. *Dendrophryniscus minutus* and most specimens of *D. brevipollicatus* have some fusion of the frontoparietal to the prootic. In one large specimen of *D. brevipollicatus*, fusion is complete. The medial part of each frontoparietal is noticeably convex above the postero-lateral portions of the frontal fontanelle.

The frontoparietal of *Melanophryniscus* is similar in shape to that of *Atelopus*. There is always medial fusion of the frontoparietal posterior to the transverse tectum. Anterior to the tectum the frontoparietal may form a medial V, exposing part of the frontal fontanelle (Fig. 5), or it may be fused completely. In the large adults of *M. moreirae* and *stelzneri*, the frontoparietal and the nasal bones are fused. The occipital groove is open except for a very short distance posteriorly. Some individuals, especially of *M. tumifrons*, have considerable sculpturing and secondary dermal ornamentation on the frontoparietal. In these instances the occipital groove usually remains open although it sometimes is set deeply into the surface of the bone. The otic portion of the frontoparietal does not fuse with the prootic lateral to the occipital groove.

The frontoparietal of *Oreophrynella quelchii* (Fig. 6) is unique among the frogs studied. The

triangular frontal fontanelle and the two parietal fontanelles are exposed in the adults. The frontoparietal bone extends laterally on each side of the frontal fontanelle to the anterior level of the orbit. The anterior edges are longest laterally; medially they converge towards the anterior portion of the fontanelle. Although the frontoparietal is fused across the transverse tectum in one specimen and separate in another, in both it surrounds the parietal fontanelles on all sides and above the

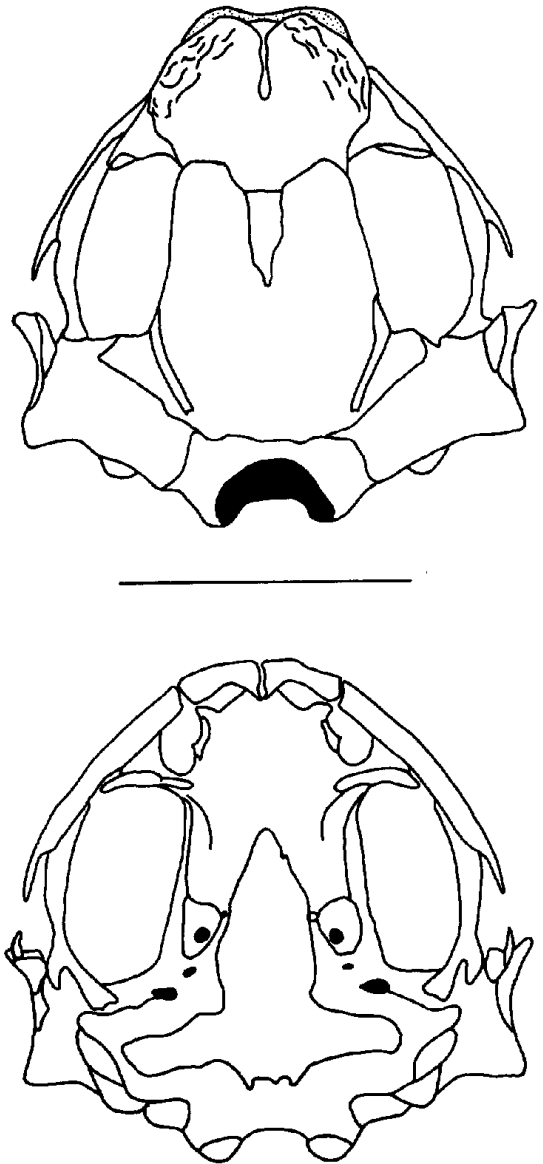


FIGURE 5. DORSAL AND VENTRAL VIEWS OF THE SKULL OF *Melanophryniscus tumifrons*, LACM 64439, ♂. LINE EQUALS 5 MM.

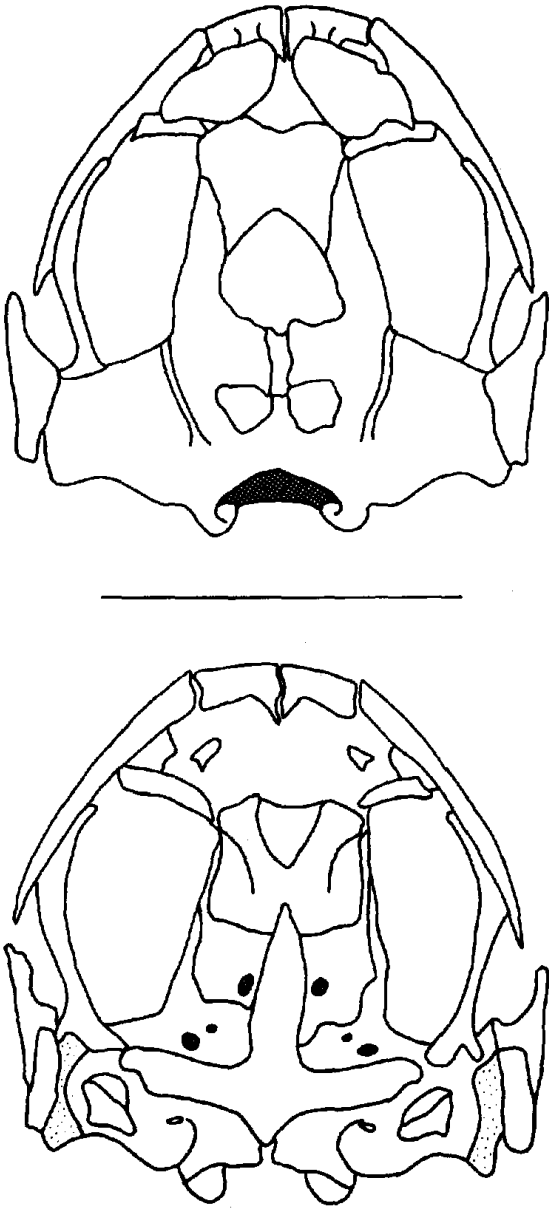


FIGURE 6. Dorsal and ventral views of the skull of *Oreophrynella quelchii*, LACM 64442, ♀. Line equals 5 mm.

medial tectum that separates the two fontanelles. The occipital groove is open along its entire length although there is a tendency for calcified cartilage to roof over the groove at its posterior end. Lateral to the groove the otic portions of the frontoparietal apparently fuse with the prootic. Only the anterior and medial portions of the frontoparietal are distinct from the underlying chondrocranium.

Premaxilla.—The premaxilla is essentially the same in all specimens examined. It consists of a basal platform and a dorsal or nasal process. *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella* have a premaxillary platform that is rectangular in shape. The anterior edge is nearly twice as long or longer than the medial edge. There is always a well-defined extension into a palatal process along the medial edge; there is no well-developed lateral process. There is a tendency in *Melanophryniscus* for the palatal process to terminate in a crescent, the ends of which point to the medial line. The palatal processes are longest in *Oreophrynella* and shortest in certain species of *Atelopus*. The palatal processes usually turn dorsally. The posterior edge of the premaxilla has a wavy appearance, the arched part of the wave lying between the lateral and medial edges. Anterior to the dorsal process, the platform turns ventrally to form the leading edge of the upper jaw.

The dorsal processes in *Atelopus* vary considerably in length and shape. However, in all species the dorsal processes diverge laterally and in profile are usually directed slightly anteriorly. In some instances this contributes to the projecting shape of the snout; in others the snout profile is determined more by the anterior projection of the nasal cartilage or the sphenethmoid complex. The dorsal processes are approximately the same in *Dendrophryniscus* except that when viewed from the front, they are nearly straight up and down rather than laterally directed. Also, in profile the dorsal processes project more anteriorly in *Dendrophryniscus* than in *Atelopus*.

In *Melanophryniscus* the dorsal processes are straight and broad from the front and directed slightly anteriorly in profile. In contrast to *Atelopus* and *Dendrophryniscus* the premaxilla contributes strongly to the nearly vertical profile of *Melanophryniscus*.

The dorsal process in *Oreophrynella* is generally the same as that in the other three genera without the strong lateral divergence. However, in profile the dorsal process is directed posteriorly and gives the snout a rounded profile.

Septomaxilla.—The small septomaxilla lies ventral to the antero-lateral margin of the nasal, usually just above the point of articulation between the maxilla and premaxilla. Parker (1882:240) stated that there are no septomaxillae in three species of *Atelopus* that he examined. My examination of these three species, as well as several other species of *Atelopus*, indicates that Parker was incorrect.

All species examined of *Atelopus* have a similar shaped septomaxilla. The lateral edge is broad, and

usually there is a moderately sized, anteriorly directed nasal process. The bone turns medially and then dorsally forming a U-shaped trough. The medial end is directed posteriorly. There is some variation in the shape and presence of a foramen in the septomaxilla; these characters were not evaluated at the specific level. A few specimens of some species of *Atelopus* have an osseous connection between the septomaxilla and the maxilla and between the septomaxilla and the sphenethmoid.

The lateral part of the septomaxilla in *Melanophryniscus* is considerably reduced compared to that of *Atelopus*. There is an elongate, anteriorly directed nasal process. The trough of the bone is broad, as is the medial edge. The medial end is directed posteriorly.

The septomaxilla of *Dendrophryniscus* is nearly the same as in *Melanophryniscus*. The only difference is the broader lateral edge in *Dendrophryniscus*. The nasal process is elongate in *D. brevipollicatus* and reduced in *D. minutus*. The trough and medial portions are broad in both. In several respects it is nearly intermediate between *Atelopus* and *Melanophryniscus*.

The septomaxilla of *Oreophrynella* is very reduced. The nasal process is nearly vertical in a lateral aspect. The trough is closed in front and more scooped. The medial process is also reduced and lacks the posterior flare characteristic of other genera.

Maxilla.—The maxilla or upper jaw bone is an elongate structure lying between the premaxilla and the quadratojugal lateral to the pterygoid. The maxilla is edentulous and forms the ventro-lateral margin of the skull.

The maxilla of *Atelopus* is deepest anteriorly at a point nearest the nasal and palatine bones. Usually, but not always, there is a nasal process. The anterior tip nearest the premaxilla is usually pointed; posteriorly the maxilla gradually is decreased in width to a rounded point at the quadratojugal. The ventral edge is nearly straight along its entire length. In most species, the ventral edge near the premaxilla is raised at about a 45° angle and pointed. The dorsal margin is raised gradually from its posterior limit to near the nasal bone where it may be raised abruptly to form a nasal process. Anterior to this process the dorsal edge is rounded and sloped gradually or abruptly down to form the anterior point. In some instances, this anterior dorsal edge is not rounded but rather is irregular in outline forming several secondary processes directed towards the anterior lateral margin of the nasal bone. A horizontal maxillary shelf extends the entire length of the maxilla about half way

down the medial side. Posteriorly this shaft supports the antero-ventral edge of the pterygoid. The shelf is widest anteriorly and is directed slightly dorsalad along its free edge. This forms a V-shaped trough beneath the nasal capsule.

The maxilla in *Melanophryniscus* is similar to that in *Atelopus*. The anterior end is rounded to nearly squared; the posterior end often widens at the pterygoid rather than narrowing gradually as is characteristic of *Atelopus*. The maxillary shelf is prominent and forms the characteristic V-shaped trough.

In *Dendrophryniscus* the maxilla rises gradually to the nasal process, which is always well developed and elongate. Posteriorly, the maxilla is pointed, and anteriorly it is rounded to blunt. The maxillary shelf is well developed and slightly wider anteriorly.

The maxilla of *Oreophrynella* is much wider and not nearly as elongate as it is in the three previous genera. The width at the pterygoid is almost equal to the nasal portion. There is a moderate to poorly developed nasal process. The anterior end is nearly square with a slightly pointed projection directed dorsally towards the septomaxilla. The posterior part of the maxillary is pointed along the ventral edge and rises rapidly at about a 45° angle to the pterygoid portion and thence nearly straight across to meet the nasal portion. The maxillary shelf is gradually reduced in width posteriorly.

Palatine.—The palatine bones are present in all species of *Atelopus* that were examined. They lie on the ventral aspect of the antorbital ridge. Generally they are subarcuate; some are nearly straight. The maxillary half of the palatine is the widest, the medial end is usually drawn to a sharp point. In *A. Boulengeri* the medial end of the palatine is widest. No attempt was made to derive specific relationships based on palatine shape.

The palatines are greatly reduced in one specimen of *D. minutus* and absent in a second specimen. If present, they have extensive lateral reduction and appear as slivers of bone. The palatines of *D. brevipollicatus* are slightly shorter than those of *Atelopus*; their anterior edge often is fused to the underlying chondrocranium and large nasal process of the maxilla. There is secondary deposition of calcified cartilage in this general region. Apparently this gives added support to the antero-lateral part of the skull at the nasal-sphenethmoid-maxillary connection.

Palatine bones are present in *Melanophryniscus tumifrons* but lacking in *moreirae*, *stelzneri*, and *rubriventris*. When present the bones are partially fused to the underlying chondrocranium. The possibility exists that the palatines are actually present

but fused to the orbitosphenoid in the latter three species. However, the general appearance of the antorbital region suggests that the palatine has been lost rather than fused. Badenhorst (1945) reported that palatines were absent from her sectioned material of *Melanophryniscus moreirae*.

Oreophrynella possesses a relatively large palatine. In ventral view it extends from the antero-medial edge of the orbit, laterally and slightly posteriorly to the maxilla. There is a connection between the palatine and the maxilla on the inner surface of the latter above the maxillary shelf.

Vomer.—The vomers (prevomers) of *Atelopus* are widely separated medially and, like the premaxilla and maxilla, are edentulous. Interspecific variation in shape of the bone was noted, but no attempt was made to group the species by vomerine shape. In general the vomer is crescent shaped and possesses a medial wing (Fig. 3). The bone is situated on the lateral edge of the sphenethmoid complex, anterior and medial to the opening of the internal nares, the choanae. The wings of the vomer are directed slightly ventrally to follow the dorsal curvature of the oral cavity formed by the sphenethmoid complex and the maxilla. The anterior wing is usually the longest and best developed, and is directed toward the anterior tip of the maxilla. The medial and posterior wings of the vomer form the anterior and medial margins of the choanae. The medial wing is pointed and extends towards the nasal portion of the maxilla. The posterior process is often more rounded than the medial process and directed parallel to the midline. The vomer of *A. Boulengeri* is blade-shaped, broadest posteriorly and lacks a medial wing.

Although the vomers of *Dendrophryniscus* also are crescent-shaped and in the same position as those of *Atelopus*, there are some differences. In *D. brevipollicatus* these bones are much larger (Fig. 4). The anterior wing extends forward to connect with the maxilla laterally and the premaxilla anteriorly at the point of juncture of the latter two. The medial wing is more elongate than in *Atelopus* and extends a greater distance towards the nasal portion of the maxilla. In some individuals the medial wing, together with the posterior wing, encloses between one-half and two-thirds of the choanae. In *D. minutus* the vomers are smaller than they are in *brevipollicatus* but the same size as in *Atelopus*. The anterior wing also resembles that of *Atelopus*, while the medial wing is reduced and the posterior wing sharply pointed.

A slightly different vomer is characteristic of *Melanophryniscus* (Fig. 5). The posterior wing is greatly reduced and sometimes absent. In con-

trast the anterior wing is usually quite extensive, reminiscent of the condition of the anterior wing obtained in some species of *Atelopus* and in *Dendrophryniscus brevipollicatus*. The extensive anterior wing is characteristic of *M. tumifrons*, *M. stelzneri*, and *M. rubriventris*. The vomers in *M. tumifrons* and *M. stelzneri* are fused to the underlying sphenethmoid complex. The vomer in *M. moreirae* is much wider and lacks the elongate anterior wing. The medial and anterior wings are of about equal length and form a crescent between them. The vomers are distinct from the underlying chondrocranium in *M. moreirae* and *M. rubriventris*. The fusion of the vomer to the chondrocranium in *M. stelzneri* and *M. tumifrons* correlates with the fusion of other skull elements.

The vomers of *Oreophrynella quelchii* are triangular and small (Fig. 6). They are widely separated medially and situated anteriorly and medial to each choana. Two corners of the vomer, probable remnants of the medial and posterior wings, and the included side outline the antero-medial edges of the choanae. The top of the triangular bone is directed towards the tip of the snout.

Parasphenoid.—The parasphenoid bone is roughly T-shaped and located ventrally on the posterior part of the skull. The top of the T lies ventral to the prootic while the upright extends anteriorly to contact the postero-ventral part of the sphenethmoid complex.

In *Atelopus* the anterior projection of the parasphenoid is as wide or wider and usually longer than the lateral arms. The anterior projection abuts against or slightly overlaps the posterior part of the sphenethmoid complex; its terminal end is rounded or slightly pointed. There are well-developed ridges medial to the point of juncture of the anterior projection and lateral wings of the parasphenoid. These ridges provide a suitable elevated area for attachment of muscles. The lateral wings extend beneath the prootic. The edges of the lateral wings usually parallel each other and are directed perpendicular to the anterior projection of the T. In some species of *Atelopus* the leading edges of the lateral wing may be directed slightly posteriorly. The posterior edge is usually straight, but some species have a slight posterior projection along the midline towards the foramen magnum.

The anterior projection of the parasphenoid is about two times the length of the lateral wings in *Dendrophryniscus*. In addition there is always a rounded posterior projection. In other details it is nearly the same as *Atelopus*.

In *Melanophryniscus* the parasphenoid is fused with the underlying base of the skull. The outline

of the parasphenoid, obvious in some individuals, indicates that the anterior projection is much broader and longer than the lateral arms. This gives an overall dagger-shape to the parasphenoid. When discernible, a posterior projection is well developed. Because of the overall fusion of this bone with the underlying chondrocranium, it is impossible to determine the extent and shape of the lateral arms and posterior projection in certain specimens and species, especially *M. stelzneri*.

The parasphenoid of *Oreophrynella* is basically the same as in the other three genera. However, the anterior projection is much narrower, covering only one-fourth of the interorbital width of the skull; in the other genera the width of the anterior projection is always more than one-third of the interorbital width. The lateral arms are directed slightly anteriorly. A posterior process is present.

Squamosal.—The squamosal consists of two parts, a shaft or stem which extends from the lateral margins of the prootic ventrally meeting the quadrate and quadratojugal at the point of articulation with the lower jaw, and a dorsal arm which bends over the lateral portion of the prootic and onto its dorsal surface. This dorsal section of bone has been referred to as the temporal plate (Sanders, 1953:38) and as the otic plate (Tihen, 1962a:160). Griffiths (1954b) discussed a bone which he referred to as an otic element. This structure will be considered in detail later.

The squamosal is basically the same in those species of *Atelopus* that were available for examination. The lower portion of the shaft is turned postero-medially. This rotation forms a prominent lateral ridge along the upper half of the shaft. In some species there is a small hook at the lower tip of this lateral ridge. The lower half of the shaft is usually flat and bladeliike with the medial edge lying more posteriorly than the lateral edge. In many species there is a flange on the upper part of the squamosal shaft which extends slightly anteriorly and bends medially. This flange, when present, gives the upper shaft of the squamosal an expanded appearance and provides greater area for attachment of some of the adductor muscles of the lower jaw. When this flange is restricted to the dorsal anterior corner of the shaft, it is referred to as an anterior projection of the dorsal arm.

The dorsal arm of the squamosal is directed posteriorly and extends onto the dorsal surface of the crista parotica or the prootic. Often the dorsal arm and the upper part of the squamosal shaft are sculptured. There is considerable interspecific variation in the angle formed by the shaft and posterior arm. The angle is nearly right in some and obtuse in other. In a few species of *Atelopus* the dorsal

arm is bent towards the shaft. This connection is best described by two obtuse angles. Considerable variation was also noted in the position and direction of the shaft in relation to the arm. In some species the shafts are straight and lie directly beneath the arm. In others, the shafts may diverge ventrally or bow inward.

The squamosal of *Dendrophryniscus* is similar to that of *Atelopus*. The lower portion of the shaft is bladeliike but is not rotated medially as much as it is in *Atelopus*. As a result, the lateral ridge is not formed. The dorsal arm has a well-developed anterior projection that bends ventrally. The dorsal arm extends medially over the prootic in *D. brevipollicatus*; it barely overlays the prootic in *D. minutus*. In occipital aspect the anterior projection extends slightly lateral to the body of the shaft. The shaft itself is bowed and slightly divergent ventrally.

In *Melanophryniscus* the squamosal stem is bladeliike; it turns medially in three species, but the broad face remains lateral in *M. moreirae*. There is no lateral ridge on the squamosal of the latter species. A lateral ridge is present in the species with the medially turned stem. An anterior projection is lacking in all *Melanophryniscus* examined. The dorsal arm is very narrow and does not overlap the prootic dorsally. Rather it abuts against the crista parotica of the prootic. The entire squamosal is situated more anteriorly than it is in either *Atelopus* or *Dendrophryniscus*.

The squamosal shaft of *Oreophrynella* is narrow and laterally flattened. There is no lateral ridge or medial rotation. The dorsal arm extends over the lateral edge of the prootic and onto its dorsal surface. There is a large anterior process that is somewhat ventrally directed. In occipital view the shaft is straight and directly below the dorsal arm.

Quadratojugal.—The quadratojugal is a small bone located slightly medial and ventral to the squamosal and fused intimately to the quadrate. In most forms it extends anteriorly towards the posterior part of the maxilla.

The quadratojugal is L-shaped and present in all species of *Atelopus* examined. Because of its close association with the quadrate, it is difficult to determine its posterior extent. The quadratojugal may or may not contact the ventral shaft of the squamosal; it rarely touches the pterygoid. In most species the anterior tip of the quadratojugal reaches to or overlaps with the maxillary. However, there is a reduction of the quadratojugal in some species of *Atelopus* (e.g. *ignescens*, *pachydermus*). In these forms there appears to be a ligamentous or cartilaginous connection between

the posterior tip of the maxilla and the quadratojugal.

In *Dendrophryniscus brevipollicatus* the quadratojugal is reduced and is situated on the antero-ventral edge of the quadrate; in *D. minutus* it is reduced to only an ossified tip of the quadrate. The posterior tip of the maxillary and the quadratojugal are widely separated.

The quadratojugal is small and restricted to the antero-ventral part of the quadrate in *Melanophryniscus*. The anterior process, if present, is very short and widely separated from the maxilla. There appears to be a ligamentous connection between these two bones. In some specimens of *M. moreirae* the quadratojugal is absent. One specimen has a trace of the bone on one side only. Badenhorst (1945) reported that the quadratomaxillary (=quadratojugal) was small in her specimens of *M. moreirae*. Apparently there is a trend toward reduction and eventual loss of this bone in species of *Melanophryniscus*. It would be interesting to know whether the absence of this bone is restricted to specimens from a single locality or widespread throughout the species.

The quadratojugal in *Oreophrynella* is absent from most specimens examined. One individual has a trace of ossification on one side. Whether this is actually a remnant of the quadratojugal or just a local calcium deposit is impossible to ascertain with the material available.

Pterygoid.—The pterygoid lies medial to the maxilla and extends posteriorly to articulate with the otic capsule and the squamosal-quadrate complex. In *Atelopus* the pterygoid is closely associated anteriorly with the posterior portion of the medial shelf of the maxilla, upon which it rests. From this point the pterygoid extends forward along the medial shelf approaching the nasal-maxilla-palatine juncture. Posteriorly the dorsal edge of the pterygoid arches dorso-medially to contact the otic capsule. The pterygoid articulates with the prootic via two heads. The medial head is the largest and attaches to the ventral surface of the otic capsule just anterior to the lateral tips of the parasphenoid and the fenestra ovalis. The lateral head attaches to the ventro-lateral tip of the prootic and the crista parotica and lies medial to the upper portion of the shaft of the squamosal. The eustachian tube passes posteriorly between these two heads. The lateral head is poorly developed or absent in those species of *Atelopus* that have middle ear bones.

The flattened postero-ventral process of the pterygoid passes medial to the squamosal shaft and folds around the quadrate. The postero-ventral process of the pterygoid together with the shaft

of the squamosal effectively enclose the quadrate. Ventrally the pterygoid forms an obtuse angle where it contacts the maxilla anterior to the posterior tip of the latter bone.

The pterygoids of both *Melanophryniscus* and *Dendrophryniscus* are basically the same as in *Atelopus*. However, in *Melanophryniscus* there is no close association between the maxilla and the anterior process of the pterygoid. In this condition *Dendrophryniscus* is closer to *Atelopus* than to *Melanophryniscus*. In both *Melanophryniscus* and *Dendrophryniscus* the posterior processes are reduced. The dorsal process connects with the antero-ventral part of the otic capsule through a large cartilaginous complex formed from the crista parotica and the process pterygoideus. The postero-ventral process is flattened and greatly reduced. The eustachian tube passes medially and dorsally to the pterygoid through the extensive cartilage on the lateral edges of the prootic.

The dorsal connection of the pterygoid to the otic capsule in *Oreophrynella* is similar to the condition obtained in the other three genera. The ventral process does not extend to the lower medial edge of the squamosal shaft, as it does in some *Atelopus* and *Dendrophryniscus*, but rather is located medial to the quadrate about half way up the squamosal shaft. There is a much more gradual slope from the dorsal process to the anterior tip of the pterygoid in *Oreophrynella*, *Melanophryniscus*, and *Dendrophryniscus* than is found in *Atelopus*.

Sphenethmoid complex.—Because of the difficulty in determining the internal construction of the nasal region and because of the almost complete fusion of endochondral elements, including the ethmoid, with the nasal cartilages anterior to the orbitosphenoid fontanelle, the entire anterior portion of the cranium is referred to as the sphenethmoid complex.

In all species of *Atelopus* (except *A. boulengeri*), *Melanophryniscus*, and *Dendrophryniscus* the sphenethmoid complex is extensively ossified and about the same shape. This ossification includes most of the endochondral structure of the olfactory capsule. None of the bufonids examined exhibit this extensive ossification. Dorsally the posterior portion of the nasals and the prefrontals anterior to the frontal fontanelle are supported by an ossified sphenethmoid complex. In most species of *Atelopus* and *Dendrophryniscus* the nasal portion of the sphenethmoid is ossified and extends anterior to the nasal bones. In some species the anterior portion of the sphenethmoid complex is cartilaginous and referred to as nasal cartilage. This anterior extension of the sphenethmoid (car-

tilaginous or ossified) contributes to the acute profile of the snout in many species. In *Melanophryniscus* the anterior extension of the nasal cartilage is present only in the species *rubriventris* and *tumifrons*. The fusion of the dorsal dermal bones in *Melanophryniscus* makes it difficult to determine the posterior and lateral extensions of the sphenethmoid unit.

In ventral aspect there are several ossified processes of the sphenethmoid complex. A palatine process extends laterally toward the maxilla and forms a postorbital ridge that supports the palatine bones. The palatine process is usually expanded distally. Ventrally the anterior portion of the sphenethmoid complex is ossified beneath the vomers in *Atelopus* and *Melanophryniscus* but only under the posterior edge of the vomers in *Dendrophryniscus*. In the single large specimen of *A. Boulengeri* available, the anterior half of the sphenethmoid complex is unossified. Both the palatines and vomers are supported by cartilaginous material rather than ossified portions of the sphenethmoid. Perhaps lack of ossification is correlated with the large size of this specimen. In specimens of *Atelopus* and *Dendrophryniscus* the tip of the parasphenoid slightly overlaps the sphenethmoid and together with the overlapping prefrontals on the dorsal surface gives added support between the anterior and posterior parts of the skull. In *Melanophryniscus* there is a more intimate connection between the two halves of the skull, especially on the ventral surface. The posterior extension of the sphenethmoid complex fuses with the anterior projection of the prootic, thus reducing the extent of the orbitosphenoid fontanelle. As previously mentioned, there is also dorsal fusion of the dermal elements of the nasal-frontoparietal, and ventral fusion of the parasphenoid-sphenethmoid complex. These fusions add rigidity to the skull.

The nasal capsules appear to be widely separated in *Atelopus*. In *Melanophryniscus* and *Dendrophryniscus* they are only narrowly separated.

The ossification of the sphenethmoid complex in *Oreophrynella* is restricted to the ethmoid or posterior section. The entire nasal capsule and anterior portion of the sphenethmoid complex are reduced and unossified. This condition is very similar to that obtained in most species of New World *Bufo* (Tihen, 1962a).

Orbitosphenoid.—The optic nerve passes from the brain into the orbit through the optic foramen in the orbitosphenoid fontanelle. This fontanelle is posterior to the sphenethmoid complex and anterior to the prootic and is floored midventrally by the anterior arm of the parasphenoid. The orbitosphenoid in most Amphibia is the thin cartilagi-

nous covering of the orbitosphenoid fontanelle that surrounds the optic nerve. In most amphibians it is unossified.

All species of *Atelopus* and *Dendrophryniscus* have an unossified orbitosphenoid. The fontanelle is irregular in shape, is continuous above the parasphenoid, and separates the prootic from the sphenethmoid complex. Basically the same condition is found in *Oreophrynella*.

In *Melanophryniscus* the fontanelle is greatly reduced by the apparent ossification of the orbitosphenoid and its fusion with the surrounding endochondral and dermal elements. Because of this extensive fusion, it is impossible to determine the limits of the orbitosphenoid in the species of *Melanophryniscus* examined. There is secondary ossification of the orbitosphenoid above the parasphenoid arm in *M. tumifrons* and *M. rubriventris*. In *M. moreirae* and *M. stelzneri* the ossification is more extensive. There is no indication of a supraparasphenoid connection between the two fontanelles. The extensive ossification in *M. moreirae* and *M. stelzneri* restricts the orbitosphenoid fontanelle to two circular openings smaller than those characteristic of *M. tumifrons* and *M. rubriventris*. All four species exhibit greater ossification of the orbitosphenoid than do species of *Atelopus*, *Dendrophryniscus*, and *Oreophrynella*.

Prootic.—The prootic forms the posterior and lateral parts of the endocranium of the skull. The auditory capsule and elements of the inner ear are contained within the prootic. Laterally the prootic ends in a cartilaginous abutment, the crista parotica, to which the suspensorium and a portion of the depressor muscle of the lower jaw attach. Posteriorly the prootic terminates in two occipital condyles which articulate with the vertebral column. The occipital condyles are the only part of the exoccipital which are distinct from the prootic. Because of the intimate fusion between these elements, the entire posterior section of the endocranium is referred to as the prootic.

There is little difference in the overall appearance and shape of the prootic in any of the genera examined. The taenia tecti transversalis and taenia tecti medialis are present in all species available of the four genera. Badenhorst (1945:18) reported the absence of the taenia tecti transversalis in *Melanophryniscus moreirae*, but it is obvious in all of my material.

Developmental series of *Atelopus ignescens* and *A. varius* indicate that the antero-ventral portion of the prootic enclosing the otic capsule anteriorly and surrounding the foramina of the third and the fifth and seventh cranial nerves is the first to ossify.

Later, the exoccipital and posterior surfaces of the prootic ossify. The remainder of the prootic and the auditory capsule follows. Nothing is known of the order of ossification in the other genera, although small specimens of *Dendrophryniscus* indicate the same sequence.

Suspensorium.—The quadrate, together with contributions from the pterygoid process, crista parotica and processes pseudobasalis, make up the suspensorium in all species of *Atelopus*, *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella*. The quadrate is restricted to the lower portion of the suspensorium and is cartilaginous except in some species where it ossifies in the immediate vicinity of the quadratojugal. The quadrate articulates with the lower jaw via two rounded condyles.

Mandibular Arch

The lower jaw is formed by the union of two arches, each composed of four basic components. The prearticular is the bony posterior portion of the mandible. It is grooved along its lateral surface and overlaps with the dentary. The dentary lies lateral to the anterior half of the prearticular and extends anteriorly and laterally to the Meckel's cartilage towards the symphysis where it fuses with the mentomeckelian. The Meckel's cartilage extends the entire length of the mandible to the symphysis in the groove of the prearticular. The anterior end is ossified to form the mentomeckelian which is connected to the other mandible by a ligament. Posteriorly the Meckel's cartilage broadens and turns slightly upward to form the articular fossa for the quadrate.

There is some interspecific variation in the relationships of the dentary to the prearticular and in the respective length of each. The medially directed curve in the prearticular is found posterior to a midpoint in all forms. The curve is farthest posterior in *Atelopus*, followed by *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*, respectively.

Hyoid Apparatus

The most important comparative study of the anuran hyoid and larynx is that by Trewavas (1933). Her exhaustive survey demonstrated the value of the hyolaryngeal apparatus in interpreting phylogenetic relationships. Parker (1940) and Griffiths (1959) also considered the hyolaryngeal apparatus and generally confirmed its importance in reflecting phylogenetic affinity. Only the hyoid portion of the hyolaryngeal apparatus was studied in this project. I have used a modified version of

the terminology of Trewavas (1933) and Peters (1964: fig. 27B).

The hyoid and its associated muscles function primarily to move the tongue in and out of the mouth during feeding. The hyoid consists of a hyoid plate which lies beneath the tongue. The hyoid plate gives rise anteriorly to two narrower processes, the manubria, which run anteriorly for a short distance and then turn laterally and continue posteriorly, paralleling the mandible as the ceratohyals. Just posterior to the point at which the mandible articulates with the quadrate, the ceratohyals turn dorsally and continue up to the skull where they attach to the lateral portion on the otic capsule near the fenestra ovalis. In some forms there is a well-developed anterior process or continuation of the manubrium. A hyoglossal sinus extends deep into the hyoid plate between the manubria. Hypobranchial 1 extends laterally from the hyoid plate posterior to the origin of the manubrium. In most frogs (see *Bufo*, Fig. 7) a posterolateral process, hypobranchial 2, extends from the lateral margins of the hyoid plate posterior to hypobranchial 1. The hyoid plate, manubria, ceratohyals, and hypobranchials 1 and 2 are cartilaginous. The postero-medial processes, hypobranchials 4, are thin bony shafts which extend dorsally and laterally from the posterior part of the hyoid plate. Hypobranchial 4 lies dorsal to the clavicle of the pectoral girdle and encloses the arytenoid and the cricoid.

In all species of *Atelopus* the hyoid plate is elongate, about three times its width at the narrowest point near the middle (Fig. 7). The hyoglossal sinus is moderate in depth and extends to a level near the origin of hypobranchial 1. The manubria are moderate in width and give rise to a narrow ceratohyal. There is a short anterior process extending from each manubrium. These anterior processes are one-half to one-third the length of the manubria and bend laterally near their tips. In some specimens the anterior processes frequently rejoin the manubria just past the point where the latter turn posteriorly. This loop formation is illustrated by Trewavas (1933: fig. 46). Hypobranchial 1 is present, has a narrow base, and exhibits an anterior flare and usually a smaller posterior flare. Hypobranchial 2 apparently is lacking in all *Atelopus* examined. Hypobranchial 4 is elongate, about equal in length to the hyoid plate, and bends sharply dorsad about midway along its length.

The hyoid apparatus of *Dendrophryniscus* (Fig. 7) is very similar to the hyoid apparatus of *Atelopus*. The hyoid plate is elongate, its length about three times its width. The manubria are short, equal to about one-third of the length of the hyoid plate.

The ceratohyals are narrow. There are no anterior processes. Hypobranchial 1 is narrow at its base and terminates with an anterior flare and sometimes a posterior flare. There is no hypobranchial 2. Hypobranchial 4 is elongate, equal in length to the hyoid plate and bends sharply dorsad about midway along its length.

The hyoid of *Oreophrynella quelchii* (Fig. 7) is similar to that of *Atelopus* in overall appearance, although the hyoid plate is not as elongate as it is in either *Atelopus* or *Dendrophryniscus*. It is only about twice as long as it is wide. The manubria are very long, approximately the same length as the hyoid plate. Accordingly, the hyoglossal sinus is

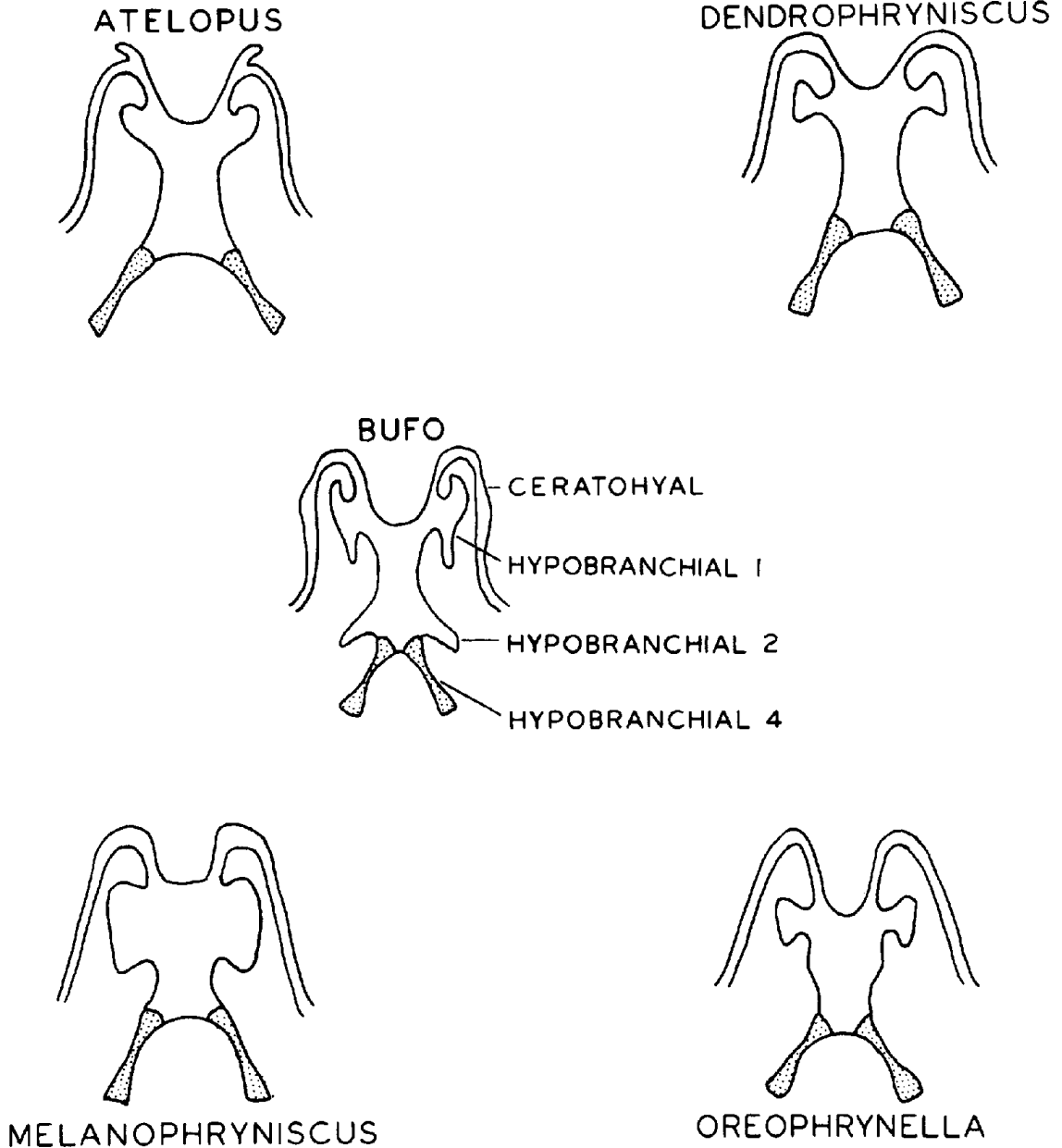


FIGURE 7. The cartilaginous and bony (stipple) portions of the hyoid apparatus of representative species of *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*. The hyoid apparatus of a typical species of *Bufo* is illustrated for comparison. Not drawn to scale.

much deeper than in *Atelopus*. The anterior portions of the ceratohyals are slightly expanded. There are no anterior processes. Hypobranchial 1 is about the same as in *Atelopus* and *Dendrophryniscus*; it is not expanded at its base and has small terminal flares anteriorly and posteriorly. Hypobranchial 2 is absent. Hypobranchial 4 is shorter than the hyoid plate. It extends laterally and slightly dorsad but does not have the sharp dorsal bend that is found in *Atelopus* and *Dendrophryniscus*.

All four species of *Melanophryniscus* have approximately the same hyoid structure (Fig. 7). The length of the hyoid plate is two to three times its width. The manubria are moderately long and slightly expanded where they give rise to the ceratohyals. There are no anterior processes. The base of hypobranchial 1 is broadly expanded and extends between one-half and two-thirds the length of the hyoid plate. Each hypobranchial 1 expands slightly to form a smaller anterior flare and a larger posterior flare. Hypobranchial 2 has been lost. Hypobranchial 4 extends laterally and bends slightly dorsad. Trewavas (1933:459, fig. 43) illustrated *Melanophryniscus moreirae* under the name *Dendrophryniscus stelzneri*. Badenhorst (1945) also illustrated the hyoid of *M. moreirae*.

In her classic work on the hyoid and larynx, Trewavas (1933) discussed the similarities between *Bufo*, *Atelopus*, *Melanophryniscus*, and *Oreophrynella*. These similarities include the absence of a constrictor laryngis posterior and a pulvinaria vocalia, the point of attachment of the hyoglossus muscle, the shape of the hyoid plate, the dorsal bending of hypobranchial 4, the well-developed lateral process of the cricoid, and the absence (except in *Melanophryniscus moreirae*) of a middle posterior petrohyoid muscle.

Trewavas (1933:517) suggested that the similarities among the hyolaryngeal apparatus would justify the retention of the family Bufonidae for the genera *Bufo*, *Atelopus*, *Oreophrynella*, and *Melanophryniscus*. My examinations of *Dendrophryniscus* indicate that it also lacks the constrictor laryngis posterior and, in this character, as well as in those previously mentioned, it should be considered with the genera *Atelopus*, *Melanophryniscus*, and *Oreophrynella*.

Vertebral Column

The nature of the vertebral centrum has been considered important in the major classification of frogs. Although some earlier workers (e.g. Cope, 1865, 1866) recognized the importance of vertebral characteristics, it was not until Nicholls (1916) divided the phaneroglossid Anura into four basic

groups and Noble (1922, 1931) verified and elaborated on Nicholls' work that the importance of vertebral characteristics was established. Several workers, especially Parker (1934), Griffiths (1963), Inger (1967), and Kluge and Farris (1969) discussed the exceptions and inadequacies in the Nicholls-Noble scheme.

Regional differentiation.—There is considerable intergeneric variation in the type and number of vertebrae in the forms studied. There is also some intrageneric variation in vertebral number.

A single cervical vertebra, the atlas, occurs in all frogs. Primitively, it lacks transverse processes. The trunk vertebrae vary in number and shape, but always possess transverse processes. A single sacral vertebra is characteristic of most frogs. It connects to the ilia by means of the lateral diapophyses. The urostyle or coccyx articulates with the sacral vertebra and extends posteriorly and dorsally between the ilia.

Cervical vertebra.—There are two basic types of cervical vertebra in the genera studied. One, found in *Melanophryniscus* and *Dendrophryniscus*, is a typical atlas lacking transverse processes. The other type is characteristic of *Atelopus* and *Oreophrynella* and consists of an atlas fused with the first trunk vertebra. This fusion results in a cervical vertebra with transverse processes, hereafter referred to as an atlas complex.

The primitive atlases have a pair of well-developed condylar articulating facets which meet the occipital condyles of the skull. These facets are slightly concave and located ventro-laterally on anteriorly directed processes. They are usually widely separated on the ventral midline.

The vertebrae of *Melanophryniscus* and *Dendrophryniscus* lack a neural ridge, although there are some irregular knobs and ridges on the dorsal surface for muscle attachment. There is a small knob on the posterior dorsal surface of the atlases of *Melanophryniscus* and *Dendrophryniscus* that comes in close association with an anteriorly directed process from the dorsal surface of the first trunk vertebra. This dorsal connection probably gives added rigidity to the anterior part of the vertebral column.

The postzygapophyses of the atlas are poorly developed in *Melanophryniscus*; the faces of the articulating facets are strongly concave and directed laterally and slightly posteriorly so that the prezygapophyses of the first trunk vertebra fit into a groove and articulate on three surfaces, one dorsally, one ventrally, and one medially. In *Dendrophryniscus* the postzygapophyses are well developed; the articulating surfaces are directed ventrally.

The atlas is fused with the first trunk vertebra in all species of *Atelopus*. Noble (1922:Plate 3, fig. 4) illustrated a ventral aspect of the vertebral column of *Atelopus varius* clearly showing the fusion of the atlas and the first trunk vertebra. The foramen for the spinal nerve is located just posterior and slightly ventral to the transverse process. In some species, including *A. ignescens*, and *A. pachydermus*, there are small slits on the dorsal surface of the atlas that indicate incomplete fusion between the atlas and the first trunk vertebra. Radiographs of *A. carrikeri* suggest very little fusion between the atlas and the first trunk vertebra; confirmation must await skeletal preparations. An ontogenetic series of *A. ignescens* and *A. varius* clearly shows the progressive fusion of these two vertebrae. In most species of *Atelopus* the dorsal surface of the atlas is ornately ridged with a cross or triangular pattern. The arms of the cross or the base of the triangle are situated above the line of fusion between the two vertebrae; the posterior projection of the cross forms a dorsal connection with the second vertebra. Apparently this gives additional rigidity to the vertebral column and perhaps represents an early evolutionary stage in fusion of the vertebral column.

The anterior facets that articulate with the occipital condyles are ventro-laterally located and separated medially. The postzygapophyses of the atlas complex are typically directed ventrally. In young specimens of *Atelopus* prior to fusion, the postzygapophysis of the atlas and the prezygapophysis of the first trunk vertebra are oriented ventrally and dorsally respectively. These apophyses are not obvious after fusion.

The only indications of fusion of the atlas and the first cervical vertebra in *Oreophrynella* are the presence of transverse processes on the first vertebra and of a foramen for a spinal nerve just anterior to each transverse process. Noble (1926:fig. 4) illustrated the vertebral column of *Oreophrynella* and showed the fusion of vertebrae one and two. An ontogenetic series is not available, so nothing can be said concerning the nature of the fusion of the zygapophyses of the atlas and first vertebra. The postzygapophysis of the atlas complex is typical; its articulating surface is directed ventrally. Dorsal ornamentation is restricted to a low λ on the posterior two-thirds of the complex. The posterior wings of the λ project between the vertebrae as short flanges and roof the gap. Because there is no connection with the next vertebra, these flanges apparently give intervertebral protection to the spinal cord rather than adding rigidity to the vertebral column.

Trunk vertebrae.—All vertebrae lying between the cervical vertebra, either the atlas or atlas complex, and the sacral vertebra are considered to be trunk vertebrae. All species of *Atelopus* examined have six trunk vertebrae, although occasionally seven are found in *A. ignescens* and *A. carrikeri*. One specimen of *A. longirostris* has only five discrete vertebrae; here the first is fused with the atlas complex. There is extreme interspecific and intraspecific variation in the shape, length, and direction of the transverse processes. The large transverse processes on the first trunk vertebra posterior to the atlas complex are rotated anteriorly and bent ventrally. There they form attachments for muscles from the scapula and suprascapula and give dorsal support to the pectoral girdle. The remaining transverse processes are directed laterally and generally are of about the same length or slightly longer posteriorly. In certain species the processes of some vertebrae are directed anteriorly, in some posteriorly, and in some laterally. The transverse processes on the second trunk vertebra are usually the broadest. The edges of each transverse process are even in some species, and scalloped in others. All postzygapophyses are directed ventrally; all prezygapophyses are directed dorsally. The dorsal surface of each neural arch is ornate and forms a cross, a diamond, or a broad triangle. Usually there is a dorsal connection or articulation between the ornamentation on the neural ridge of consecutive vertebrae.

Individuals from some populations, especially of *Atelopus varius* and *A. senex*, have fusions of trunk vertebrae and irregular placement of the ultimate transverse process. Noble (1926:14) mentioned abnormal specimens of *A. varius*. One specimen of *A. senex* has the fourth and fifth trunk vertebrae and their transverse processes fused; another has the third and fourth and the fifth and sixth fused with all their transverse processes separated except on the right side of the three-four fusion where the processes also are fused. In another specimen from this same locality, there is a transverse process typical of trunk vertebrae on the right side of the sacral vertebra; the preceding trunk vertebra has an expanded process characteristic of the sacral vertebra.

There are only four trunk vertebrae in *Oreophrynella quelchii*. The first transverse process is the longest and broadest; it is rotated slightly anteriorly and directed posteriorly and ventrally. The transverse processes on trunk vertebrae two, three, and four decrease in length posteriorly and extend laterally. The third and fourth are directed slightly anteriorly. The dorsal surface of each neural arch has an inverted Y design, the posterior arms of

which overhang the intervertebral space. The postzygapophyses are well developed, and their facets are directed ventrally. The facets of the prezygapophyses are directed dorsally.

Usually there are seven trunk vertebrae in *Melanophryniscus*, although eight were observed in a radiograph of a single specimen of *M. stelzneri*. The extra vertebra appears to be between the first and second or second and third trunk vertebrae. The transverse processes on the first vertebra are directed anteriorly. Those on the second are the longest and broadest; they are rotated anteriorly and directed ventrally and slightly posteriorly. The transverse processes on vertebrae three through seven decrease in length and width posteriorly. The edges of the transverse processes are scalloped and irregular in *M. tumifrons*, *rubriventris*, and *stelzneri*; they are nearly smooth in *M. moreirae*. In *M. stelzneri* the last transverse process is reduced to a nubbin.

In *M. tumifrons*, *rubriventris*, and *stelzneri* there is considerable dorsal ornamentation on the neural arch. This ornamentation consists of an irregular elevated cross or triangle design. In the latter the edges may be straight or concave. The ornamentation is best developed in the anterior four or five trunk vertebrae and serves for muscle and ligament attachment. The posterior extensions of the dorsal ornamentation overlap the intervertebral spaces and in one specimen of *M. tumifrons* actually form bony connections at paravertebral points between two vertebrae. The zygapophyses are well developed in *M. stelzneri*, *rubriventris* and *tumifrons*. The articulating facets of the postzygapophyses are directed ventrally and medially; those of the prezygapophyses are directed dorsally and slightly laterally. This type of articulation restricts the lateral movement of the vertebrae and together with the dorsal ornamentation apparently gives added rigidity to the vertebral column.

In *Melanophryniscus moreirae* there is very little to no dorsal ornamentation or overhang; this leaves a wide intervertebral gap. The pre- and postzygapophyses are well developed and have dorsally and ventrally directed articulating facets. This condition is more similar to that found in *Atelopus* than to that in other species of *Melanophryniscus*. It apparently allows for a more flexible vertebral column than is found in the other three species of *Melanophryniscus*.

There are normally seven trunk vertebrae in *Dendrophryniscus*, although several specimens have only six. In those specimens with six vertebrae, obvious fusion has occurred between trunk vertebrae one and two or between the sixth and seventh or between the seventh and the sacral

vertebra. Some specimens show no sign of fusion; in these it is anticipated that the terminal trunk vertebra was incorporated into the sacral vertebra. There are transverse processes on all trunk vertebrae; none are scalloped. The first is directed anteriorly and slightly ventrally. The second is the broadest; it is rotated anteriorly and directed ventrally and slightly posteriorly. The third is directed posteriorly. The fourth through the seventh are thinner and point laterally or slightly anteriorly in *D. brevipollicatus*. The fourth and fifth point posteriorly, while the sixth and seventh are directed laterally in *D. minutus*. There is very little dorsal ornamentation on the neural arch. Two small dorso-lateral projections extend over the intervertebral gap but never connect with the next vertebra. The postzygapophyses are large and articulate on their ventral face with the dorsally directed prezygapophyses.

Sacral vertebra.—The sacral vertebra is single. Posteriorly it articulates with the urostyle, and laterally it articulates with the ilia of the pelvic girdle.

The primary difference between the sacral vertebra and the trunk vertebrae is the condition of the sacral diapophyses. In *Atelopus*, *Melanophryniscus*, *Oreophrynella*, and *Dendrophryniscus* the sacral diapophyses are flattened and greatly expanded distally. The ilia attach on the ventral surface of the distal edge of each diapophysis. If there is dorsal ornamentation on the neural arch of the trunk vertebrae, it is usually repeated on the sacral vertebra, although the ornamentation is often less extensive.

The sacrum of *Oreophrynella* includes two trunk vertebrae that are fused with the normal sacral vertebra. This fusion is clearly shown by the presence of three spinal nerve foramina on the ventral part of the sacral vertebra (Noble, 1926: fig. 4).

Centrum.—In all forms studied the intervertebral body is fused to the anterior end of the centrum. This condition is typically procoelous. The posterior portion of each centrum is rounded and fits into a cup of the centrum of each successive vertebra. The centrum is continuous ventrally in all forms. The centrum begins about midway along the ventral part of the cervical vertebra and is continuous through the sacrum. The only divergence from the typical procoelous pattern is found in the nature of the articulation of the urostyle with the sacral vertebra. In all forms this is accomplished by a bicondylar (rather than unicondylar) articulation with the coccyx. In some specimens the sacrum and coccyx are fused.

Development.—Mookerjee (1931, 1936) and Mookerjee and Das (1939) traced the develop-

ment of the vertebral column in several species of Anura and recognized two different modes of vertebral development, perichordal and epichordal. Griffiths (1963:258) also outlined the development of the vertebral centrum in Amphibia. He presented a scheme deriving the three types of centra, stegochordal, ectochordal, and holochordal, through four different pathways. Griffiths fails to give any evidence to support his contention that there are two distinct pathways of stegochordal central development. Inger (1967) followed Griffiths' proposal of three centra types but questioned the primitiveness of the ectochordal type. Kluge and Farris (1969:21-25) reviewed the pertinent literature and presented an excellent discussion of vertebral development. They pointed out the inconsistencies of Griffiths' proposal and concluded that the apparent intrafamilial variability and overlap among vertebral categories mitigates against the use of this suite of characters in defining inter-familial relationships. They suggested that detailed study of continuous developmental series of many species is necessary before the nature of vertebral ossification can be generally applied to anuran phylogeny.

In this effort, I examined three specimens of *Atelopus varius* measuring 8.5, 12, and 15 mm and three specimens of *A. ignescens* measuring 12, 18, and 20 mm to determine the sequence of vertebral ossification. Dorsally, with the exception of the first two vertebrae that are separate from each other and unossified on the midline, the neural arch of *A. varius* is narrow and complete in the smallest specimen. In the 12 mm specimen, each vertebra has closed dorsally, and the first two are nearly completely fused with each other. At 15 mm the first two vertebrae have fused to form the atlas complex. There is also a gradual widening of the neural arch from the smallest to the largest specimens. All other dorsal and lateral components of the vertebrae (zygapophyses, transverse processes), with the exception of dorsal ornamentation, are present in the smallest specimen.

The centra are completely ossified ventrally in the 8.5 mm specimen but are not connected by ossification to the lateral portions of the vertebrae. In the 12 mm specimen ossification has begun to connect the four ventral corners of the centra to the lateral portions of the vertebrae. This ossification is nearly complete in the 15 mm specimen. In the larger specimens, there is a thin line of ossification that connects successive vertebrae in the middle of the centrum. This probably represents the notochord. Only in the largest specimen (15 mm) is there any indication of ossification and fusion of the intervertebral disc to form the procoelous ver-

tebrae. The bicondylar articulation of the coccyx to the sacrum is obvious at the 12 mm stage.

The three stages of *A. ignescens* are almost identical in the sequence of vertebral ossification. I consider this sequence to represent perichordal development (= ectochordal of Griffiths, 1963). The ossification of the centra to the rest of the vertebrae occurs first in the posterior vertebrae in the 18 mm stage. Distinct posterior procoelous central facets are apparent in the 20 mm stage. Unfortunately, earlier stages of *Atelopus* are not available, nor are developmental stages of the other genera. Kluge and Farris (1969:23) indicated that the Atelopodidae have both perichordal and epichordal vertebrae. This conclusion was based on an examination of *Dendrophryniscus minutus* (*Atelopus minutus*) and *Atelopus cruciger*. They indicated that the former is "very likely epichordal" while the latter is almost certainly "perichordal." I can find no indication of epichordal vertebrae in *Dendrophryniscus minutus*. Accordingly I consider all four genera perichordal, until developmental series prove otherwise.

Coccyx.—Griffiths (1963:277-78) reviewed the literature concerned with morphogenesis of the coccyx (urostyle) and unequivocally demonstrated that this bone is formed by the fusion of caudal vertebrae with a single, medial hypochord. This is the same conclusion reached by Mookerjee (1931). Griffiths goes on to discuss the evolutionary implications and early history of the coccyx.

The coccyx usually articulates via a bicondylar socket with the sacral vertebra in *Atelopus*. However, it is fused to the sacrum in some specimens of *A. spurrelli* and *A. varius* from Panama, and in *A. glyphus*, *A. oxyrhynchus*, and an undescribed form from Ecuador. Cope (1865:101) indicated that the coccygeal condyle is simple in *A. flavescens*. However, examination of *A. flavescens* shows the typical bicondylar condition. There is a well-developed lateral flange at the anterior end of the coccyx in most specimens of *A. spurrelli*, *A. varius* and related species. This flange is present but narrow and extends nearly the entire length of the coccyx in *A. flavescens*, *A. spumarius*, and *A. zeteki*. The lateral flange is absent from *A. boulengeri*, *A. ignescens*, *A. ebenoides*, *A. carrikeri* and other closely related species. Most forms have a dorsal ridge which may be slightly expanded on the top to form a cap. Normally there is a wide gap between the dorsal surface of the sacral vertebra and the ridge of the coccyx. A dorsal ridge is reduced or absent in some species, including *A. boulengeri*, *A. ignescens*, *A. oxyrhynchus* and *A. pachydermus*. An expanded diapophysis of a transverse process of a presacral vertebra sometimes is

found on the coccyx just posterior to its articulation with the sacrum.

Only in one specimen of *Melanophryniscus stelzneri* was the coccyx fused to the sacrum; all other specimens of the genus had the normal articulation. All four species have a dorsal ridge and a slightly expanded flange anteriorly.

The coccyx is fused to the sacral vertebrae in four cleared specimens of *Dendrophryniscus brevipollicatus* and one cleared specimen of *D. minutus*. Radiographs of a few specimens indicate an articulation, but confirmation must await additional skeletal preparations. There is no lateral flange or dorsal ridge. Izecksohn (1968) reported that most of the specimens of *D. leucomystax* studied had bicondylar articulation. However, in three specimens the coccyx and sacral vertebra were fused.

The coccyx of *Oreophrynella* is typically fused to the sacrum and has a greatly expanded lateral flange which extends from near the posterior distal tip of the sacral diapophyses postero-medially almost to the tip of the coccyx. There is a low, but well-defined, dorsal ridge on the coccyx.

Appendicular skeleton

Pectoral girdle.—Cope (1864, 1865, 1866, 1867) recognized the importance of the structure of the pectoral girdle to salientian classification. Following the classical works by Parker (1868) and others, and the modifications by Boulenger (1882), the Cope scheme became generally accepted. Noble (1922, 1926) pointed to certain problems of a classification based on the condition of the pectoral girdle and considered the girdle condition useful only as secondary evidence in showing relationships. Griffiths (1963) argued that most Anura can be divided into two phylogenetic groups based on the presence or absence of epicoracoidal horns. Inger (1967) pointed out that several groups of frogs apparently achieved the firmisternal (fused) condition independently. Inger also argued that the arciferal (overlapping) condition probably is primitive. Kluge and Farris (1969) also concluded that the arciferal condition is primitive. The arciferal nature of the girdle is characteristic of most salamanders (Noble, 1931; Eaton, 1959) and occurs in developmental stages of many firmisternal forms (Noble, 1926; Griffiths, 1963). These data support the assumption that the arciferal condition of the pectoral girdle is primitive.

The clavicles form the anterior portion of the girdle; the coracoids form the posterior part. Medially, epicoracoidal cartilage connects the clavicles and coracoids to each other and their respective halves. Anteriorly, there is a continuous connection between the clavicles; this is characteristically

a firmisternal union and occurs in all forms examined. The coracoids maintain this firmisternal connection on the posterior midline only in *Atelopus*. The epicoracoidal cartilages between each coracoid overlap in *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*, thus obtaining the arciferal condition posteriorly. Noble (1926) illustrated the nature of the overlap in *Melanophryniscus stelzneri* and *M. moreirae* and *Dendrophryniscus brevipollicatus*. He referred to this condition as arciferofirmisternal and considered it to be an intermediate step between the arciferal and the firmisternal conditions. Apparently *Atelopus* represents the end point in this shift to firmisterny.

All species of *Atelopus*, *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella* have basically the same shaped pectoral girdle, whether the condition be one of overlap or fusion (Fig. 8). However, *Oreophrynella* has a much deeper clavicular area than the other forms, and *Dendrophryniscus minutus* has a more rectangular shaped girdle. The medial border of each coracoid foramen is formed of cartilage in all four genera. Also the clavicles and coracoids are fused laterally in all *Atelopus* (except a large specimen of *A. bouleengeri*) and *Melanophryniscus* but are separate in most specimens of *Dendrophryniscus* and *Oreophrynella*. The lateral fusion of these two bones is considered to be a derived state, apparently correlated with the shift towards a more firmisternal condition.

Griffiths (1963) focused attention on the development of epicoracoidal horns as a systematic character potentially of greater use than the arciferal or firmisternal nature of the pectoral girdle. His argument centered on the taxonomic usefulness of a character, whose states are based only on degree of fusion or overlap. Griffiths contended that those species which have posteriorly directed epicoracoidal horns are generally the arciferal families, and those that lack well-developed epicoracoidal horns are generally the firmisternal families. Based on Griffiths taxonomic survey and in the absence of contrary data, Kluge and Farris (1969) accepted these criteria as useful in defining families of frogs.

In developing the above outlined argument, Griffiths (1963:270) discussed the trend towards firmisterny in the atelopodid genera using an illustration (264, Fig. 8) of a proposed morphological continuum starting with the arciferal girdle of *Bufo*, continuing through *Dendrophryniscus* (probably *Melanophryniscus*?), *Oreophrynella* and a hypothetical condition, to the firmisternal *Atelopus* and *Brachycephalus* (discussed elsewhere, MS). This trend purportedly is characterized by an

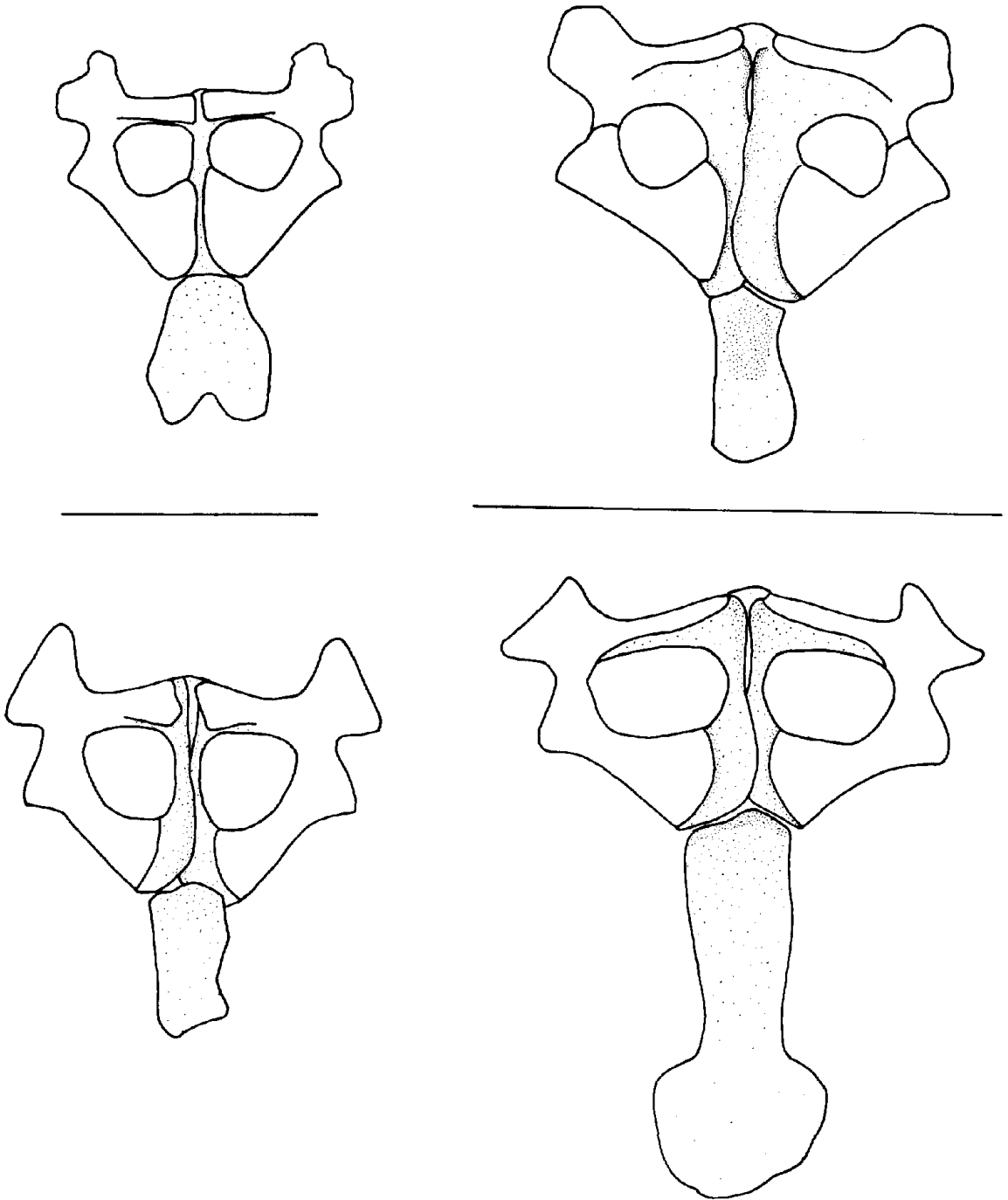


FIGURE 8. Ventral view of the pectoral girdle of (upper left) *Atelopus varius* LACM 64440, (lower left) *Melanophryniscus rubriventris* LACM 64441, (upper right) *Oreophrynella quelchii* LACM 64443, and (lower right) *Dendrophryniscus brevipollicatus* LACM 64444. Lines equal 5 mm.

increase in epicoracoidal horn development and a corresponding suppression or loss of the sternal element. He argued that with the increase in depth of the precoracoidal bridge, the sternal primordium is separated later and the migrating anlagen is reduced while that of the epicoracoidal horns is increased. Griffiths stated that "*Atelopus* has carried the trend farther: zonally, epicoracoid fusion is complete but, behind [posterior to] the coracoids, they [the epicoracoids] overlap extensively, the sternum being completely suppressed" (italicized words are mine).

Melanophryniscus, *Dendrophryniscus*, *Oreophrynella*, and all species of *Atelopus* which I examined have a discrete sternal element (Fig. 8). This element probably represents the mesosternum. It shows some variation in the degree of ossification but in all cases it is ossified. In some species of *Melanophryniscus* and *Atelopus* the posterior portion of this sternal element is cartilaginous and may represent the xiphisternum. Griffiths (1963: 270) mentioned occasionally encountering "incipient abdominal cartilages" in some atelopodids. He gave no further information concerning the distribution, position or function of these cartilages. I am convinced that the element which I am calling a sternum is homologous among the four genera and is the same element called a sternum by many anuran biologists (e.g. Noble, 1931; Goin and Goin, 1962), and illustrated by Griffiths in *Bufo*. Further, I could find no indication of the extensive epicoracoidal horn development in either *Atelopus*, *Melanophryniscus*, *Dendrophryniscus*, or *Oreophrynella* nor the extensive posterior overlap of the epicoracoids in *Atelopus* that were repeatedly mentioned (Griffiths, 1959:459; 1963:264-270, fig. 8).

Pelvic girdle.—The pelvic girdle of all five genera has the typical V-shape. The pubis and ischia fuse to form the posterior parts of the girdle and acetabulum; the ilia form the arms of the V and fuse together posteriorly with the ischia and pubis to complete the girdle and form the anterior lip of the acetabulum. The ilia are nearly round in cross section and articulate with the ventral surface of the expanded sacral diapophyses in *Atelopus*, *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella*.

Limb elements.—The relative length of the limbs is extremely variable and generally conforms to the relationships discussed below with respect to habitus of each form. The differences in limb length, especially among species of *Atelopus*, reflect interspecific variation and in certain cases may be attributed to ontogenetic, sexual, or geographic variation. There are no distinct differences in shape of the forelimbs; all forms have a humeral ridge.

The hindlimbs are typical of most frogs. There is a slight bend in the shaft of the femur of most of the forms; the bend becomes weakly S-shaped in some of the long-legged species of *Atelopus*.

Mesopodial elements.—Because of the inherent difficulty in determining homologous elements and because of the current confusion in terminology, no attempt has been made to standardize names of the mesopodial elements. My terminology is a composite from several sources that seems to most adequately describe the situation in the genera studied.

The carpal elements vary in number from six to four. All genera have two proximal elements, a radiale and an ulnare. Apparently the intermedium has fused with one of these elements. Ritland (1955a) indicated that the intermedium fused with the ulnare in *Ascaphus*.

The central carpals or centralia are represented by two elements in *Melanophryniscus* and *Oreophrynella* but only a single element in *Atelopus* and *Dendrophryniscus*. The proximal centrale, which probably represents a fusion of centralia II and III, is smaller in *Oreophrynella* than in the other four genera. Another central carpal element, perhaps centrale I, is located distally to centrale II-III and medial to distal carpal I. Centrale I articulates with the medial edge of metacarpal I. A distinct bony element is located distal to and articulates with centrale I. This element is considered to be a prepollex. However, the possibility exists that it represents centrale I and that the other central carpal elements would have to be numbered accordingly; centrale I would become II, and centrale II-III would become III. Eaton (1959) and Romer (1962) suggested that the fourth central carpal is fused with the radiale in modern anurans. The large size of centrale II-III in *Melanophryniscus* might be the result of a fusion of central elements II-III-IV. The carpal bone that lies distal to this centrale and medial to distal carpal I would then be homologous to the element referred to as a prepollex in *Oreophrynella*. However, its position suggests that the prepollex has been lost in *Melanophryniscus* and that the distal element is I and the proximal element is centrale II-III.

In *Atelopus* and *Dendrophryniscus* the first centrale has fused with centrale II-III, and together they form a single central carpal element, centrale I-II-III, that lies between the radiale and metacarpal I.

The distal elements in the manus are referred to as distal carpals. They are numbered according to the digit which they support. All forms have two distinct distal carpal elements. The first supports digit 1; the second, third, and fourth are

fused into a single unit and support digits 2, 3 and 4. Distal carpals II, III and IV are fused into a single element as is characteristic of the other four genera.

The tarsal elements, including the tibiale and fibulare (astragalus and calcaneum, respectively) number four or five. Digits 4 and 5 articulate with the distal head of the fibulare, suggesting a fusion of distal tarsal elements IV and V with the fibulare. *Oreophrynella* has distal tarsals I, II, and III at the base of digits 1, 2, 3. This same arrangement is characteristic of most *Melanophryniscus*. A single specimen of *M. tumifrons* has tarsals I and II fused. *Dendrophryniscus* also usually has three, but a single specimen of *D. brevipollicatus* has a fusion between distal tarsals II and III. All specimens of *Atelopus* possess two distal tarsal elements; the second and third are fused. A single specimen of *Atelopus varius* has a fusion between distal tarsal I and the centrale that forms the base for the prepollex.

The metacarpal elements are consistent among the genera. There are four metacarpals, and they generally increase in size in the following order: 1, 2, 4, 3. The metatarsals of *Atelopus*, *Melanophryniscus*, and *Dendrophryniscus* have the same general size relationship, listed in order of increasing length: 1, 2, 3, 5, 4. In *Oreophrynella* metatarsals 1, 2, and 3 are of about equal length and slightly more than two-thirds the length of metatarsals 4 and 5, which are of about equal length.

A distinct prepollex is found in *Oreophrynella*; it may consist of a single or two distinct elements. Apparently the prepollex is absent in *Melanophryniscus* and *Dendrophryniscus*, although both have a small lateral, irregular spine or ridge that might be a remnant of a prepollex that fused to the side of metacarpal 1. This is better developed in males than in females. In *Atelopus* there is a single or double element that is usually fused to the lateral edge of the metacarpal 1. Frequently, it forms a lateral ridge on the metacarpal. This element may articulate with centrale I-II-III or be separated proximally and fused to the metacarpal. In some specimens, it extends nearly the entire length of the metacarpal; in others it may be restricted to the middle half of the metacarpal. In a few specimens, this ridge is free from the metacarpal; usually it is partially or completely fused to it as least at its proximal end. Laurent (1942) showed it completely separate from the metacarpal in *Atelopus varius*. This irregular structure is better developed in males than in females. Because of the wide range of both inter- and intraspecific variation in *Atelopus*, there are two possible interpretations concerning the nature of this element. First, it may

be derived from metacarpal 1, in connection with the male holding of the female during amplexus, or it may be a remnant of the prepollex that fused to the first metacarpal unit. I consider it to be a remnant of the prepollex until contrary evidence becomes available.

A prehallux is present in all forms and may consist of one or two fused elements or three discrete elements. The structure is best developed in some *Atelopus* and poorly developed in *Dendrophryniscus*.

Digits.—All forms typically have four digits on the front foot and five digits on the hind foot, although in some species of *Atelopus* the fifth digit of the foot is greatly reduced and incorporated into the sole.

The common phalangeal formula for the hand is 2-2-3-3 and is found in *Oreophrynella* and *Melanophryniscus*. Each element is short and robust in *Oreophrynella*, and the terminal element is stout and only slightly expanded. The condition in *Melanophryniscus* is similar, but each phalanx is slightly more elongate, and the terminal tips are very irregular though slightly expanded. There is a reduction in the number and length of the phalanges in the first digit in *Atelopus*. Several species exhibit the typical 2-2-3-3 formula, but specimens of several species have only a single unit in digit 1 giving a formula of 1-2-3-3. In some specimens the formula is 1-2-3-3 in one hand and 2-2-3-3 in the other. Apparently there is a trend towards reduction in length and ultimate loss of the phalanges in the first digit in some species of *Atelopus*. The tips of the terminal phalanges are generally expanded and slightly rounded.

Specimens of *Dendrophryniscus minutus* have a 2-2-3-3 phalangeal formula and slightly expanded tips while *D. brevipollicatus* has lost the terminal phalanx in digit 1 and has a formula of 1-2-3-3. In addition the terminal tips of *D. brevipollicatus* are expanded and T-shaped.

The phalangeal formula for the foot is consistently 2-2-3-4-3 for *Atelopus*, *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella*. The length and width of the phalanges in digit one in *Atelopus* are greatly reduced. A single specimen of *A. spumarius* has a phalangeal formula of 1-2-3-4-3. In each of the species, the terminal tips of the feet have the same general shape that is characteristic of the hands.

AUDITORY APPARATUS

The value of the middle ear as a taxonomic character in frogs has been recognized for a considerable period of time. The perfect or imperfect condition of the ear was considered by Günther

(1858a, b) and Mivart (1869) to be of primary importance in the classification of anurous Batrachia. More recent authors (Noble, 1931; Parker, 1934; Griffiths, 1954b, 1959) have demonstrated that the absence of a middle ear apparatus is characteristic of several unrelated species of frogs and questioned its value as a higher taxonomic character.

Parker (1932) implied that the absence of a complete ear apparatus in so many different groups of Anura is the result of convergent evolution through loss. Later (1934) he reversed himself and suggested that the absence of a middle ear structure was indeed a primitive character, an interpretation formulated following the report by Du Toit and de Villiers (1932) that the developing ear of young *Hyperolius horstocki* passes through an incomplete ear stage, almost exactly the same as the condition in earless frogs, before attaining the typical complete ear of the adult.

Griffiths (1954b) interpreted the absence of an ear apparatus in the African frog *Didynamis sjostedti* and the neotropical species of *Dendrophryniscus* and *Atelopus* as indicating relationships and suggested that the African and neotropical frogs were evolved from a common stock in Africa; the neotropical group subsequently dispersed. Later (Griffiths, 1959) he changed his mind and decided that the absence of a complete ear in the African and South American species was the result of parallel loss in the two groups. Each group was evolved independently from an ancestral bufonid stock residing in the same area as their respective descendants. He considered the absence of the complete ear as a pedomorphic character of relatively common occurrence in Salientia.

Ramaswami (1939) reviewed much of the earlier work on the middle ear of frogs. Eiselt (1941) made an exhaustive study of the opercular muscle and the middle ear in Anura. Tumarkin (1955) and Sedra and Michael (1959) discussed the current ideas concerning the ontogenesis of the anuran auditory mechanism. In general, their terminologies are incorporated into this study.

The middle ear of frogs consists of a tympanum, a middle ear cavity, and ear bones. The tympanum is a thin membrane which covers the external opening of the middle ear. It may be covered by a thin differentiated portion of skin and be apparent externally; this is referred to as an external tympanum. It may be covered by undifferentiated skin and not be visible externally; this is referred to as an internal tympanum. Some frogs have various degrees of intermediacy between an external and internal tympanum. The tympanic

annulus surrounds the tympanic membrane. It is a cartilaginous ring derived from the quadrate.

The middle ear cavity surrounds the ear bones and lies between the tympanum and the inner ear. The Eustachian tube connects the middle ear cavity with the pharyngeal cavity. The openings of the Eustachian tubes in the pharyngeal region of the mouth are called the ostia pharyngea. The ear bone in frogs is called a pseudocolumella and is composed of three parts: 1) a cartilaginous footplate (pars interna plectri or interstapedial) which is derived from and abuts against the otic capsule in the fenestra ovalis; 2) a bony stylus (pars media plectri or mediostapedial) which also is derived from the otic capsule and connects to 3) a cartilaginous extracolumella (pars externa plectri or extrastapedial) lying across the inner surface of the tympanic membrane. The extrastapedial apparently is derived from the quadrate. The fenestra ovalis (oval window) is the membranous area on the ventro-lateral wall of the otic capsule that separates the middle ear from the inner ear.

In frogs with a tympanic-middle ear apparatus, hearing in adults is accomplished in at least two ways. Airborne sounds, picked up by the tympanum, are passed down the ear ossicles to the fenestra ovalis and then to the inner ear. In frogs that lack a tympanic-middle ear apparatus apparently "hearing" is accomplished by a muscular connection between the suprascapula and the otic capsule. Posterior and medial to the footplate of the pseudocolumella and lying in the fenestra ovalis is a bony element called the operculum. The movable operculum is derived from the otic capsule and connects to the suprascapula via the opercular muscle. The opercular muscle is a specialized derivative of the levator muscles of the scapula. In a terrestrial environment vibrations from the ground are transmitted through the pectoral girdle to the operculum and then to the middle ear via the tensed opercular muscle. This pathway is available to frogs with a typical tympanic-middle ear apparatus.

In addition to examining the auditory apparatus, the ability of these frogs to call was investigated with reference to the presence of vocal slits and the nature of the vocal sac. The terminology used in their descriptions follows Peters (1964).

Middle ear.—A tympanum, annulus tympanicus and ear ossicles are absent from all species of *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella* examined. All species of *Atelopus* also lack these structures with the exception of *A. flavescens*, *A. spumarius*, and an undescribed species, each of which lacks an external tympanum but possesses a moderate to well-developed internal

tympanum, annulus tympanicus and ear ossicles.

Opercular structure.—All specimens of *Atelopus*, *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella* have a well-developed operculum. Similarly, they all have a well-developed opercularis muscle which arises on the operculum and inserts on the ventral surface of the anterior distal part of the suprascapula. This condition, as well as the typical middle ear structure, is present in the three species that have the middle ear.

Ostia pharyngea.—No specimens of *Dendrophryniscus* have ostia pharyngea. *Oreophrynella quelchii* has small indentations that appear to be remnants of the pharyngeal opening of the Eustachian tubes, but there are no ostia pharyngea. All species of *Melanophryniscus* have ostia pharyngea. There is some variation in the size of the opening. *M. stelzneri* has the largest opening, and *M. moreirae* has the smallest. Species of *Atelopus* show as much variation among themselves as is shown by the other genera. Specimens of *A. flavescens* always have very large ostia pharyngea. Some species of *Atelopus* include individuals with ostia pharyngea and individuals without them. Ostia pharyngea are lacking completely in all specimens of some species.

Vocal apparatus.—There are no vocal slits in available specimens of *Dendrophryniscus* or *Oreophrynella*. All specimens of the four species of *Melanophryniscus* examined have vocal slits. The vocal slits may be on one side or on both sides, but their positions are constant for each species. Males of *M. stelzneri* have a well-developed external vocal pouch. External vocal pouches are not evident in the other species. In species of *Atelopus*, vocal slits may be absent or present. When present, they may be on the right side only, the left side only, or on both sides. External vocal sacs were not observed in specimens of *Atelopus*, *Oreophrynella*, or *Dendrophryniscus*.

EXTERNAL MORPHOLOGY

Habitus

Frogs of the genus *Atelopus* are considerably different from most frogs in overall appearance and are referred to as atelopodid-like: the head is usually longer (snout to end of lower jaw) than it is wide (at the point of jaw articulation); the snout is strongly acuminate from a dorsal aspect and typically acute from a lateral profile; round nares open laterally and generally are situated closer to the tip of the snout than to the eye; the moderately sized eyes may be longer than, equal to, or shorter than the distance between the eye and the naris; the pupil is horizontally elliptical; there is no external tympanum, although there may be an elevated

(supratympanic) area dorsal to where a tympanum is normally located. The body length (snout to vent) of adult males is generally greater than three times the body width (at sacrum). The limbs are usually long and spindly. Many species are brightly colored with vivid shades of red, yellow, or green, often contrasted in irregular patterns with dark colors, especially black.

Dendrophryniscus brevipollicatus and *D. minutus* are smaller than most *Atelopus* species but very similar in head proportions (head length longer than or equal to head width) and snout shape. The round nares are closer to the tip of the snout than to the eye; the eye is proportionally smaller than in *Atelopus*, less than or equal to the distance from the eye to the naris. An external tympanum is absent; there is no indication of a supratympanic elevation. The species of *Dendrophryniscus* are slightly more robust than *Atelopus*; the body length ranges from two and one-half to three and one-quarter times the body width. The limbs are moderately long and thin. *Dendrophryniscus* is not brightly colored but possesses a cryptic pattern of brown or tan, often barred with darker markings dorsally.

The species of the two remaining genera, *Melanophryniscus* and *Oreophrynella*, are different from both *Atelopus* and *Dendrophryniscus* in habitus. They generally resemble toads in overall appearance and are referred to as bufonidlike: heads are wider than they are long; from a dorsal aspect the snout is acuminate or slightly rounded; in profile the snout is rounded or vertical; the laterally opening nares are round and close to the tip of the snout; the eye is moderate in size and equal to or slightly less than the distance from the eye to the naris; the pupil of the eye is horizontally elliptical; an external tympanum is lacking. A supratympanic elevation is absent in *Melanophryniscus* and poorly developed in *Oreophrynella*. These genera are represented by more robust species than are found in either *Atelopus* or *Dendrophryniscus*. Dorsally the species of *Melanophryniscus* and *Oreophrynella* are usually uniform dark brown or black often spotted or marked with yellow. The bottoms of the hands and feet are bright orange, yellow, or red. The bright colors on the ventral surface of the body are marbled with black except in *M. rubriventris* which is uniformly red beneath.

Integument

The skin of anurans has certain specific peculiarities which may be valuable in appraising relationships. Of primary concern in this study are the texture of the epidermis and the nature and arrangement of the glands as they contribute to the

general appearance of the frog. Wherever possible, I have attempted to utilize the nomenclature proposed by Elias and Shapiro (1957) to describe the glandular development.

The skin of most species of *Atelopus* is smooth to slightly rugose; in some forms (*cruciger* and *oxyrhynchus*) there is a dorso-lateral row of rounded warts (verrucae) along the body. Laterally on certain other species (*carrikeri*, *ignescens*, and *walkeri*) there are warts with a thickened stratum corneum at their apex. These warts are different from those forming the dorso-lateral row and are referred to as conical apical. No species have parotoid glands, although in some, including *A. ignescens*, there is glandular development in the parotoid region. cursory examination of these glands in *A. ignescens* indicates that they are of the same type as those found on the dorso-lateral regions of the head, above the eyes, in scattered areas on the back, sides, and dorsal surfaces of the humerus and femur, and over the entire dorsal surface of the distal sections of each limb, onto the hands and feet. Microscopic examination of a thin section of glandular tissue indicates that the glands are strikingly different in size and structure from those that form the parotoid glands of most species of *Bufo*.

Dendrophryniscus has a minutely glandular skin with small scattered warts, some of which are topped with low conical apical. There is no glandular development in the parotoid area. Low elevation in this area results from the dorso-lateral extensions of the posterior arm of the squamosal and the lateral part of the prootic.

All specimens of *Melanophryniscus* that were examined possess a rugose skin covered with verrucae. These warts are rounded in *M. moreirae* and *rubriventris*; in *tumifrons* the warts are tipped with one to several conical apical, usually lighter in color than the verrucae. *M. stelzneri* has an intermediate condition. These conical are best developed in the lateral areas of the head and neck between the eye and the foreleg insertion. In all *Melanophryniscus* examined the warts on the dorsal surfaces are more abundant and better developed than those on the ventral surfaces. There are no discrete parotoid glands in any species. However, *M. tumifrons* has two nearly confluent large verrucae on the snout.

The skin of *Oreophrynella quelchii* is rugose and covered with many small rounded warts. In overall appearance it is very similar to *M. moreirae*. There are no distinct or enlarged warts in the parotoid region.

Other integumentary characters are the presence and configuration of a ridge along the upper eyelid. This ridge is found in some species of *Atelopus*

and is absent from others. When the ridge is present, it forms a thickened brow. In *Dendrophryniscus* the ridge is formed by about 12 small warts; in *Melanophryniscus* it is thickened in all species. In *M. moreirae* this thickening is edged with four or five warts that are rounded; in *tumifrons* the warts are pointed.

Hands and Feet

Several characters of varying significance which pertain to the hands and the feet have been used by anuran systematists in the past. The presence of a tarsal fold, the number of digits on the hands and feet, the shape of the terminal ends of the digits, the presence and configuration of tubercles on the palms and soles of the hands and feet, and the condition of the interdigital webbing are considered in this study.

A tarsal fold has been reported for some species of *Atelopus* (Rivero, 1963:115) but is absent from most species which I have examined. There is no tarsal fold in species of the other four genera.

All species of *Atelopus* have four fingers and five toes, although the first digit of the hand may be reduced in length, fully webbed, and therefore, not immediately apparent. The digital tips of all species examined vary from slightly to not expanded. Four fingers and five toes are also characteristic of all species of *Dendrophryniscus*, *Melanophryniscus* and *Oreophrynella*. The inner two digits on the hind foot of *Oreophrynella quelchii* are opposable; the first toe is longer than the second and gives the foot an overall broader appearance, quite distinct from species in the other genera. The digital tips are expanded in *Dendrophryniscus brevipollicatus* but not in *D. minutis*. In contrast, the tips of the digits in *Melanophryniscus* are slightly thickened, and in *Oreophrynella* they are markedly thickened; the digits are not expanded in species of either genus.

Many species of *Atelopus* have marked interspecific variation in the condition of the tubercles on the hands and feet. Some species have moderately developed palmar tubercles. Subarticular tubercles, if present, are usually small and indistinct. The species of *Dendrophryniscus*, *Melanophryniscus* and *Oreophrynella* are consistent in having tubercles on both the hands and the feet. *Dendrophryniscus* has a large outer palmar tubercle and some subarticular tubercles on the hands and an outer metatarsal tubercle and several subarticular tubercles on the feet. Species of *Melanophryniscus* have a moderate to well developed outer metacarpal tubercle and inner and outer metatarsal tubercles. Additional metacarpal, metatarsal, and subarticular tubercles are also present.

All tubercles are well developed in specimens of *M. tumifrons* and *stelzneri* and poorly to moderately developed in *M. moreirae* and *rubriventris*. In *Oreophrynella quelchii* there are two flat metacarpal tubercles, an inner and an outer, and an inner metatarsal tubercle. There are no distinct subarticular tubercles. Rather, there are three to five smaller tubercles on the ventral surfaces of the hands and feet near the bases of the digits. The rest of the palmar and soler surfaces are irregularly wrinkled and folded and covered with many small tubercles.

The interdigital webbing in the genera studied differs from that observed in other frogs, such as hylids or ranids. It is not a membrane as defined by Peters (1964) but rather a thickened integumentary connection between digits, similar to the webbing encountered in many of the more terrestrial anurans, such as toads of the genus *Bufo*.

The condition of the interdigital webbing shows a great deal of variation in species of *Atelopus*. The fingers generally are not, or are only slightly, webbed, with the greatest development between the first and second digit. The toes vary from a slightly to fully webbed condition. *Dendrophryniscus* has no, or very rudimentary, webbing on the hands and rudimentary webbing on the feet. The specimens of *Melanophryniscus* and *Oreophrynella* show no webbing on the hands. The digits of the feet are joined at their bases by a fleshy extension of thick skin from the sole. While this has been interpreted as "webbing" by some authors (Cochran, 1955:3), it is different from the webbing characteristic of some species of *Atelopus* and *Dendrophryniscus*.

REPRODUCTIVE BIOLOGY

Several aspects of the reproductive biology of Anura provide information valuable to an understanding of generic relationships (Jameson, 1957). Because of the lack of adequate knowledge concerning the life histories and reproductive behavior of the majority of the species studied, most of these characters concern morphology. Therefore, it is difficult to determine relationships based on similarities or differences in morphological characteristics alone.

Urogenital System

Uterus.—Bhaduri (1953) made an exhaustive survey of the urogenital system in Anura. In general he concluded that the urogenital apparatus has no great significance for defining major taxonomic groups. He pointed out that the uterine condition generally is constant within a genus and sometimes within a family, although the extremes of uterine modification are found within the limits

of some families. Bhaduri (1953:64) described the uterus of *Bufo* and referred to this condition as *uterus septatus*. In this condition there is a partition of varying length between the uteri except posteriorly where a common uterus forms. This condition is intermediate between those frogs which have two uteri separate along their entire length (*uterus separatus*) and those frogs which lack any partition, having the uteri confluent, forming an unpaired common uterus (*uterus communis*).

All specimens of the five genera that I examined seem to fall into Bhaduri's *uterus septatus* group. Some species of the bufonid *Nectophrynoides* apparently have this condition as well.

Bidder's Organ.—The anterior portion of the progonad retains its ovarian nature in males of some frogs and is referred to as the Bidder's organ. This structure has been subjected to intensive study for nearly 200 years. Witschi (1933) presented a review of this structure and discussed its morphology with reference to sex determination and differentiation in several species of toads. He demonstrated that the cortical layer of the progonad supplies the germ cells of the Bidder's organ and postulated that the ovarian nature of this structure results from the withdrawal of medullary or testes-forming tissue from the anterior part of the progonad. He suggested that the ancestral form of the bufonids must have possessed a long gonad. In living species during the differentiation of the gonad, the functional testes or ovaries are restricted to the posterior segment, while the anterior portion of the gonatomes give rise to Bidder's organ and fat bodies.

Davis (1936) surveyed the distribution of Bidder's organs in Anura and found that this peculiar structure was restricted to bufonid toads. He reported the presence of Bidder's organs in several species of *Bufo*, *Nectophrynoides*, *Pedostibes*, and *Pseudobufo*. He reported their absence from *Cacophryne borbonica* and *Nectophryne afra*. Davis considered the bufonids to be derivatives from a leptodactylid stock and favored the hypothesis that the Bidder's organ originated with the Bufonidae. He pointed out that certain leptodactylids have elongate testes. This fact lends support to Witschi's proposition that the ancestral bufonid possessed long gonads.

Dubois (1947) reported the presence of a Bidder's organ in a juvenile *Cacophryne borbonica* and an adult male *C. cruentata*. He concluded that Bidder's organs are found in all genera of Bufonids, including *Bufo*, *Pseudobufo*, *Pedostibes*, *Pelophryne*, *Nectophryne*, *Nectophrynoides*, and *Cacophryne*.

ryne. He considered it a characteristic of the Bufonidae lacking in other anuran families.

Dubois (1947) mentioned the presence of a Bidder's organ in the Australian leptodactylid *Pseudophryne bibronii* and in *Rhinophrynus*. The report of a Bidder's organ in *Pseudophryne* is based on Stohler's work (1932). Rau and Gatenby (1923) and Ponce (1924) reported this organ lacking from *Pseudophryne bibronii*. Dubois does not mention the source of his information concerning *Rhinophrynus*. Rau and Gatenby (1923) examined several specimens of *Rhinophrynus dorsalis* and could find no trace of a Bidder's organ. I also examined several specimens of *Rhinophrynus* and found no indication of a Bidder's organ.

Griffiths (1954b, 1959) confirmed the presence of a Bidder's organ in *Bufo*, *Nectophrynoides*, *Pedostibes*, and *Pseudobufo* and reported this structure from several species of *Atelopus*, *Melanophryniscus stelzneri*, *Oreophrynella quelchii*, *Cacophryne borbonica*, and *Nectophryne afra*. Inger (1954) reported the presence of Bidder's organs in *Ansonia* and *Pelophryne*. Griffiths (1954b) indicated that the Bidder's organ is better developed in young individuals than in old individuals and pointed out that the structure may be degenerate in fully adult individuals, especially in genera other than *Bufo*. Witschi (1933) and Davis (1936) also reported that the Bidder's organ is better developed in the juveniles of some species of *Bufo*. Griffiths maintained that the presence of a Bidder's organ in a species is proof of bufonid affinities, but that its absence need not, on its own merit, establish that such affinities do not exist. He further contended that the degeneration or disappearance of the organ might be expected either ontogenetically or phylogenetically. Later Griffiths (1959: 477) stated that the presence of Bidder's organs in *Atelopus*, *Dendrophryniscus*, *Oreophrynella*, *Didynamipus*, and *Cacophryne* makes their origin from the Bufonidae indisputable.

A Bidder's organ has been reported from several specimens of *Atelopus*, *Melanophryniscus*, *Oreophrynella quelchii*, and *Dendrophryniscus brevipollicatus*.

Gonads.—There is very little information available concerning the evolutionary importance of differences in size, shape, and coloration of the gonads of frogs. Witschi (1933) and Davis (1936) mentioned that the ancestral forms of bufonids possessed long gonads. Davis (1935) reported that *Cacophryne borbonica* lacks the lengthened testes characteristic of other toads. Inger (1966:74) indicated that the snout-vent length to testes length ratios of *C. borbonica* and *C. cruentata* range be-

tween four and five to one. In *Bufo biporcatus* the ratio was eight to one.

The testes of some specimens of *A. varius* from near La Hondura, Costa Rica, and of some specimens of *A. longirostris* and *A. senex* have a black testicular peritoneum. In all the other species of *Atelopus*, the testes are white; apparently the testicular peritoneum is colorless. It is possible that the black coloration of testicular peritoneum is correlated with the breeding condition of males of some species and may shield the testes from ultraviolet light. Lack of adequate knowledge concerning the breeding cycles of *Atelopus* prevents further discussion at this time.

In most species of *Atelopus* the ratios of snout-vent lengths to testes lengths for mature males range from about seven to one in *A. ignescens* to ten to one in *A. flavescens*. These data are difficult to evaluate because of the probable increase in size of the testes during the breeding season.

No males of *Dendrophryniscus minutus* were available; in males of *D. brevipollicatus* the testes are covered with a black peritoneum. The testes are not elongated. Ratios of snout-vent length to testes length range between 13 and 14 to 1. The testicular peritoneum of *Melanophryniscus moreirae* is unpigmented; in *M. stelzneri*, *rubriventris*, and *tumifrons* the peritoneum is moderately to heavily pigmented black. Snout-vent length to testes length ratios vary between seven and eight to one. The testes of *Oreophrynella quelchii* are elongate and appear white. Snout-vent length to testes length ratios average less than five to one.

The only information gathered concerning the ovaries was the number, size, and pigmentation of the eggs they contained. Only animals with well-developed eggs were examined.

Noble (1927) indicated that the eggs of *Atelopus* are very small and pigmented. Apparently Noble was referring to eggs of a species of *Melanophryniscus*. In 1926 he listed *M. stelzneri* and *moreirae* as species of *Atelopus*. The ovarian eggs of several species of *Atelopus* are moderate in size and lack pigment. The number of eggs in both ovaries varies among the species. As few as 350 and 372 eggs were found in *A. gracilis* and *A. ignescens*; 910 eggs were taken from a female *A. varius*. Mature ovarian eggs average about 0.8 mm in a female *A. gracilis* (36 mm snout-vent length), about 1.3 mm in a female *A. ignescens* (45 mm snout-vent length) and about 1.0 mm in a female *A. varius* (40 mm snout-vent length). There is no apparent correlation between the size of the female and the number of eggs laid, although only three specimens were examined in detail. Ap-

parently there is a correlation between the size of the eggs and the size of the animal; the smaller eggs are found in smaller animals. There is a suggestion that the size of eggs increases as the number of eggs decreases (comparison of *A. ignescens* and *A. varius*), but probably this size increase is subject to limitations imposed by the size of the females (*A. gracilis* and *A. ignescens*).

The only report of eggs of *Atelopus* refers to *A. varius* from Costa Rica. Starrett (1967) observed egg deposition in the laboratory and stated that the average diameter of the eggs is 1.6 mm. She reported that the eggs are uniformly white and laid in strings. The longest string contained 23 eggs and measured 35 mm; her measurements of the eggs and string may have been affected by handling and the artificial conditions in the laboratory. I suspect that the eggs are deposited in continuous strings.

Carvalho (1949) described the eggs and tadpoles of *Dendrophryniscus brevipollicatus*. Apparently the eggs are relatively large and deposited in groups of five or six. The eggs are yellow and measure about 2 mm in diameter.

Two females of *Dendrophryniscus brevipollicatus* contained 52 and 65 eggs in the ovaries. The female with 52 eggs measured 25 mm snout-vent length and had 23 eggs in the left ovary and 29 eggs in the right. Most of the eggs are about equal in size; the largest measures 1.6 mm. The second female was approximately the same size but showed a definite differential maturation of the eggs. This frog contained eight large and 30 smaller eggs on the left and seven large and 20 smaller eggs on the right. Unfortunately the eggs were not measured before the frog was skeletonized. In all cases the eggs had a black animal pole and a light vegetal pole. Carvalho (1949) indicated that *Dendrophryniscus brevipollicatus* lays yellow eggs and deposits them at intervals. My information from one female seems to support his field observations concerning the spacing between egg deposition. It is difficult to explain the discrepancy in egg coloration. Perhaps there is a dispersal of dark pigment following fertilization, and the resulting zygote, because of the large amount of yolk, appears yellow.

Duellman and Lynch (1969) described the eggs and tadpoles of *Dendrophryniscus minutus* from Ecuadorian specimens. Two females laid gelatinous strands of eggs measuring 245 and 285 mm and containing 245 and 291 eggs respectively. The eggs have a dark brown animal pole. They are not partitioned from each other as was described for *Atelopus* (Starrett, 1967). The strands of the

two females measure 5.0 and 7.5 mm in diameter. The eggs measure about 0.8 mm in diameter.

Two females of *D. minutus* measuring 18 and 25 mm snout-vent length contained about 175 and 420 eggs respectively. All the eggs are black on the animal pole and measure about 0.8 mm. The eggs completely filled the body cavity from just behind the heart to the cloaca.

The eggs of *D. leucomystax* are smaller, more numerous than those of *D. brevipollicatus* (Carvalho, 1949), and have a black animal pole (Izecksohn, 1968).

A female of *Melanophryniscus moreirae* (26 mm snout-vent length) contained 78 eggs in the ovaries. The eggs, about 1.7 mm average diameter, are black with a light vegetal pole. Starrett (1967) reported 70 eggs laid in the laboratory by one individual. Eggs are laid singly but adhere to each other in small clumps. She stated that the average diameter of the eggs is 2.0 mm. Bokermann (1967) examined 20 females and found 33 to 60 eggs ($\bar{x} = 48$). He suggested that females deposited eggs over a period of several days.

Two female *M. stelzneri*, 24 and 28 mm snout-vent lengths, contained 206 and 237 eggs respectively. Each egg measures about 1.2 mm in diameter. Their eggs are black with a light vegetal pole. Females of *M. stelzneri* lay more eggs than female *M. moreirae* of the same size. Apparently this increase in egg number corresponds to the decrease in egg size. Fernandez (1927) reported 201, 351, and 91 eggs each from three pair of *M. stelzneri*. Budgett (1899) and Fernandez (1927) reported a very rapid rate of development, 48 hours or less, from egg to tadpole in *M. stelzneri*. The eggs of *Melanophryniscus moreirae* hatch in about 100 hours (Starrett, 1967). The more rapid rate of development of *M. stelzneri*, as compared to *M. moreirae*, may be reflected in the higher number of eggs characteristic of *M. stelzneri*. Less yolk material is required for early development of each egg, and therefore more eggs of smaller size can be produced with the same amount of material and can fit in the same space. The eggs of *M. rubriventris* also have a dark animal pole (McDiarmid, 1971). No female specimens of *M. tumifrons* were available for examination.

Two females of *Oreophrynella quelchii* were examined. The first measured 22 mm snout-vent length and contained four eggs in the left ovary and six eggs in the right. All the eggs are large, uniformly light (probably yellow) and contain much yolk. The four eggs on the left average 1.9 mm in diameter; five of those on the right measure about 2.8 mm and a sixth measures 1.4 mm in diameter. This difference in egg size suggests that

O. quelchii may lay two clutches of eggs. A second female contained 15 large unpigmented eggs. There were six eggs in the left ovary and nine in the right. Unfortunately these eggs were not measured before the specimen was skeletonized.

Breeding Biology

Mating call.—Bogert (1960) classified frog calls into several categories and characterized the mating call as the vocalization of adult frogs most commonly heard in breeding aggregations. Duellman (1967) described the different types of mating calls based on the social organization of anurans.

Males of *Atelopus varius* utter a weak call in the field and often in the laboratory. Our lack of knowledge concerning the breeding behavior of these frogs makes it impossible to categorically state that this vocalization is a mating call and serves to attract frogs of the same species. Sexton (1958) found resident males of *A. cruciger* calling throughout the summer, and yet only a single individual was known to have mated. Starrett (1967) mentioned a weak call emitted by a male after it separated from a female following amplexus. She illustrated a sound spectrogram of a more typical call of *A. varius*. My field experience with *Atelopus* leads me to suspect that this call is not a mating call but may represent a form of male release call or possibly function as a territorial call (see Bogert, 1960, for discussion). I heard this type of call from a male *Atelopus varius* that was several hundred meters from the nearest breeding site. Some forms of *Atelopus* emit a soft "chirp" when they come into contact with each other in collecting sacks (Campbell, personal communication); others apparently do not. Dunn (1933) also reported this chirping call.

I suspect that the effectiveness of a weak mating call for a frog that breeds along fast moving, noisy streams is limited, especially since *Atelopus varius* lacks a tympanum and middle ear. However, only extensive field work using tape recordings of male calls to determine their effect on other males as well as on females will clarify the nature of this supposed mating call.

Lutz (1932) briefly reported on the breeding biology of *Dendrophryniscus brevipollicatus*. Carvalho (1949) discussed the breeding habits of this species in more detail and described the call. Apparently this frog spends most of its time in bromeliads on trees and emits a weak "tic . . . tic", presumably its mating call. Nothing is known concerning the mating call of *D. minutus*. Izecksohn (1968) described the call of *D. leucomystax* as consisting of weak peeps.

Much more information is available concerning the mating calls of species of *Melanophryniscus*. Budgett (1899) described the mating call of *Melanophryniscus stelzneri* from the Paraguayan Chaco as consisting of two clear musical "pings," followed by a long descending "trill." He mentioned that both the males and females have a call. Fernandez (1927) reported mating calls of *M. stelzneri* from the Sierra de Cordoba, Argentina. Barrio (1964) described the mating call of *Melanophryniscus stelzneri* by means of sound spectrograms of tape recorded calls. Starrett (1967) and Bokermann (1967) reported mating calls for *M. moreirae*. These reports, together with information obtained from Werner C. A. Bokermann (personal communication) and Jay M. Savage (personal communication) indicate that mating calls are characteristic of and important in the breeding biology of *Melanophryniscus*.

Nothing is known about the mating calls, breeding habits, or behavior of *Oreophrynella*.

Breeding behavior.—All references to breeding behavior in *Atelopus* are based on the reports by Starrett (1967), Duellman and Lynch (1969), my own field experience with *Atelopus varius* in Costa Rica, and the report by Sexton (1958) on the life history of *Atelopus cruciger* in Venezuela. As far as is known, *Atelopus* utilizes streamside habitats for breeding. Apparently males spend most of their time along the streams while the females are often encountered on the hillsides and some distance from the streams. The breeding season apparently extends throughout the year as amplexing pairs have been collected in March, July, August, and November. Whether females move down to the streams in response to some environmental cue, such as rainfall, or whether they are attracted by the vocalization of males, is unknown. Whatever the reason, the frogs locate each other, perhaps by visual recognition, and pair by means of axillary amplexus. The pairs remain in amplexus for a long period, a minimum of 19 days in the field (Sexton, 1958) and a minimum of 20 days in the laboratory (Starrett, 1967), during which time the female carries the male on her back. Apparently, the female searches for a place to deposit her eggs. During these movements, the pair seldom moves more than a meter from the stream and often is found sitting on rocks along the edge or in the shallows. Starrett (1967) suggested that these frogs probably deposit their eggs beneath or around rocks in the stream. I suspect that the eggs are attached to rocks or other objects in the stream to avoid being washed away. The eggs hatch in about six days. Tadpoles of *A. varius* have been taken in March, June, and September in Costa

Rica; those of *A. certus* in May in Panama; those of *A. ignescens* in Ecuador in August; and those of *A. spumarius* in July in Ecuador. Recently metamorphosed specimens of *Atelopus varius* have been collected in Costa Rica in August and October. Specimens of *A. ignescens* and *A. spurrelli* at a similar stage were taken in Colombia in July and April respectively.

Dendrophryniscus brevipollicatus spends most of its time in bromeliads. Apparently males call from these sites during the rainy parts of the year. The eggs are deposited at intervals in small clumps in the axils of the plant. The tadpoles spend their entire lives in the bromeliads (Carvalho, 1949). Melin (1941) reported an amplexing pair of *Dendrophryniscus minutus* in February or March in Brazil. Duellman and Lynch (1969) collected two amplexing pairs of *D. minutus* at the edge of a quiet, murky swamp at the edge of the forest in July in Ecuador.

The species of *Melanophryniscus* apparently breed in temporary, rain filled ponds. *Melanophryniscus stelzneri* breeds in January in Argentina; *M. moreirae* breeds in October and November in Brazil. Budgett (1899) stated that the eggs of *stelzneri* are laid in separate globules of jelly which float on the water. Fernandez (1927) and Barrio (1964) indicated that breeding commences in ponds formed by heavy rains. Similar breeding behavior was described for *M. stelzneri* by Fernandez (1927), and by Starrett (1967) and Bokermann (1967) for *M. moreirae*. Females of both species deposit eggs singly or in small groups.

Amplexus is axillary in *Atelopus*, *Dendrophryniscus*, and *Melanophryniscus*.

Larvae

Goin (1960) indicated that all members of the family Atelopodidae have indirect development, that is, they lay eggs in water and pass through a tadpole stage before transformation. This has been confirmed for *Atelopus*, *Dendrophryniscus*, and *Melanophryniscus*. Starrett (1967) described and illustrated the tadpoles of *Atelopus varius* and Duellman and Lynch (1969) described and illustrated the larvae of *A. certus*, *A. ignescens*, and *A. spumarius*. The larva of *Dendrophryniscus brevipollicatus* was described and illustrated by Carvalho (1949); that of *D. minutus* was described and illustrated by Duellman and Lynch (1969).

The larva of *Melanophryniscus stelzneri* was described and illustrated by Fernandez (1927). Ahl (1938) and later Starrett (1967) and Bokermann (1967) described and illustrated the larvae of *M. moreirae*. The characteristics of larvae of known species are summarized in Table 1.

Starrett (1967) and Duellman and Lynch (1969) discussed the similarities between the tadpoles of *Atelopus*, *Melanophryniscus*, *Dendrophryniscus*, and *Bufo*. They indicated their close relationships with other forms (e. g. *Ansonia*) of the family Bufonidae. All have the typical 2/3 tooth row pattern and a sinistral spiracle. The anus is median in *Bufo* and *Atelopus*; it is dextral in *Melanophryniscus* and *Dendrophryniscus*. The lateral margins of the mouth have an indented row of papillae in *Bufo* and *Melanophryniscus stelzneri*; in *M. moreirae* the papillae are restricted to the lateral margins but do not exhibit the indentation. *Dendrophryniscus brevipollicatus* has nearly a complete

TABLE 1
Summary of Larval Characteristics

| | <i>Spiracle</i> | <i>Anal Tube</i> | <i>Tooth Rows</i> | <i>Labial Papillae</i> | <i>Mouth</i> |
|--------------------------------------|-------------------|------------------|-------------------|--------------------------------------------------------------|---------------------------------------------|
| <i>Atelopus</i> ¹ | single, sinistral | median | 2/3 | single row, interrupted on lower lip | large, ventral, large suctorial disc |
| <i>Dendrophryniscus</i> ² | single, sinistral | dextral | 2/3 | single row, interrupted on upper lip; or single row, lateral | small, antero-ventral, no suctorial disc |
| <i>Melanophryniscus</i> ³ | single, sinistral | dextral | 2/3 | single row, lateral | moderate, antero-ventral, no suctorial disc |

¹ = *Atelopus certus*, *A. ignescens*, *A. spumarius*, *A. varius*

² = *Dendrophryniscus brevipollicatus*, *D. minutus*

³ = *Melanophryniscus moreirae*, *M. stelzneri*

cies for which specimens were not available for detailed examination are listed as referred forms based on their descriptions and available data. The general geographic range of each genus is briefly outlined.

ATELOPUS Duméril and Bibron 1841

Definition: 1) tensor fasciae latae muscle strap-like and elongate, originating on anterior third of ilium and inserting on proximal third of cruralis muscle; 2) semitendinosus muscle a thin slip visible two-thirds of its length, inserting via a long tendon; 3) adductor longus muscle absent; 4) depressor mandibulae muscle present in SQ or SQat condition; 5) adductor mandibulae muscle present in S condition; 6) frontoparietal bone of normal extent, separate or fused on midline; 7) occipital groove closed; 8) leading edge of premaxillary platform twice as wide as medial edge; 9) septomaxilla U-shaped with trough; 10) palatines present; 11) vomers present; 12) parasphenoid pointed anteriorly, overlapping sphenethmoid complex medially; 13) squamosal stem rotated, anterior process usually present, dorsal arm extending over prootic; 14) quadratojugal well developed or reduced; 15) pterygoid well developed and of normal extent; 16) sphenethmoid complex ossified; 17) orbitosphenoid unossified; 18) quadrate cartilaginous, restricted to lower part of suspensorium; 19) prearticular curve in mandible posterior to midpoint, Meckel's cartilage unossified; 20) anterior processes of ceratohyal very small and directed laterally; 21) hypobranchial 1 present with narrow base, hypobranchial 2 absent; 22) constrictor laryngis posterior muscle absent; 23) seven presacral vertebrae; 24) atlas fused with first trunk vertebra; 25) sacrum usually separate from trunk vertebra; 26) coccyx with bicondylar articulation or fused with sacrum; 27) sacral diapophyses greatly expanded, elliptically flattened in cross section; 28) pectoral girdle firmisternal; 29) sternum present; 30) ilia, sacral diapophyses articulate in a flat joint; 31) one centrale in hand; 32) two distal carpals; 33) phalangeal formula of hand, 2-2-3-3 or 1-2-3-3; 34) phalangeal formula of foot, 2-2-3-4-3; 35) middle ear apparatus absent, except in *A. flavescens*, *A. spumarius* and an undescribed species; 36) ostia pharyngea present or absent; 37) vocal slits present or absent; 38) habitus atelopodiform, body length greater than three times body width; 39) skin smooth or with rounded warts or conical apical; 40) Bidder's organ present; 41) testicular peritoneum black or unpigmented; 42) eggs white, 350-910 total counts; 43) larvae aquatic.

Range: tropical areas of central Costa Rica southward through Panamá, Colombia, Ecuador,

into Peru and Bolivia and northeastward through northern Venezuela; disjunct populations in Guyana, Surinam, French Guiana, and northeastern Brazil (Fig. 9).

Content: *boulengeri* Peracca 1904; *carrikeri* Ruthven 1916; *certus* Barbour, 1923; *chiriquiensis* Shreve 1936; *cruciger* (Lichtenstein and von Martens 1856); *ebenoides* Rivero 1963; *elegans* (Boulenger 1882); *exigua* Boettger 1892; *flavescens* Duméril and Bibron 1841; *glyphus* Dunn 1931; *ignescens* (Cornalia 1849); *longirostris* Cope 1868; *oxyrhynchus* Boulenger 1903; *pachydermus* (Schmidt 1857); *senex* Taylor 1952; *spumarius* Cope 1871; *spurrelli* Boulenger 1914; *varius* (Lichtenstein and von Martens 1856); *walkeri* Rivero 1963; *zeteki* Dunn 1933.

Referred forms: *bibronii* (Schmidt 1857); *bicolor* Noble 1921; *bufoniformis* Peracca 1904; *carinatus* Andersson 1945; *erythropus* Boulenger 1903; *longibrachius* Rivero 1963; *nicefori* Rivero 1963; *palmatus* Andersson 1945; *pedimarmoratus* Rivero 1963; *pernambucensis* Bokermann 1962; *planispinus* Jiménez de la Espada 1875; *rugulosus* Noble 1921; *seminiferus* Cope 1874; *tricolor* Boulenger 1902; *willmani* Donoso Barros 1969.

DENDROPHRYNISCUS Jiménez de la Espada 1870

Definition: 1) tensor fasciae latae muscle short and broad, originating on middle third of ilium and inserting on distal third of cruralis muscle; 2) semitendinosus muscle a thin slip not visible along its length, inserting via a long tendon; 3) adductor longus muscle absent; 4) depressor mandibulae muscle present in SQ or SQm condition; 5) adductor mandibulae muscle present in S condition; 6) frontoparietal bone of normal extent, separate along midline except in largest adults, fused in posterior one-quarter; 7) occipital groove open; 8) leading edge of premaxillary platform twice as wide as medial edge; 9) septomaxilla U-shaped with trough; 10) palatines present or absent; 11) vomers present; 12) parasphenoid pointed anteriorly, overlapping sphenethmoid complex medially; 13) squamosal stem slightly rotated, anterior process well developed, degree dorsal arm extends over prootic variable; 14) quadratojugal reduced; 15) pterygoid well developed and of normal extent; 16) sphenethmoid complex ossified; 17) orbitosphenoid unossified; 18) quadrate cartilaginous, restricted to lower part of suspensorium; 19) prearticular curve in mandible posterior to midpoint, Meckel's cartilage unossified; 20) anterior processes of ceratohyal absent; 21) hypobranchial 1 present with narrow base, hypobranchial 2 absent; 22) constrictor laryngis posterior muscle ab-

cies for which specimens were not available for detailed examination are listed as referred forms based on their descriptions and available data. The general geographic range of each genus is briefly outlined.

ATELOPUS Duméril and Bibron 1841

Definition: 1) tensor fasciae latae muscle strap-like and elongate, originating on anterior third of ilium and inserting on proximal third of cruralis muscle; 2) semitendinosus muscle a thin slip visible two-thirds of its length, inserting via a long tendon; 3) adductor longus muscle absent; 4) depressor mandibulae muscle present in SQ or SQat condition; 5) adductor mandibulae muscle present in S condition; 6) frontoparietal bone of normal extent, separate or fused on midline; 7) occipital groove closed; 8) leading edge of premaxillary platform twice as wide as medial edge; 9) septomaxilla U-shaped with trough; 10) palatines present; 11) vomers present; 12) parasphenoid pointed anteriorly, overlapping sphenethmoid complex medially; 13) squamosal stem rotated, anterior process usually present, dorsal arm extending over prootic; 14) quadratojugal well developed or reduced; 15) pterygoid well developed and of normal extent; 16) sphenethmoid complex ossified; 17) orbitosphenoid unossified; 18) quadrate cartilaginous, restricted to lower part of suspensorium; 19) prearticular curve in mandible posterior to midpoint, Meckel's cartilage unossified; 20) anterior processes of ceratohyal very small and directed laterally; 21) hypobranchial 1 present with narrow base, hypobranchial 2 absent; 22) constrictor laryngis posterior muscle absent; 23) seven presacral vertebrae; 24) atlas fused with first trunk vertebra; 25) sacrum usually separate from trunk vertebra; 26) coccyx with bicondylar articulation or fused with sacrum; 27) sacral diapophyses greatly expanded, elliptically flattened in cross section; 28) pectoral girdle firmisternal; 29) sternum present; 30) ilia, sacral diapophyses articulate in a flat joint; 31) one centrale in hand; 32) two distal carpals; 33) phalangeal formula of hand, 2-2-3-3 or 1-2-3-3; 34) phalangeal formula of foot, 2-2-3-4-3; 35) middle ear apparatus absent, except in *A. flavescens*, *A. spumarius* and an undescribed species; 36) ostia pharyngea present or absent; 37) vocal slits present or absent; 38) habitus atelopodiform, body length greater than three times body width; 39) skin smooth or with rounded warts or conical apical; 40) Bidder's organ present; 41) testicular peritoneum black or unpigmented; 42) eggs white, 350-910 total counts; 43) larvae aquatic.

Range: tropical areas of central Costa Rica southward through Panamá, Colombia, Ecuador,

into Peru and Bolivia and northeastward through northern Venezuela; disjunct populations in Guyana, Surinam, French Guiana, and northeastern Brazil (Fig. 9).

Content: *boulengeri* Peracca 1904; *carrikeri* Ruthven 1916; *certus* Barbour, 1923; *chiriquiensis* Shreve 1936; *cruciger* (Lichtenstein and von Martens 1856); *ebenoides* Rivero 1963; *elegans* (Boulenger 1882); *exigua* Boettger 1892; *flavescens* Duméril and Bibron 1841; *glyphus* Dunn 1931; *ignescens* (Cornalia 1849); *longirostris* Cope 1868; *oxyrhynchus* Boulenger 1903; *pachydermus* (Schmidt 1857); *senex* Taylor 1952; *spumarius* Cope 1871; *spurrelli* Boulenger 1914; *varius* (Lichtenstein and von Martens 1856); *walkeri* Rivero 1963; *zeteki* Dunn 1933.

Referred forms: *bibronii* (Schmidt 1857); *bicolor* Noble 1921; *bufoniformis* Peracca 1904; *carinatus* Andersson 1945; *erythropus* Boulenger 1903; *longibrachius* Rivero 1963; *nicefori* Rivero 1963; *palmatus* Andersson 1945; *pedimarmoratus* Rivero 1963; *pernambucensis* Bokermann 1962; *planispinus* Jiménez de la Espada 1875; *rugulosus* Noble 1921; *seminiferus* Cope 1874; *tricolor* Boulenger 1902; *willmani* Donoso Barros 1969.

DENDROPHRYNISCUS Jiménez de la Espada 1870

Definition: 1) tensor fasciae latae muscle short and broad, originating on middle third of ilium and inserting on distal third of cruralis muscle; 2) semitendinosus muscle a thin slip not visible along its length, inserting via a long tendon; 3) adductor longus muscle absent; 4) depressor mandibulae muscle present in SQ or SQm condition; 5) adductor mandibulae muscle present in S condition; 6) frontoparietal bone of normal extent, separate along midline except in largest adults, fused in posterior one-quarter; 7) occipital groove open; 8) leading edge of premaxillary platform twice as wide as medial edge; 9) septomaxilla U-shaped with trough; 10) palatines present or absent; 11) vomers present; 12) parasphenoid pointed anteriorly, overlapping sphenethmoid complex medially; 13) squamosal stem slightly rotated, anterior process well developed, degree dorsal arm extends over prootic variable; 14) quadratojugal reduced; 15) pterygoid well developed and of normal extent; 16) sphenethmoid complex ossified; 17) orbitosphenoid unossified; 18) quadrate cartilaginous, restricted to lower part of suspensorium; 19) prearticular curve in mandible posterior to midpoint, Meckel's cartilage unossified; 20) anterior processes of ceratohyal absent; 21) hypobranchial 1 present with narrow base, hypobranchial 2 absent; 22) constrictor laryngis posterior muscle ab-

sent; 23) eight presacral vertebrae; 24) atlas not fused with first trunk vertebra; 25) sacrum usually separate from trunk vertebra; 26) coccyx fused with sacrum; 27) sacral diapophyses greatly expanded, elliptically flattened in cross section; 28) pectoral girdle firmisternal anteriorly, arciferal posteriorly; 29) sternum present; 30) ilia, sacral diapophyses articulate in a flat joint; 31) one centrale in hand; 32) two distal carpals; 33) phalangeal formula of hand 2-2-3-3 or 1-2-3-3; 34) phalangeal formula of foot, 2-2-3-4-3; 35) middle ear apparatus absent; 36) ostia pharyngea absent; 37) vocal slits absent; 38) habitus atelopodiform, body length greater than two and one-half times width; 39) skin minutely glandular with small scattered warts; 40) Bidder's organ present; 41) testicular peritoneum black; 42) eggs with black animal

pole and light vegetal pole, 52-64 total counts for *brevipollicatus*, 175-420 total counts for *minutus*; 43) larvae aquatic.

Range: tropical lowland areas of the Amazon Basin in Brazil, Peru, Ecuador, Surinam, French Guiana, Guyana, and mountainous areas of south-eastern Brazil (Fig. 9).

Content: *brevipollicatus* Jiménez de la Espada 1870; *leucomystax* Izecksohn 1968; *minutus* (Melin 1941) by present arrangement.

Referred forms: *proboscideus* (Boulenger 1882) by present arrangement.

MELANOPHRYNISCUS Gallardo 1961

Definition: 1) tensor fasciae latae muscle short and broad, originating on middle third of ilium and inserting on distal half of cruralis muscle; 2) semi-

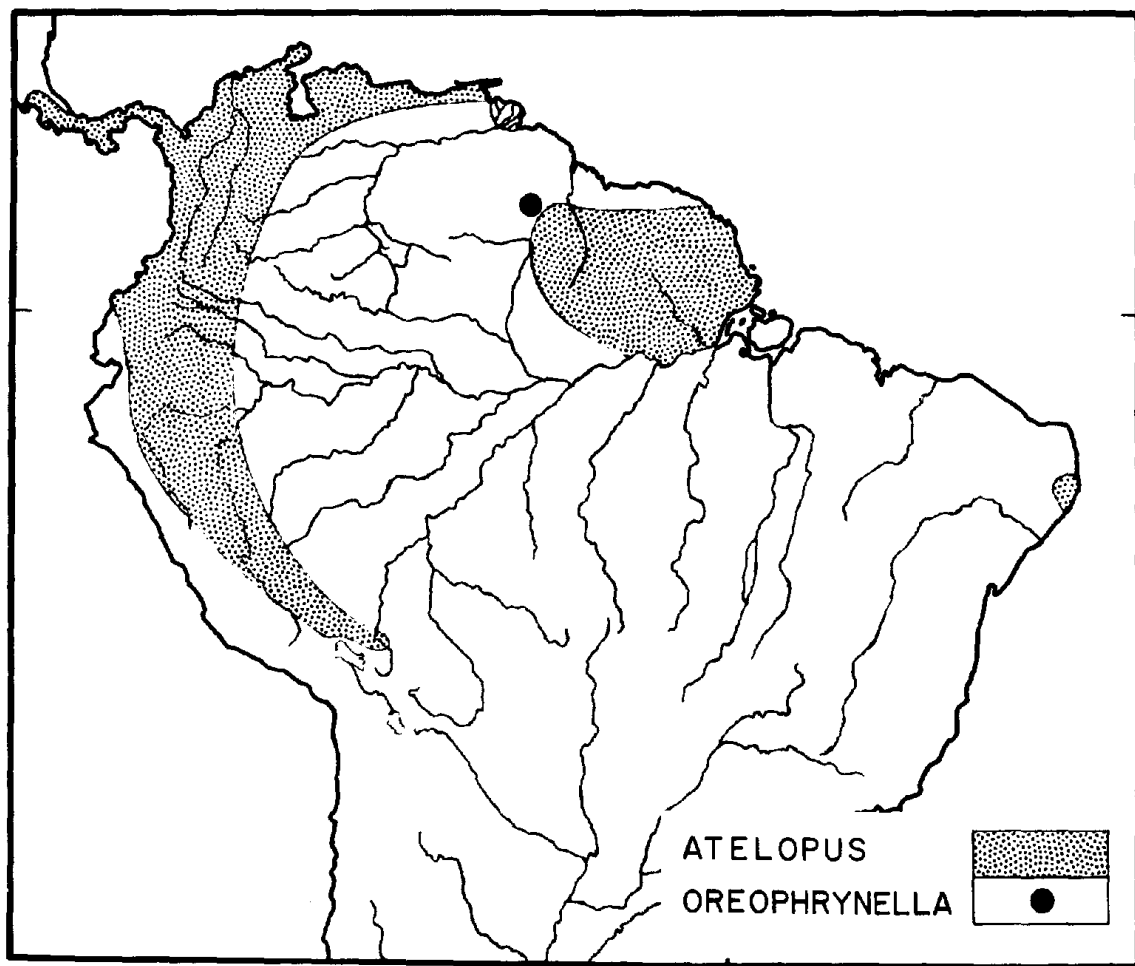


FIGURE 9. Map depicting the known ranges of species of *Atelopus* and *Oreophrynella*.

tendinosus muscle a thin slip visible two-thirds of its length, inserting via a long tendon; 3) adductor longus muscle absent; 4) depressor mandibulae muscle present in SQ condition; 5) adductor mandibulae muscle present in S condition; 6) frontoparietal bone of normal extent, anterior half fused or separate on midline, posterior half always fused; 7) occipital groove open except posteriorly; 8) leading edge of premaxillary platform twice as wide as medial edge; 9) septomaxilla U-shaped with trough; 10) palatines present or absent; 11) vomers present; 12) parasphenoid pointed anteriorly, overlapping sphenethmoid complex medially; 13) squamosal stem rotated in three species, anterior process lacking, dorsal arm not extending over prootic; 14) quadratojugal reduced or absent; 15) pterygoid well developed and of normal extent; 16) sphenethmoid complex ossified; 17) orbito-sphenoid ossified; 18) quadrate cartilaginous, restricted to lower part of suspensorium; 19) prearticular curve in mandible posterior to midpoint, Meckel's cartilage unossified; 20) anterior processes of ceratohyal absent; 21) hypobranchial 1 present with wide base, hypobranchial 2 absent; 22) constrictor laryngis posterior muscle absent; 23) eight presacral vertebrae; 24) atlas not fused with first trunk vertebra; 25) sacrum usually separate from trunk vertebra; 26) coccyx with bicondylar articulation with sacrum; 27) sacral diapophyses greatly expanded, elliptically flattened in cross section; 28) pectoral girdle firmisternal anteriorly, arciferal posteriorly; 29) sternum present; 30) ilia, sacral diapophyses articulate in a flat joint; 31) two centralia in hand; 32) two distal carpals; 33) phalangeal formula of hand 2-2-3-3; 34) phalangeal formula of foot 2-2-3-4-3; 35) middle ear apparatus absent; 36) ostia pharyngea present; 37) vocal slits present; 38) habitus bufoniform, body length never exceeds three times width; 39) skin rugose, covered with rounded warts or conical apical; 40) Bidder's organ present; 41) testicular peritoneum black or unpigmented; 42) eggs with black animal pole and light vegetal pole, 78-237 total counts; 43) larvae aquatic.

Range: southern temperate and tropical areas of Argentina, Paraguay, Uruguay, and southeastern Brazil; an allopatric population of one species described from the Amazon Basin in Pará, Brazil (Fig. 10).

Content: *moreirae* (Miranda-Ribeiro 1920); *rubriventris* (Vellard 1947) by present arrangement; *stelzneri* (Weyenbergh 1875); *tumifrons* (Boulenger 1905).

Referred forms: *devincenzii* Klappenbach 1968; *sanmartini* Klappenbach 1968.

OREOPHRYNELLA Boulenger 1895

Definition: 1) tensor fasciae latae muscle short and broad, originating on middle third of ilium and inserting midway along cruralis muscle; 2) semitendinosus muscle a thin slip visible two-thirds of its length, inserting via a long tendon; 3) adductor longus muscle absent; 4) depressor mandibulae muscle present in SQ condition; 5) adductor mandibulae muscle present in E condition; 6) frontoparietal bone greatly reduced anteriorly exposing frontal fontanelle, fused in midline posterior to parietal fontanelles; 7) occipital groove open; 8) leading edge of premaxillary platform twice as wide as medial edge; 9) septomaxilla U-shaped with trough; 10) palatines present; 11) vomers present; 12) parasphenoid pointed anteriorly, overlapping sphenethmoid complex medially; 13) squamosal stem not rotated, large anterior process, dorsal arm extending over prootic; 14) quadratojugal absent; 15) pterygoid well developed and of normal extent; 16) ethmoid portion only of sphenethmoid complex ossified; 17) orbitosphenoid unossified; 18) quadrate cartilaginous, restricted to lower part of suspensorium; 19) prearticular curve in mandible posterior to midpoint, Meckel's cartilage unossified; 20) anterior processes of ceratohyal absent; 21) hypobranchial 1 present with narrow base, hypobranchial 2 absent; 22) constrictor laryngis posterior muscle absent; 23) five presacral vertebrae; 24) atlas fused with first trunk vertebra; 25) sacrum fused with trunk vertebrae; 26) coccyx fused with sacrum; 27) sacral diapophyses greatly expanded, elliptically flattened in cross section; 28) pectoral girdle firmisternal anteriorly, arciferal posteriorly; 29) sternum present; 30) ilia, sacral diapophyses articulate in a flat joint; 31) two centralia in hand; 32) two distal carpals; 33) phalangeal formula of hand, 2-2-3-3; 34) phalangeal formula of foot, 2-2-3-4-3; 35) middle ear apparatus absent; 36) ostia pharyngea vestigial; 37) vocal slits absent; 38) habitus bufoniform, body length never exceeds three times width; 39) skin rugose, covered with rounded warts; 40) Bidder's organ present; 41) testicular peritoneum unpigmented; 42) eggs yellow, 10-15 total counts; 43) larvae probably aquatic.

Range: restricted to the immediate vicinity of Mount Roraima on the Guayanan, Venezuelan, and Brazilian borders (Fig. 10).

Content: *quelchii* (Boulenger 1895a).

Referred form: *macconnelli* Boulenger 1900.

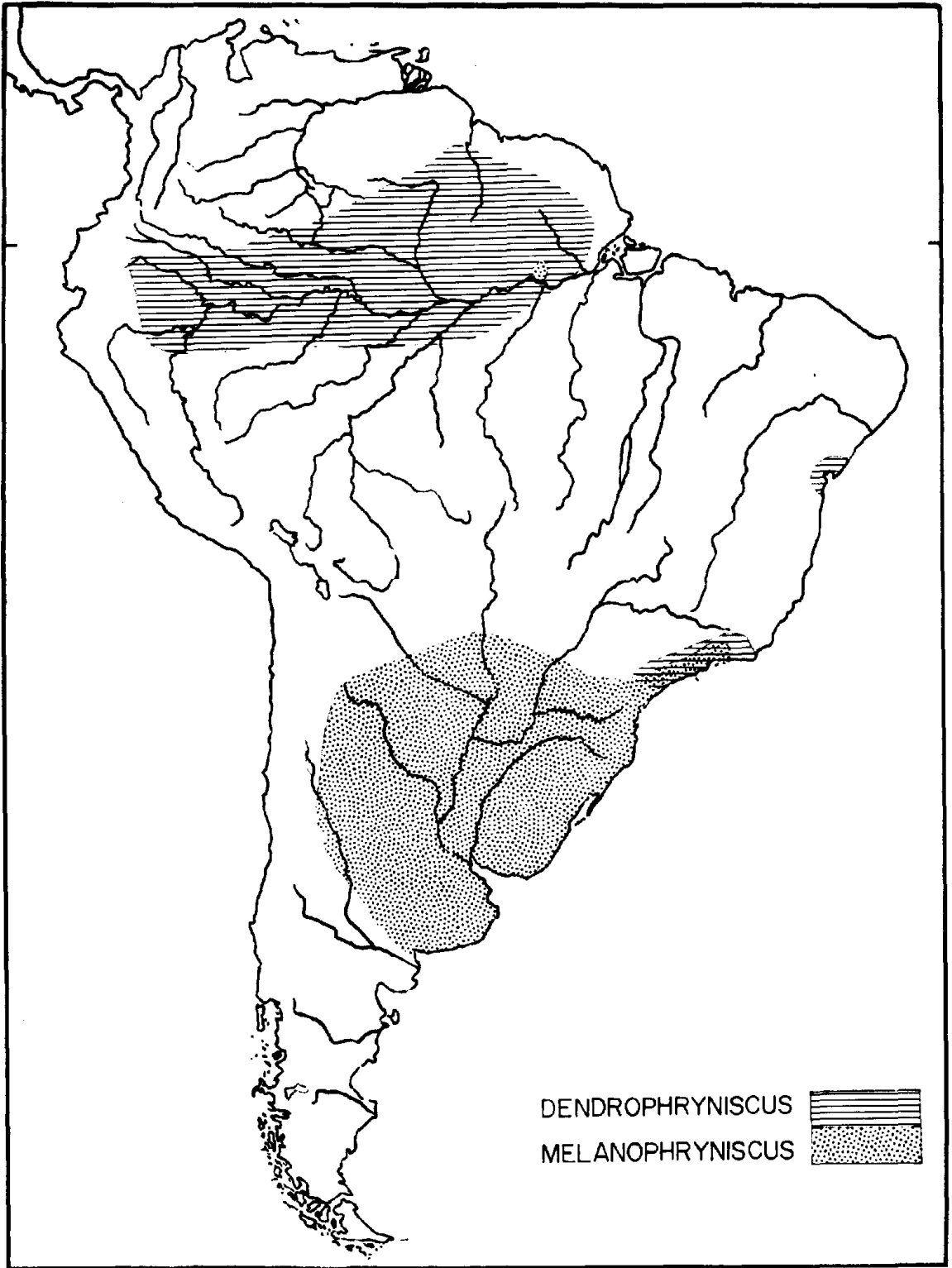


FIGURE 10. Map depicting the known ranges of species of *Dendrophryniscus* and *Melanophryniscus*.

EVOLUTION

At the outset of this project several basic assumptions were deemed essential to completion of the study. One of these assumptions was that the genera included in the Atelopodidae by Noble (1922, 1926) and Davis (1935) were a natural group. Even though Griffiths (1959) removed *Oreophrynella* and *Dendrophryniscus* (= *Melanophryniscus*) from the Atelopodidae and put them in Bufonidae, I thought that their inclusion in this study was necessary. Griffiths shifted these two genera from one family to another on the basis of the nature of their epicoracoidal fusion and arbitrarily defined the family Atelopodidae. In addition, he did not examine *Dendrophryniscus brevipollicatus*; therefore the position of this genus in his scheme is unknown.

EVALUATION OF CHARACTER STATES

To determine the evolutionary patterns among the four genera, the characters utilized in the generic definitions must be evaluated as to their primitive (ancestral) or advanced (derived) states. This kind of analysis assumes that those taxa having the greater numbers of primitive character states are nearer the ancestral stock than are those with a small number of primitive character states.

The evolutionary changes in a character from a primitive to an advanced state have been evaluated in accord with the following postulates:

- 1) character states of modern species which also are found in fossils of presumed ancestors or of forms considered closely related are considered primitive;
- 2) character states based on structures that show a reduction in number of parts or a simplification of existing parts are considered advancements. This postulate is referred to as Williston's Rule. It states that the number of parts of an organism tends to be reduced, with the fewer parts greatly specialized in function (Simpson, 1949, 1953; Gregory, 1951). This postulate does not assume irreversibility of characters;
- 3) character states that are universal or frequent in other modern groups or widespread within the taxonomic group being studied are considered to be primitive. This postulate may be derived from the Rule of Parsimony (Kluge, 1967; Kluge and Farris, 1969) and has been discussed by Throckmorton (1968).

INTERGENERIC RELATIONSHIPS

Several characters are the same among the four genera and are used in the generic definitions only

to elucidate the differences between these four genera and other procoelous Anura (e.g. *Brachycephalus*). These characters are not discussed in this section unless they are important to the later treatment of familial relationships. To facilitate comparison among the genera, each character is numbered as it was in the generic definitions. Each state is designated primitive or advanced according to one of the above postulates. Where necessary, a brief discussion is presented to support the designation. It is impossible to designate certain character states as either primitive (P) or advanced (A); these are not rated but simply numbered.

- 1) tensor fasciae latae muscle—two character states:

P. short, origin on middle third of ilia—primitive.

A. elongate, origin on anterior third of ilia—advanced.

Dunlap (1960) and Tihen (1960) indicated that the elongate tensor condition is only found in four other genera of frogs. An anterior origin occurs also in the bufonids *Ansonia* and *Mertensophryne* and in the leptodactylids *Limnodynastes* and *Eleutherodactylus*. I suggest that the elongation of this muscle in *Atelopus* reflects a change in patterns of locomotion from hopping to walking. Since most frogs exhibit a short condition, and because all evidence indicates that the earliest known frogs were "hoppers", I have followed the Rule of Parsimony in determining the evolutionary stage.

- 2) semitendinosus muscle—two character states:
 1. visible two-thirds of length, inserting via long tendon.
 2. invisible, inserting via long tendon.

- 3) adductor longus muscle—one character state:
 - A. absent—advanced.

Inger (1967) pointed out that there has been a progressive trend towards fragmentation and specialization of musculature in the series from fish to mammal. Tihen (1965) also suggested that there has been a general trend towards increasing complexity of musculature. Noble (1922) indicated that the adductor longus muscle is a separate slip of the pectineous muscle. He supported the undifferentiated nature (absence) of the muscle as the primitive condition. However, Kluge and Farris (1969) pointed out that absence of the adductor longus muscle in some primitive frogs might be the result of a secondary loss

- to increase locomotor efficiency. Tihen (1960) argued that the muscle probably was present in early salientians and has been lost in some forms. Until more information is available and in accord with Williston's Rule, I consider the absence of the adductor longus muscle in the forms studied an advanced state.
- 4) depressor mandibulae—three character states:
 P. SQat—primitive.
 A₂. SQ—advanced.
 A₃. SQm—advanced.
 The attachment of a slip of the depressor mandibulae muscle to the annulus tympanicus must be considered primitive. The presence of an annulus tympanicus is associated with the presence of a middle ear, which, as indicated by the fossil record, is a primitive condition. When the middle ear is lost, the annulus tympanicus and its associated depressor slip are also lost. Starrett (1968) has shown that the SQ condition has been independently derived in several families. Postulates one and two are applicable.
- 5) adductor mandibulae muscle—two character states:
 A₁. S—advanced.
 A₂. E—advanced.
 The S and E conditions are independent derivatives of an S and E ancestral condition (Starrett, 1968). Once a muscle has been lost, it is not reacquired (Tihen, 1965 and Williston's Rule).
- 6) frontoparietal bone—two character states:
 P. normal size, separate or fused on midline—primitive.
 A. greatly reduced exposing frontal and parietal fontanelles—advanced.
 The advanced condition is attributed to arrested development. The primitive condition is implied from postulates one and three.
- 7) occipital groove—three character states:
 1. open.
 2. open except posteriorly.
 3. closed.
- 10) palatine bone—two character states:
 P. present—primitive.
 A. absent—advanced.
 The primitive condition was designated according to Williston's Rule.
- 13) squamosal—three character states:
 1. stem rotated, anterior process present, dorsal arm over prootic.
 2. stem rotated, no anterior process, no dorsal overlap of prootic.
 3. stem not rotated, anterior process present, dorsal arm over prootic.
- 14) quadratojugal—three character states:
 P₁. well developed—primitive.
 P₂. present but reduced—primitive.
 A. absent—advanced.
 The primitive states were designated according to Williston's Rule. It was impossible to determine whether the well developed state or the reduced state was ancestral; therefore both were designated primitive.
- 16) sphenethmoid complex—two character states:
 P. only ethmoid portion ossified—primitive.
 A. completely ossified—advanced.
 Designation of the primitive state was based on the Rule of Parsimony.
- 17) orbitosphenoid—two character states:
 P. unossified—primitive.
 A. ossified—advanced.
 The primitive state was determined according to the Rule of Parsimony.
- 20) anterior process of ceratohyal—two character states:
 P. absent—primitive.
 A. small and directed laterally—advanced.
 Since none of the bufonid (closely related modern group) genera have an anterior process of the ceratohyal (Trewavas, 1933), the Rule of Parsimony would indicate that the absence of an anterior process is primitive. In addition, in both *Melanophryniscus* and *Dendrophryniscus*, the anterior part of the ceratohyal is expanded; I consider the process in *Atelopus* to be the culmination of a trend toward an increase in the cartilaginous extent of this part of the ceratohyal. This treatment follows that part of Williston's Rule referring to specialization of parts.
- 21) hypobranchial 1—two character states:
 1. narrow base.
 2. wide base.
 hypobranchial 2—one character state:
 A. absent—advanced.
 The advanced state of hypobranchial 2 was designated according to Williston's Rule and the Rule of Parsimony.
- 23) number of presacral vertebrae—three character states:
 P. eight—primitive.
 A₂. seven—advanced.
 A₃. five—advanced.
 Griffiths (1963) indicated that higher numbers of presacral vertebrae are primitive. Tihen (1965) pointed out that the number of presacral vertebrae may decrease but does not

- increase. Both Inger (1967) and Kluge and Farris (1969) agreed that high numbers of presacral vertebrae in frogs appear to be more primitive. Fossil evidence also suggests that higher numbers are primitive. Postulates one, two, and three are applicable.
- 24) atlas—two character states:
P. separate from first trunk vertebra—primitive.
A. fused to first trunk vertebra—advanced.
Bones, once fused, rarely become independent elements again (Tihen, 1965). This is in accord with Williston's Rule and also with the Rule of Parsimony.
- 25) sacrum—two character states:
P. separate from trunk vertebrae—primitive.
A. fused to trunk vertebrae—advanced.
The reasons given under character 24 also apply here.
- 26) coccyx—two character states:
P. articulates with sacrum—primitive.
A. fused to sacrum—advanced.
The reasons given under character 24 also apply here.
- 28) pectoral girdle—two character states:
A₁. anteriorly firmisternal, posteriorly arciferal—advanced.
A₂. entirely firmisternal—advanced.
The arciferal condition occurs in most Bufonidae, in primitive amphibians and salamanders and in the developmental stages of firmisternal forms. Therefore, it must be primitive. The arcifero-firmisternal and firmisternal girdles represent stages in an evolutionary continuum from an overlapping to a fused condition. Postulates one and three are applicable here.
- 31) centralia of hand—two character states:
P. two—primitive.
A. one—advanced.
The primitive state was determined according to Williston's Rule.
- 33) phalangeal formula of hand—two character states:
P. 2-2-3-3—primitive.
A. 1-2-3-3—advanced.
The primitive state was determined according to Williston's Rule.
- 35) middle ear apparatus—two character states:
P. internal tympanum and middle ear present—primitive.
A. absent—advanced.
The fossil record clearly indicates that a middle ear was present in the primitive frog. Tihen (1965) also suggested that the middle ear was originally present, and once lost is not reacquired.
- 36) ostia pharyngea—three character states:
P. present—primitive.
A₂. vestigial—advanced.
A₃. absent—advanced.
The ostia pharyngea are associated with hearing and vocalization. When the middle ear degenerates, the ostia pharyngea also degenerate. Their absence is, therefore, a derived condition.
- 37) vocal slits—two character states:
P. present—primitive.
A. absent—advanced.
The presence of vocal slits is frequently but not invariably associated with the presence of a middle ear and ostia pharyngea. Once the ability to hear is lost, there is a degeneration of the vocal apparatus. As with characters 35 and 36, the absence of vocal slits is derived.
- 38) habitus—two character states:
1. atelopodiform.
2. bufoniform.
- 39) skin texture—four character states:
1. smooth.
2. scattered warts.
3. minutely glandular with small warts.
4. rugose and covered with warts.
- 40) Bidder's organ—two character states:
A. present—advanced.
The presence of a Bidder's organ only in the Bufonidae and the atelopodid genera indicates that it is an advanced character according to the Rule of Parsimony.
- 41) color of testicular peritoneum—two character states:
1. unpigmented.
2. black.
- 42) egg color and number—three character states:
P₁. unpigmented, 350 to 910 eggs—primitive.
P₂. black animal pole, light vegetal pole, 52 to 420 eggs—primitive.
A. unpigmented, ten to 15 eggs—advanced.
Tihen (1965) suggested that numerous, fully aquatic eggs probably are primitive and that any departure from this trend is derived. It is difficult to ascertain whether a black or a white egg is primitive, therefore, the primitive allocation of the first two states is based on the large number of eggs and not the color. Eggs which are often exposed to sunlight are usually black.
- Twenty-nine characters and their 65 associated character states were used in this analysis. Two characters, 3 and 40, exhibit the same state in the

TABLE 2
Distribution of 29 Characters among
Atelopus, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*

| | | | | | | | | | | | | | | | |
|-------------------------|----------------|----|----|---------------------------------|----------------|----|------|------|-------------------|---------------------------------|----|------|----|------|----------------|
| Characters* | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 10 | 13 | 14 | 16 | 17 | 20 | 21 | |
| <i>Atelopus</i> | A* | 1* | A | P, A ₂ | A ₁ | P | 3 | P | 1 | P ₁ , P ₂ | A | P | A | 1 | |
| <i>Dendrophryniscus</i> | P* | 2 | A | A ₂ , A ₃ | A ₁ | P | 1 | P, A | 1 | P ₂ | A | P | P | 1 | |
| <i>Melanophryniscus</i> | P | 1 | A | A ₂ | A ₁ | P | 2 | P, A | 2 | P ₂ , A | A | A | P | 2 | |
| <i>Oreophrynella</i> | P | 1 | A | A ₂ | A ₂ | A | 1 | P | 3 | A | P | P | P | 1 | |
| Characters | 23 | 24 | 25 | 26 | 28 | 31 | 33 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 |
| <i>Atelopus</i> | A ₂ | A | P | P, A | A ₂ | A | P, A | P, A | P, A ₃ | P, A | 1 | 1, 2 | A | 1, 2 | P ₁ |
| <i>Dendrophryniscus</i> | P | P | P | A | A ₁ | A | P, A | A | A ₃ | A | 1 | ? | A | 2 | P ₂ |
| <i>Melanophryniscus</i> | P | P | P | P | A ₁ | P | P | A | P | P | 2 | 4 | A | 1, 2 | P ₂ |
| <i>Oreophrynella</i> | A ₃ | A | A | A | A ₁ | P | P | A | A ₂ | A | 2 | 4 | A | 1 | A |

*Characters numbered as in generic definitions; A = advanced state, A₁, A₂, etc. = different advanced states; 1, 2, etc. = different neutral states; P = primitive state, P₁, P₂, etc. = different primitive states.

four genera but are included because of their importance in later comparisons. *Atelopus* has undergone the greatest radiation in terms of component species and, hence, has the greatest number of character states, 37. *Melanophryniscus* and *Dendrophryniscus* have about the same number of states, with 31 and 32 respectively. *Oreophrynella* is represented by a single species and thus has only 29 character states.

In Table 2 the distribution of the 65 character states among the four genera is listed. *Melanophryniscus* has the greatest number of the 20 primitive states with 14, followed by *Atelopus* with 13, *Dendrophryniscus* with 11 and *Oreophrynella* with only seven. This comparison would seem to indicate that *Melanophryniscus* is the most primitive and that *Oreophrynella* is the least primitive. While this analysis gives some indication of relative primitiveness among the four genera, it fails to consider the number and distribution of shared primitive characters.

Ten of the 14 primitive character states found in *Melanophryniscus* are shared with *Dendrophryniscus*. Five of these 10 are also shared with *Atelopus* (Table 2). Characters 10 and 14 actually are the same in some species of *Dendrophryniscus*, *Melanophryniscus*, and *Atelopus*. However, in *Melanophryniscus* and *Dendrophryniscus*, there are independent trends towards fusion and loss of the palatines and reduction and loss of the quadratojugal. These two characters, therefore, are indicative of greater similarities among the three genera than apparent in the original analysis. The three genera show similarities in numbers of eggs, but egg color clearly allies *Dendrophryniscus* with *Melanophryniscus*.

Oreophrynella has seven primitive characters, five of which it shares with *Melanophryniscus*. Four of these five states are also shared with *Dendrophryniscus*, and two of them with *Atelopus* as well. A fourth character state (17) is found in *Oreophrynella*, *Dendrophryniscus*, and *Atelopus*. The absence of this primitive state in *Melanophryniscus* indicates divergence in this character from the primitive stock which probably had an unossified orbitosphenoid. Only in character 16 does *Oreophrynella* have a primitive state not found in the other three genera.

With the exception of the state of character 17, all the primitive character states of *Dendrophryniscus* are also found in *Melanophryniscus*. The sharing of 10 primitive character states clearly indicates that *Dendrophryniscus* was derived from the same stock that gave rise to *Melanophryniscus*.

Atelopus has 13 primitive characters, two of which are common to all the genera. Characters 6, 14, 25 and 42 are primitive in *Atelopus*, *Melanophryniscus*, and *Dendrophryniscus*, although characters 14 and 42 have different primitive states in *Atelopus*. *Atelopus*, *Dendrophryniscus*, and *Oreophrynella* share only character state 17. Although this character is advanced in *Melanophryniscus*, the ancestral stock undoubtedly had the primitive state. It is noteworthy that no primitive characters are common only to *Atelopus*, *Melanophryniscus* and *Oreophrynella*. This again indicates the similarity between *Melanophryniscus* and *Dendrophryniscus*. Nearly all character states present in the former are also present in the latter.

Atelopus has two primitive character states not found in the other genera. The presence of a middle ear and the closely associated presence of

a depressor slip to the annulus tympanicus are unique to three species of *Atelopus*. This condition can only be interpreted as the retention of a primitive character state.

Three remaining primitive character states, 26, 36, and 37, are shared only between *Atelopus* and *Melanophryniscus*. Two of these characters, 36 and 37, are closely associated with hearing and are being lost. The bicondylar articulation of the coccyx in the two genera again suggests common ancestry.

Analysis of shared primitive character states indicates that *Melanophryniscus* is more primitive than *Dendrophryniscus* though both probably were derived from the same ancestor. *Atelopus* probably was derived from this same ancestral stock, diverging much earlier, however. Several primitive states were retained in the *Atelopus* line. Most of the primitive states retained in the *Melanophryniscus* line are also found in *Dendrophryniscus*. *Oreophrynella* apparently is closer to the *Melanophryniscus* line than it is to the *Atelopus* line. The derivation of *Oreophrynella* and *Melanophryniscus* from a common ancestor could have occurred prior to the split of *Melanophryniscus* and *Atelopus* stocks or after the separation of the *Atelopus* line.

An analysis of relationships based on the grouping of entities according to their shared primitive character states is very useful. However, this approach does not consider the advancements or evolutionary change of each unit. Once relationships have been established on the basis of similar primitive character states, the evolutionarily important characters of advancement must be incorporated into the study. The patterns of relationships established on the basis of advanced character states may be compared to those established on degree of similarity in primitive states.

There are 22 characters that have 27 different advanced character states (Table 2). *Melanophryniscus* has the least number of advanced states with ten, followed by *Dendrophryniscus* with 14, *Oreophrynella* with 15, and *Atelopus* with 16.

All advanced character states (10) found in *Melanophryniscus*, except that of characters 14 and 17, are also found in *Dendrophryniscus*. This supports the close relationship between these two genera established from the primitive character states analysis. *Melanophryniscus* also shares six states with *Oreophrynella*, four of which are found in all the genera. The fifth character state, the condition of the pectoral girdle (28), is advanced in all four genera, but differs between *Melanophryniscus*, *Dendrophryniscus* and *Oreophrynella*, and

Atelopus. The advanced state in *Atelopus* represents the culmination of an evolutionary trend towards fusion. Of the remaining five character states, two are common to *Melanophryniscus*, *Dendrophryniscus*, and *Atelopus* which clearly sets *Oreophrynella* off from these three genera. Character state 10, shared only by *Melanophryniscus* and *Dendrophryniscus*, reflects the independent loss of palatines in these genera. Only *Melanophryniscus* has an ossified orbitosphenoid; this state generally coincides with the increased skull ossification characteristic of the genus. The absence of the quadratojugal (14) in some species of *Melanophryniscus* and *Oreophrynella* probably indicates independent losses.

Dendrophryniscus has 14 advanced character states, only one of which is unique. The secondary modification of the depressor mandibulae distinguishes *Dendrophryniscus minutus* from *D. brevipollicatus* and the other genera. Of the remaining 13 states, eight are shared with *Melanophryniscus*, and most of these are also found in *Atelopus*.

The remaining five character states of *Dendrophryniscus* are shared with *Atelopus* or with *Atelopus* and *Oreophrynella*. The coccyx (character 26) is fused with the sacrum in some *Atelopus*, in *Dendrophryniscus* and *Oreophrynella*. It is free and articulates with the sacrum in other species of *Atelopus* and all *Melanophryniscus*. Therefore, it seems likely that this advanced state has been independently derived in each of the three lines. Character 37 has exactly the same distribution as character 26. In this instance the loss of vocal slits is obviously correlated with the loss of the middle ear (see discussion below). There is also a progressive loss of the ostia pharyngea (character 36) associated with the loss of the middle ear.

The two remaining character states are the loss of a digit of the hand (31), which may be the result of arrested development, and fusion of centralia in the hand (33). Apparently, both of these states were derived independently in *Atelopus* and *Dendrophryniscus*. Each may be the result of a shift in locomotory patterns.

Most of the advanced character states of *Oreophrynella* are either common to all genera or restricted to *Oreophrynella*. Of its 15 advanced states, *Oreophrynella* shares six with *Melanophryniscus* and seven each with *Atelopus* and *Dendrophryniscus*. Of the six shared with *Melanophryniscus*, four are common to all genera. The fifth (28), as previously discussed, is part of an evolutionary continuum; the sixth (14) represents the parallel loss of the quadratojugal.

The fusion of the atlas with the first trunk verte-

bra (24) and the fusion of the coccyx with the sacrum (26) are independent advancements shared between *Oreophrynella* and *Atelopus* in the former case and among *Oreophrynella*, *Atelopus*, and *Dendrophryniscus* in the latter case. The loss of vocal slits has also occurred in these three genera.

In three (6, 25, 42) of the six remaining characters, *Oreophrynella* has an advanced state while the other three genera have primitive states. In the remaining three characters *Oreophrynella* is very different from the other genera in which the characters are either primitive or in a different advanced state (5 and 23). The condition of the ostia pharyngea (36) is different in *Oreophrynella* but probably of less significance than are the other six states.

Atelopus, with 16, has the greatest number of advanced states. As previously mentioned, four of these are found in all genera. Two states (5 and 16) are shared with *Melanophryniscus* and *Dendrophryniscus*. Several (24, 26, 31, 33, 36 and 37) are shared with either *Dendrophryniscus* or *Oreophrynella* or both. These states were discussed above and represent parallel advancements. The four other advanced character states are restricted to *Atelopus*. Character states 1 and 20 are advanced only in *Atelopus*; character state 28 is more advanced than the advanced states in the other genera. Character state 23 is also advanced in *Oreophrynella* though apparently it was achieved independently.

The comparison of advanced character states indicates that *Atelopus*, *Oreophrynella*, and *Dendrophryniscus* are specialized in more characters than *Melanophryniscus*. *Atelopus* has the most advanced states, but only four of the 16 are restricted to *Atelopus*. *Oreophrynella* has 15 advanced character states, but has six states which are unique. *Dendrophryniscus* and *Melanophryniscus* have 14 and ten advanced states, respectively, but each has only a single unshared state.

It appears that the primitive character state analysis and the advanced character state analysis show similar results. In general these same results are indicated in an examination of the neutral characters. *Dendrophryniscus* is most closely related to *Melanophryniscus* in both analyses. Its similarity to *Melanophryniscus* in shared primitive states as well as the presence in *Dendrophryniscus* of all the advanced states of *Melanophryniscus* except two suggests that *Dendrophryniscus* was derived from a *Melanophryniscus* ancestral stock. Similarities between *Atelopus* and *Dendrophryniscus*

in advanced character states are attributed to parallel evolution probably the result of similar selective forces.

Melanophryniscus has the greatest number of primitive and least number of advanced states among the genera. These data indicate that *Melanophryniscus* is most similar to the ancestral stock which gave rise to the four genera.

Melanophryniscus shares more primitive and more advanced characters with *Atelopus* than it does with *Oreophrynella*.

Oreophrynella has the least number of primitive characters and the most advanced states of any of the other genera. I interpret these data to mean that the *Oreophrynella* line and the *Melanophryniscus-Atelopus-Dendrophryniscus* line diverged from the ancestral stock at different times.

The high number of advanced states in *Oreophrynella* indicates that it subsequently has become greatly specialized. *Atelopus* also has specialized in several characters but has retained some primitive states not found in *Oreophrynella* or *Melanophryniscus* and its derivative *Dendrophryniscus*. That this condition has evolutionary advantage is indicated by the complex radiation of several different species groups in *Atelopus*. *Oreophrynella*, however, is a much more specialized frog and as such has a restricted range and few species. The high number of primitive character states and the low number of advanced states characteristic of *Melanophryniscus* suggest that this genus is more generalized than either *Atelopus* or *Dendrophryniscus* and probably resembles the ancestral stock more closely than do either of the latter two genera.

My interpretation of the relationships among the four genera is shown by a dendrogram (Fig. 11). This representation is based on two factors, the number of shared primitive character states and the number and sequence of advancements. The first establishes the basic relationships, while the second is useful in drawing the phylogeny.

To elucidate the two lineages that gave rise to *Atelopus*, *Melanophryniscus*, and *Dendrophryniscus* on the one hand and *Oreophrynella* on the other, the major character states of the first group of genera are contrasted with those of the second lineage. The characteristics of *Oreophrynella* are placed in parentheses: adductor mandibulae muscle, S (E); frontoparietal bone normal, covering most of frontal and all of parietal fontanelles (greatly reduced exposing entire frontal and parietal fontanelles); quadratojugal usually present (absent); sphenethmoid complex ossified (only the ethmoid portion ossified); presacral vertebrae,

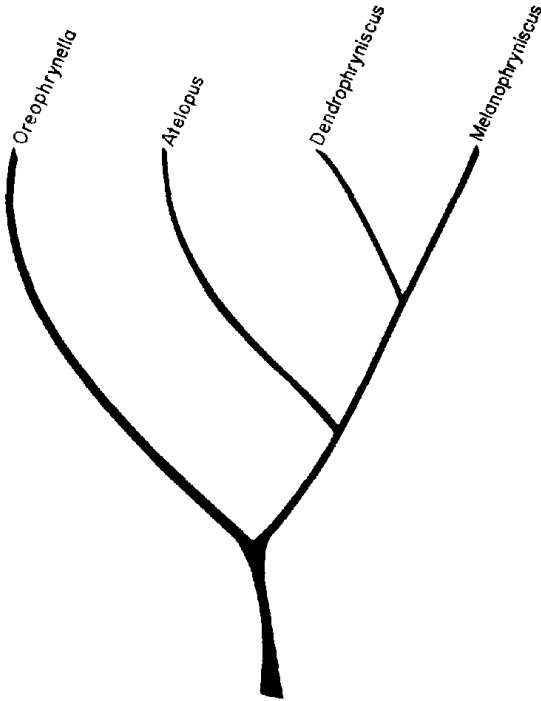


FIGURE 11. Diagrammatic representation of the evolutionary relationship among *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*.

seven or eight (five); sacrum usually separate from trunk vertebra (fused with trunk vertebra); and eggs unpigmented or with a pigmented animal pole, from 50 to 900 in number (unpigmented, 10 to 15).

The major character shifts that occurred in the evolution of *Oreophrynella* involved the loss of the adductor mandibulae posterior subexternus muscle; the differential metamorphosis of the frontoparietal bone; the loss of the quadratojugal; the reduction of presacral vertebral elements from eight to five; the fusion of the atlas and first trunk vertebra, the terminal trunk vertebra and the sacrum, and the sacrum and the coccyx. *Oreophrynella* retains the primitive condition in most of the thigh muscle characters; in the palatines; in the unossified anterior portion of the sphenethmoid; in the hyoid structure; in the arcifero-firmisternal pectoral girdle; and in the higher number of centralia and higher phalangeal formula of the hand.

The *Atelopus*-*Melanophryniscus*-*Dendrophryniscus* lineage retains the primitive condition in the nature of the frontoparietal, palatine, and quadratojugal; in the separate condition of the sacrum and trunk vertebrae; and in the higher number of eggs. These three genera lack the adductor externus

muscle, have an ossified sphenethmoid, and possess seven or eight presacral vertebrae, all differences from *Oreophrynella*.

Melanophryniscus retains most of the primitive character states. *Dendrophryniscus* was derived from *Melanophryniscus* but differs from it in the modified depressor mandibulae muscle condition, in the fusion of coccyx and sacrum, in the reduction of centralia in the hand from two to one, and in the loss in one species of the distal element on the first digit of the hand.

Atelopus has a few primitive character states which are not found in either *Melanophryniscus* or *Dendrophryniscus*. The more important of these are the presence in one species of a middle ear and its associated annulus tympanicus slip of the depressor mandibulae muscle and the presence of a well-developed quadratojugal. *Atelopus* has several character states that distinguish it from the other genera. These are advancements and are of major importance in the evolutionary history of the genus. They include an elongation of the tensor fasciae latae muscle; reduction to seven presacral vertebrae; fusion of the atlas and first trunk vertebra; attainment of a firmisternal condition in the pectoral girdle; and the development of unpigmented, heavily yolk-laden eggs and specialized larvae associated with the mountain stream habitat.

EVOLUTIONARY TRENDS

The small size of the family (four genera and about 50 species) makes it difficult to evaluate in detail character trends which might be important in determining evolutionary changes. Nevertheless, several evolutionary trends became apparent during the course of this study. Some of these trends are important to an understanding of the history of the group and probably reflect major functional shifts in the biology of the organism. Other character trends are indicated but cannot be associated with any major shift, functional or otherwise.

Locomotion

There are several changes in character states which apparently are correlated with changes in basic locomotory patterns. Although observations on live material are limited to seven species of *Atelopus* and *Melanophryniscus moreirae*, some conclusions concerning patterns of locomotion can be made. These frogs are walkers rather than hoppers. Although they are capable of jumping, they usually move each limb independently rather than moving the hind legs together in a coordinated jump.

The shortening of the vertebral column by fusion of the atlas and first trunk vertebra and of the posterior trunk vertebra and sacrum suggests close association with walking locomotion. The trend

towards fusion at the atlas is indicated in *Melanophryniscus* and *Dendrophryniscus* where there is close association between the first two vertebrae. Apparently the fusion in *Atelopus* represents a culmination of this trend. The fusion of trunk vertebrae with the sacrum occurs in some species of *Atelopus*, *Melanophryniscus*, and *Dendrophryniscus* but is present in all specimens of *Oreophrynella quelchii*. It is important to note that *Oreophrynella* has a reduced number of vertebral elements through both anterior fusion at the atlas and posterior fusion at the sacrum.

Another feature probably correlated with the reduction in number of vertebral elements is the shift towards a firmisternal girdle. Even though a firmisternal pectoral girdle occurs in several unrelated groups of frogs, there is little doubt that it is a derived condition. The functional aspects of a firmisternal as opposed to an arcifero-firmisternal or an arciferal condition are unknown. The shift from a hopping to a walking pattern of locomotion apparently has dictated a more rigid union between the two halves of the pectoral girdle to give added support to the limbs and perhaps has given rise to the firmisternal condition. The fusion apparently begins at the anterior end of the girdle and proceeds posteriorly on the midline. *Oreophrynella* and *Melanophryniscus* have slightly more overlap than is found in *Dendrophryniscus*.

It seems apparent that limb elongation as well as a change in habitus are results of the shift to walking. *Atelopus* and *Dendrophryniscus* have the atelopodid habitus and more elongate legs than the more primitive *Melanophryniscus* and *Oreophrynella* which resemble the arciferal "hopping" *Bufo*. It is also assumed that the forward shift of the origin of the tensor fasciae latae muscle may reflect an advancement and, hence, specialization associated with the walking. With the walking type of locomotion, the hind legs often are directed much more posteriorly than in hopping. If the tensor arose on the posterior part of the ilium, as it does in most frogs, efficiency would be greatly decreased when the leg was directed posteriorly. Only by moving the origin anteriorly on the ilium is the efficiency of the muscle increased so that it can function to tense the adductor of the hind leg thus initiating motor response.

The ancestral form must have had eight presacral vertebrae, free vertebral elements, an arciferal girdle, a posterior origin of the tensor muscle, and a hopping locomotion. Toads of the genus *Bufo* fit this description very well. The trends in the derived forms have been toward increased rigidity along the longitudinal axis of the body by

reducing the number of functional vertebral elements from eight to seven and five through fusion of the vertebrae and of the coccyx with the sacrum, to shift to an arcifero-firmisternal or firmisternal condition, to move the origin of the tensor muscle anteriorly on the ilium, and to shift to walking locomotion.

Without much additional field experience with these frogs, it is difficult to postulate what environmental or biological factors contributed to and selected for the apparent shift in locomotory pattern. Several ideas are put forward concerning what may be important factors contributing to the locomotory shift. These ideas are hypotheses and are proposed in the hope of stimulating additional work.

These shifts may be in response to a shift from a terrestrial to an arboreal existence. *Melanophryniscus* is entirely terrestrial; some species of *Atelopus* climb onto bushes at night; *Dendrophryniscus brevipollicatus* is arboreal. The T-shaped terminal phalanges in *D. brevipollicatus* increase the surface area of the toe tip and are directly correlated with its climbing habits. Perhaps the apparent opposable digits of the feet in *Oreophrynella* also reflect a partially arboreal existence.

A second possible explanation is associated with the aposematic coloration and diurnal habits of most of these frogs. Diurnal frogs are more susceptible to predators that hunt by sight than are nocturnal species. A slow, methodical pattern of locomotion such as walking may have a higher selective value than an erratic, abrupt pattern such as jumping. It also may be true that an aposematic device is more effective when the predator can easily discern the warning color pattern. If aposematic coloration is effective in protecting the frog, then walking may be more efficient than jumping or hopping in terms of energy utilization.

Finally, these frogs feed primarily on ants; there is no need for quick movements during feeding. These myrmecophagous habits also may have contributed to shifts in locomotory patterns.

Hearing

One of the most interesting evolutionary shifts found in several different lineages of frogs is the loss of the auditory apparatus. Probably the hearing apparatus of early Amphibia evolved in response to the shift from an aquatic to a terrestrial habitat and functioned primarily in environmental adjustment. It generally is agreed (Eaton, 1959) that the primitive frog probably had a well-developed tympanum and middle ear. Vocalization is characteristic of most frogs and could only have developed after the means for reception of airborne sound, the ear apparatus, was already

present. Therefore it seems that the absence of an ear apparatus is secondarily achieved.

Only a few species of *Atelopus* (e.g. *flavescens*, *spumarius*) have any remnant of an ear apparatus. The retention of an internal tympanum and middle ear in these forms is a primitive condition. The other species of *Atelopus* investigated, as well as the species of the other genera, lack an ear apparatus.

Although the biological factors important in initiating the loss of the external tympanum and middle ear are unknown, it is clear that once the ear starts to degenerate, the vocal apparatus also begins to degenerate. Species of *Melanophryniscus* are the only forms studied which always have external vocal pouches, visible ostia pharyngea, and vocal slits. Mating calls are common in the breeding biology of these frogs. *Oreophrynella* and *Dendrophryniscus* lack an ear apparatus; these frogs also lack ostia pharyngea and vocal slits. Many species of *Atelopus* lack ostia pharyngea and vocal slits. Only in the species which still have an internal tympanum and middle ear are the ostia pharyngea well developed. Thus it seems that the ancestral stock of these forms had a well-developed hearing apparatus. It also is likely that vocalization was an important component of their breeding biology. Vocalization is still prominent in the breeding behavior of the more primitive *Melanophryniscus*, but I suggest that because of their apparent inability to hear, vocalization is becoming less important in their reproductive behavior and will eventually be lost. The same seems to be true of several species of *Atelopus*, some of which may already have abandoned the vocal portions of their reproductive behavior.

Earlessness is more prevalent in frogs which occur at very high elevations, especially in the families Bufonidae and Leptodactylidae. Most of these earless frogs also occur in tropical areas and probably were derived from ancestors that lived in the warmer lowlands. Possibly a shift to diurnal activity patterns which allows the frogs to take advantage of warmer daytime temperatures was necessary for successful colonization of colder montane habitats. Once the frogs moved into this new environment, their reproductive behavior was modified in accord with the shift to diurnal activity. Frogs in which breeding calls or choruses formed an integral part of the reproductive behavior would be subject to strong selection by predators that were attracted by the calls. In fact, a shift to diurnal patterns for any reason would subject the frogs to strong selection by sound hunting predators during the reproductive season if vocalization was important in their breeding behavior.

These hypotheses could be invoked to explain the loss of the ear in those species of *Atelopus* which apparently do not vocalize. The latter hypothesis, correlating earlessness with high elevation, seems more reasonable, because those species with middle ears are found at low to intermediate elevations today.

Once the middle ear apparatus has been lost, apparently the ability to receive airborne sounds also is lost. What effect this has on species that relied on vocalization as an important factor in their reproductive behavior is unknown.

Aposematic Coloration

There is overwhelming morphological evidence of a trend towards the loss of the middle ear apparatus and its associated structures and hence the loss of the ability to detect airborne sounds. There also is evidence that the degeneration of the vocal apparatus is associated with the loss of the ear and that vocalization is becoming less important in the reproductive behavior of these frogs. With the loss of vocalization as a behavioral means of recognition, there apparently has evolved a secondary means of recognition in these frogs. I suggest that specific modifications of the basic aposematic coloration and subsequent visual recognition by most species, at least of *Atelopus*, replaces the role of vocal recognition and is of primary importance in mate selection.

Aposematic coloration is a well-known feature of many tropical frogs (Cott, 1957). Many of these brightly colored species are diurnal and thus subjected to sight hunting predators (e.g., birds, snakes). However, most of these bright diurnal frogs, including *Melanophryniscus* and *Atelopus*, possess poisonous glandular skin secretions, an effective defense against predators. Daly and Myers (1967) discussed the biological and chemical aspects of the toxins of poison frogs of the family Dendrobatidae. Fuhrman, Fuhrman and Mosher (1969) discussed the toxic qualities of the skin secretions of *Atelopus zeteki* and commented on its distinctive properties.

Cott (1957:292) made reference to the discriminatory feeding of a Crested Seriemma (*Cariama cristata*) which refused specimens of *Melanophryniscus stelzneri*. Budgett (1899:310) described a grass snake which fed only on a specimen of *Physalaemus cuvieri* although several specimens of *Melanophryniscus stelzneri* were available. Cochran (1961) reported the unken reflex in *Melanophryniscus stelzneri*. This peculiar behavioral response is part of an aposematic display to reveal the bright colors of the ventral surface. The

skin secretion of this frog is reported to be very poisonous; increases in amount of secretion have been recorded during this display. All these reports confirm the aposematic nature of the bright color in *Melanophryniscus*. The same is suggested for *Atelopus*.

There is little doubt that the aposematic coloration would have evolved after the frogs acquired the diurnal habit and probably after the skin developed the toxic secretory glands. Also there is little doubt that the original function of the bright coloration was to act as a warning device for predators.

Cott (1957) stated that conspicuous coloration is known to have little, if any, sexual significance in frogs. Muntz (1964), however, has shown that some frogs have color vision. Daly and Myers (1967) suggested that bright coloration might serve for intraspecific recognition in some populations of *Dendrobates*. Savage (1967) indicated that bright coloration and sexual dichromism in *Bufo periglenes* was intimately related to their breeding behavior and mate selection. I suspect that the aposematic coloration of several species of *Atelopus* and *Melanophryniscus* has secondarily become extremely important in their reproductive behavior and that mate selection is accomplished primarily through visual recognition. Once the middle ear and vocal apparatus started to degenerate, the preadaptation of aposematic coloration would be favored by selection in terms of reproduction as well as subject to selective forces from predators. The additive selection by two very different forces might well account for the tremendous amount of inter- and intrapopulational variation found in forms of *Atelopus varius*, *Atelopus ignescens*, and *Melanophryniscus stelzneri*. Sexual dichromism is well marked in many populations of *Atelopus* in Costa Rica, Panamá, and Colombia. This fact lends additional support to the hypothesis that mate selection depends on visual rather than vocal recognition. The realization that visual cues might be important in reproductive biology and that color pattern alone could serve as the premating isolating mechanism introduces a new dimension into anuran systematics.

Paedomorphosis

Wake (1966) has demonstrated the importance of paedomorphosis in the evolution of plethodontid salamanders. It appears that paedomorphosis has played a minor role in the evolution of atelopodid frogs probably because of their terrestrial habits.

There is clearly a paedomorphic character in *Oreophrynella quelchii*. In this species the fronto-

parietal fails to complete metamorphosis and in the adult appears as two separate elements that fuse only posteriorly. Thus, the frontal and parietal fontanelles are exposed. The functional or evolutionary significance of this differential metamorphosis is unknown.

Griffiths (1954a) has shown the developmental patterns of metamorphosis of the frontoparietal bone in *Bufo marinus*. Examination of sequential stages of two species of *Atelopus* and *Bufo marinus* confirms his findings and indicates that the same basic metamorphic patterns of frontoparietal development also occur in the atelopodid genera. It is assumed that the ancestral form of *Oreophrynella* exhibited a similar pattern of metamorphosis and that the adult had a well-developed frontoparietal bone. In *Oreophrynella*, however, a paedomorphic trait has been substituted for the ancestral adult condition by means of a modification of the ontogeny of the ancestor in the descendant.

The absence of palatine bones and quadratojugals and the reduction of the terminal phalanges in several species of *Atelopus* and *Dendrophryniscus* could be attributed to arrested development. The absence of palatine bones in some species of *Melanophryniscus* may be due to fusion and subsequent incorporation into the underlying chondrocranium rather than failure to develop.

There is a trend towards increasing the rigidity of the skull by either fusion of dermal bones, such as the nasals, frontoparietals and parasphenoid, to each other or to the underlying chondrocranium, or by secondary dermal ossification. This trend is especially noticeable in *Melanophryniscus* and may reflect a tendency of these frogs to be slightly more fossorial than are other species. The strengthening of the skull by fusion of elements is a common occurrence in certain fossorial forms.

FAMILIAL RELATIONSHIPS

Removal of *Brachycephalus ephippium* from the Atelopodidae (McDiarmid, MS) leaves Griffiths' family with only a single genus, *Atelopus*. I have shown the close relationship between *Atelopus*, *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella*, although the latter genus apparently is representative of a slightly different lineage. To evaluate the evolutionary status of the Atelopodidae, these four genera must be considered as a unit.

The four genera have eight or fewer procoelous presacral vertebrae; an SQ depressor condition; separate sartorius and semitendinosus muscles; the tendon of the semitendinosus muscle lying ventral to the tendon of the gracilis muscle; larvae with horny beaks and denticles and a single

sinistral spiracle; and pectoral (axillary) amplexus. The genera lack ribs and a parahyoid. This combination of features characterizes the four genera as members of the suborder Procoela. They differ from the Hylidae and Centrolenidae by lacking teeth, toe discs, and intercalary cartilages and by having arcifero-firmisternal or firmisternal pectoral girdles. They are distinguished from the Leptodactylidae (*sensu strictu*) by lacking an omosternum and teeth and from the Dendrobatidae by the absence of teeth, an omosternum and hypobranchial 2, and by the presence of expanded sacral diapophyses. These genera differ from the Pseudidae by the presence in the latter of an omosternum, teeth on the maxilla, premaxilla and vomer, and an accessory phalanx in each digit. They differ from all these families in their constant SQ depressor condition and the presence of a Bidder's organ. Most of their characters are found, however, in the remaining procoelous family, Bufonidae.

Before discussing the familial status, I should like to consider the ancestral stock and those characteristics which must have been present in the form that gave rise to the *Atelopus-Melanophryniscus-Dendrophryniscus* line and to the *Oreophrynella* line. The primitive states of all the characters used in the previous analysis are assumed to be in the composite ancestral line. This hypothetical atelopodid is compared to the genus *Bufo* in Table 3. The comparison shows that the hypothetical ancestor shares most of its 23 characters with *Bufo*. The only major difference between the two is in character 40. The absence of a Bidder's organ is considered primitive and so postulated for the ancestor. However, *Bufo*, like the four atelopodid genera, also has a Bidder's organ. Therefore, the immediate ancestral form probably also had a Bidder's organ.

The striking similarities in shared primitive characters between the hypothetical ancestral atelopodid and *Bufo* suggest that a *Bufo*-like frog is the ancestor of the atelopodid genera. However, there are several characters which distinguish members of the genus *Bufo* from the four atelopodid genera. As was pointed out earlier, phylogenies are based on evolutionary change and character advancement and not on shared character states alone. Therefore, although the ancestral form had many characters found in contemporary *Bufo*, I do not think that it was a *Bufo* as we know the genus today.

Before continuing this comparison, it is necessary to clarify an osteological relationship which has been used to show close relationship between

Atelopus and *Bufo*. Griffiths (1954b) described an otic element in atelopodid and bufonid species and stated that it was not found in members of any other families. In an effort to verify Griffiths' work, a series of eight metamorphosing *Bufo marinus*, including tadpoles measuring 24.6 mm total length (hind legs only) to metamorphosed individuals measuring 11.9 mm snout-vent length, and a recently metamorphosed series of *Atelopus ignescens* and *A. varius* were prepared in the same manner as was Griffiths' material. Griffiths stated that the otic element appears over the crista parotica just after the squamosal passes the posterior border of the eye. He presented a semi-diagrammatic illustration and a photomicrograph showing this condition in *A. ignescens* (Griffiths, 1954b: Plate 2, figs. 5, 6). According to Griffiths, after the otic element has fused with the squamosal, the resulting compound bone stops its backward migration and begins to rotate postero-laterally through 70 degrees. Thus the otic component of the squamosal passes over the lateral portion of the auditory capsule coming to lie apposed to the lateral edge of the ear capsule in adults. Griffiths stated (op. cit.:39) that the rotation is completed well after the tail has disappeared.

I could find no indication of a separate otic element in the specimens of *Atelopus* examined. A separate center of ossification was found in two metamorphosing specimens of *Bufo marinus*. In *Bufo* this element fuses with the squamosal and then with the lateral (otic) portion of the frontoparietal. Griffiths claimed that the dorsal arm or otic portion of the squamosal (his latero-otic) of *Atelopus* persisted because it continued to function as the origin of the depressor muscle. It has been shown previously that the depressor muscle attaches to the dorsal arm of the squamosal in all four atelopodid genera.

I interpret the otic element, as described initially by Sedra (1949) and later by Griffiths (1954b), to be a second center of ossification of the squamosal bone. This second center over the crista parotica may have developed in response to environmental pressure correlated with a particular behavior (fossorial existence) or in those forms in which dermal ornamentation (e.g., cranial crests of bufonids) is characteristic. Two centers of ossification do not necessarily indicate two distinct bones, as claimed by Griffiths. Two centers of ossification are known in other bony elements and it is not unreasonable to postulate their existence in the squamosal bone considering the tremendous reorganization of the cranium during metamorphosis. This proposal would be particularly ap-

TABLE 3

Comparison of Characters of the
Hypothetical Atelopodid Ancestor and the Genus *Bufo*

| <i>Character*</i> | <i>Hypothetical Ancestor</i> | <i>Bufo</i> |
|--------------------------------|-------------------------------------------|-------------------------------------------|
| 1. tensor fasciae latae | short, origin on middle third of ilia | short, origin on middle third of ilia |
| 3. adductor longus | present | present or absent |
| 4. depressor mandibulae | SQat | SQ |
| 5. adductor mandibulae | S and E | S and E |
| 6. frontoparietal | normal size, separate or fused on midline | normal size, separate or fused on midline |
| 10. palatine | present | present |
| 14. quadratojugal | present | present |
| 16. sphenethmoid complex | only ethmoid portion ossified | only ethmoid portion ossified |
| 17. orbitosphenoid | unossified | unossified |
| 18. ceratohyal | anterior process absent | anterior process absent |
| 21. hypobranchials 1 and 2 | present | present |
| 23. presacral vertebrae | eight | eight |
| 24. atlas | separate from first trunk vertebra | separate from first trunk vertebra |
| 25. sacrum | separate from trunk vertebra | separate from trunk vertebra |
| 26. coccyx | articulates with sacrum | articulates with sacrum |
| 28. pectoral girdle | arciferal | arciferal |
| 31. centralia of hand | two | two |
| 33. phalangeal formula of hand | 2-2-3-3 | 2-2-3-3 |
| 35. middle ear apparatus | present | present or absent |
| 36. ostia pharyngea | present | present or absent |
| 37. vocal slits | present | present or absent |
| 40. Bidder's organ | absent | present |
| 42. eggs | black and white or white, 52-910 | black and white, 31-30,000 |

*Characters numbered as in generic definitions.

plicable to those elements of the skull which are important in feeding, such as the squamosal.

The use of this character to indicate close relationship between groups of frogs is unwarranted until we know more about the distribution and variability of the element in other frog families. Reinbach (1939) discussed the otic element in the leptodactylid *Calyptocephalella gayi*. Examination of a metamorphosing tadpole of this species (FMNH 23829, 126 mm total length, 52.5 mm snout-vent length) confirms his findings concerning the presence and development of the element in the Leptodactylidae. Thus, Griffiths' arguments (1954b:45) concerning the homology

of the otic element in *Calyptocephalella* are at least partially unfounded. Until we know more about morphogenesis of bony elements in the skull of many more species of frogs, attempts to homologize this element, even if it is a discrete bone, are fruitless. This is especially true with reference to homologies between bones in modern frogs and fossil amphibians. Jarvic (1968) used Griffiths' work with the otic element to support his contention of an origin of the Anura independent of other modern Amphibia. Taken to its logical conclusion, this would place the Anura in closer relationship to reptiles than to Urodeles. Jarvic based this interpretation of anuran relation-

ships in part upon the homology of the otic element with the intertemporal of osteolepiforms because the otic element "arises at a place corresponding to the centre of radiation of the intertemporal . . ."

Griffiths (1954b) did not find a discrete otic element in all species of *Bufo* which he examined. Because the otic element is present in some members of the Leptodactylidae, as well as in the Bufonidae and the Atelopodidae, and because the element is variable in form or absent in some members of the latter two families, Griffiths' claim that the otic element, as a separate bone, is diagnostic of and restricted to the Bufonidae and Atelopodidae is rejected.

Since *Bufo* possesses many of the characters postulated for the ancestral atelopodid, it seems reasonable to compare the four atelopodid genera with the Bufonidae. This comparison will allow for an evaluation of their familial status.

For this comparison I examined specimens of several species of *Bufo*, the neotropical bufonid *Crepidophryne epioticus*, representatives of several Asian bufonid genera including *Ansonia*, *Cacophryne*, *Pelophryne*, and *Pedostibes*, and the African bufonid *Nectophrynooides vivipara*. For

information concerning the African genera *Wolterstorffina*, *Mertensophryne*, *Laurentophryne*, *Nectophryne*, and the Asian genus *Pseudobufo*, I referred to Tihen's paper (1960). Additional material was obtained from Tihen's papers on *Bufo* (1962a, b) and from Savage and Kluge's paper on *Crepidophryne* (1961). Very little has been written about *Didynamipus* and *Werneria*. In fact the proper familial allocation of the latter genus is questionable.

The characterization of the family Bufonidae is based on a combination of data obtained by examinations of the previously mentioned genera, of information contained in the literature, and of the characteristics used by Noble (1922, 1931) and Griffiths (1963) to define the family. Major characters common to the Bufonidae and the Atelopodidae are listed for comparison in Table 4.

A comparison shows the similarities that exist between the two groups. Ten character states are the same in both families, while six characters have different states. Each of these six different states is clearly a stage in an evolutionary continuum, and as such, should not be used to differentiate these two units at the familial level.

TABLE 4
Comparison of 16 Major Characters
in the Bufonidae and the Atelopodidae

| Character | Bufonidae | Atelopodidae |
|----------------------------------------------------------|--------------------------------------------------|--------------------------------------------------|
| vertebrae | holochordal, procoelous | holochordal, procoelous |
| coccyx | bicondylar articulation or fusion with sacrum | bicondylar articulation or fusion with sacrum |
| presacral vertebrae | seven or eight | five, seven or eight |
| pectoral girdle | arciferal or arciferal- firmisternal | arciferal-firmisternal or firmisternal |
| sacral diapophyses | greatly dilated | greatly dilated |
| tensor fasciae latae | short or elongate | short or elongate |
| adductor longus | present or absent | absent |
| tendon of semitendinosus | ventral to gracilis | ventral to gracilis |
| depressor mandibulae | SQ | SQ |
| adductor mandibulae | S and E or E | S or E |
| Bidder's organ | present | present |
| posterior laryngeal constrictor and pulvinaria vocale | absent | absent |
| hypobranchials 1 and 2 | both present | 1 present, 2 absent |
| maxillary and vomerine teeth | absent | absent |
| omosternum | present or absent | absent |
| sternum | present | present |

The reduction in number of vertebral elements has been discussed previously. The trend towards reduction is well documented in the atelopodids and also is characteristic of the Asian bufonid *Pelophryne* and the African bufonids *Mertensophryne*, *Laurentophryne*, and *Nectophryne* (Tihen, 1960). The primitive number of eight is reduced to a low of five in *Oreophrynella*.

The shift from an arciferal to a firmisternal girdle must have passed through an arcifero-firmisternal condition. This apparently is what is found in three of the atelopodid genera as well as in the Asian bufonid *Cacophryne* and the African *Didynamipus*. A firmisternal girdle is found only in *Atelopus*. Griffiths (1959) suggested that *Cacophryne* had its origin in the genus *Pedostibes*. Parker (1932) indicated that *Didynamipus* originated independently from an ancestor which also gave rise to *Nectophryne*. The shift from arciferal to firmisternal apparently has occurred or is still occurring in at least three different lines within the two major groups.

Tihen (1960) argued that the presence of an adductor longus muscle was a primitive condition and indicated that it was present in all members of the genus *Bufo*. However, my observations and those of Limeses (1964) indicate the absence of this muscle from some species of *Bufo*. Its absence from the other bufonid genera and the atelopodid genera as well suggests a closer relationship between the two groups than originally indicated.

The differences in the adductor mandibulae muscles are the result of at least two and probably more independent losses of either the externus or the subexternus muscles. The only condition from which both an S and an E condition could be derived is the primitive S and E condition which characterizes *Bufo*. All of the Asian and African genera which have been examined (*Ansonia*, *Pedostibes*, *Nectophrynoides*) to date, the Neotropical bufonid *Crepidophryne*, and the atelopodid *Oreophrynella* show an E condition. The three other atelopodid genera, *Melanophryniscus*, *Dendrophryniscus*, and *Atelopus*, have an S condition which probably arose only once. The E condition, however, probably arose at least twice, once in the Neotropics and once in the Old World Tropics.

The absence of hypobranchial 2 suggests that the atelopodid genera were derived from an ancestor which possessed both hypobranchial 1 and 2. The presence of hypobranchial 2 in *Bufo*, *Nectophrynoides*, *Cacophryne*, and the Neotropical *Crepidophryne* is considered the primitive state.

This character together with several others indicates that *Crepidophryne* is part of a Neotropical lineage more closely related to *Bufo* than to the atelopodid genera.

An omosternum is present in *Nectophrynoides* and absent from the other bufonid genera. Its absence from the atelopodid genera does not constitute any greater a difference than exists between *Nectophrynoides* and the other bufonid genera.

Of the 16 characters used in the comparison, the atelopodid genera are distinct from all members of the Bufonidae in only two characters, the S condition of the adductor mandibulae muscle (except in *Oreophrynella*) and the absence of hypobranchial 2.

Because of the close similarities between the Bufonidae and the four genera previously considered in the Atelopodidae, because the two character states which distinguish these four genera from the Bufonidae obviously are derived, and because the family Bufonidae, especially *Bufo*, is most closely related to the ancestral stock of the atelopodid genera, I consider the genera *Atelopus*, *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella* to be members of the family Bufonidae. These four atelopodid genera together with *Crepidophryne* and *Bufo* represent the Neotropical segment of the wide-ranging family Bufonidae which apparently has undergone several major, independent radiations in the three tropical regions of the world.

The Bufonidae may be distinguished from other frog families by the following combination of characters.

Bufonidae Gray 1825

Definition: 1) eight, seven or five presacral vertebrae; 2) vertebrae holochordal, procoelous; 3) coccyx with bicondylar articulation or fused with sacrum; 4) pectoral girdle arciferal, arcifero-firmisternal, or firmisternal; 5) sacral diapophyses greatly dilated; 6) tensor fasciae latae muscle short or elongate; 7) tendon of semitendinosus muscle lying ventral to gracilis muscle; 8) adductor longus muscle usually absent (present in most species of *Bufo*); 9) depressor mandibulae muscle in SQ; 10) adductor mandibulae muscle in S and E, S, or E; 11) Bidder's organ present; 12) hypobranchial 1 present, hypobranchial 2 present or absent; 13) posterior laryngeal constrictor muscle and pulvinaria vocale absent; 14) maxillary and vomerine teeth absent; 15) omosternum usually absent (present but cartilaginous in *Nectophrynoides*); 16) sternum present; 17) aquatic larva or viviparity; 18) karyotype, $2N = 20$ or 22.

HISTORICAL PERSPECTIVE

It was difficult to relate ideas concerning the phylogeny of the Neotropical bufonid genera to the paleogeographic development of South America, primarily because so little is known about the geological history of most of South America. Harrington (1962) and several other workers (Childs and Beebe, 1963) have summarized our geological knowledge. Most works have dealt with the Andean area and represent efforts of petroleum geologists in their search for oil deposits. While useful, these works rarely are pertinent to an interpretation of the early history of the South American frog fauna.

A second difficulty is the virtual absence of an adequate fossil record. Hecht (1962, 1963) has summarized what little is known about the early history of frogs. He concluded that the major adaptive radiation of frogs was completed by the Early or Middle Jurassic and that by Cretaceous the higher groups of frogs had evolved. Most, if not all, of the procoelous families probably were distinct by the beginning of Tertiary. Tihen (1962b) reviewed the New World fossil bufonids and assigned the Argentinian Oligocene fossil described as *Neoprocoela edentata* by Schaeffer (1949) to the genus *Bufo*. Tihen referred this form to the *calamita* group of *Bufo*, that today is restricted to the Old World. Estes and Wassersug (1963) described a Miocene fossil from Colombia which they referred to the modern species *Bufo marinus*. Thus, the genus *Bufo* was in South America as early as the Oligocene. Such evidence indicates that Blair's hypothesis (1963) that *Bufo marinus* invaded South America during the Tertiary isolation of that continent from North America is unsatisfactory. Cole, Lowe, and Wright (1968) indicated that the *marinus* species group of *Bufo* is karyotypically distinct from North American species groups of *Bufo* and suggested a long term isolation and independent evolutionary divergence of the *marinus* group in South America. These data and the South American fossils suggest that *Bufo* reached South America prior to the disruption of the Panamanian land connection as early as the Late Cretaceous or Paleocene.

Darlington (1957) postulated that the bufonids and the genus *Bufo* probably originated in the Old World Tropics and that they migrated to the New World across the Bering Land Bridge early in the Tertiary. However, the fossil record neither supports nor denies Darlington's postulate. In fact, Hecht (1963) pointed out that the present distributions of modern frogs offer very few clues to the center of origin of frogs much less to the origin

of the family Bufonidae. The present distribution of the bufonids, as well as that of certain other circum-tropical families, may be explained better by invoking a pre-Jurassic contact of the Old and New World continents.

Another problem is the lack of agreement among anuran systematists about a classification of higher frogs. A brief comparison of the phylogenies and classifications proposed by Noble (1931), Reig (1958), Griffiths (1963), Inger (1967), and Kluge and Farris (1969) adequately illustrates this disagreement. Hecht (1963) summarized the current patterns of classification and proposed his own. While some of Hecht's proposals suffer from lack of detailed knowledge of many procoelous genera, his phyletic interpretation placed on a time axis is extremely useful in appraising the relationships among modern families in light of their fossil record.

I have shown that the New World bufonid genera, with the possible exception of *Bufo*, were derived from an ancestral form that probably was present in South America by the beginning of the Tertiary. The overall similarities among all species of *Bufo*, whether African, European, Asian, North American or South American, suggest that *Bufo* is an extremely successful frog which has been in the three major tropical areas since the Early Tertiary and remained about the same, or which evolved in a single area and subsequently dispersed into the rest of the world. The first hypothesis assumes that the primitive bufonid from which most of the modern bufonid genera were derived, was very similar to the modern genus *Bufo*. The absence of bufonids from Madagascar and Australia probably precludes their differentiation in Africa prior to the Cretaceous and in the Indo-Australian area prior to the Upper Cretaceous. These assumptions are not in disagreement with the fossil record nor with current ideas concerning the age of most procoelous anuran families.

The second hypothesis assumes either a South American origin for the genus and dispersal into the Old World prior to the Paleocene or an Old World origin, probably Africa, for *Bufo* and subsequent dispersals into the New World. Tihen (1962a, b) favored an Old World origin for the genus and indicated that every major line of diversification within the family is represented among the various African forms. The primitive condition of *Nectophrynooides vivipara* (Tihen, 1960) and recent karyological data (Bogart, 1968) seem to support an African ancestry. The original location of the ancestral bufonid is not critical to this discussion because, despite the place of origin, it or

its descendants had to have been in South America by the beginning of the Cenozoic.

I am assuming that the Neotropical genera, with the possible exception of *Bufo*, were derived from a single ancestral group that was in South America prior to the opening of the Panamanian portal. The ancestral form from which *Melanophryniscus* and *Atelopus* were derived probably occupied savanna like habitats in areas that today form the Paranaíba, San Francisco, and Paraná Basins of Brazil. Harrington (1962) showed continental facies in these areas in the Late Cretaceous and throughout most of the Tertiary.

Melanophryniscus has retained many of the generalized characteristics of the ancestral form and generally has remained in seasonal areas of subtropical savanna, pampean grassland, and deciduous forest (Smith and Johnson, 1945). The presence of a population of *Melanophryniscus moreirae* in the Amazon Basin suggests that the genus ranged further north, probably sometime during the Late Tertiary. Today it is found there only in relict patches of savanna. Haffer (1967, 1969) discussed the isolated remnants of savannas in the forests of the lower Amazon. Gallardo (1966) suggested that a majority of the Chacoan amphibian species, including species of *Melanophryniscus*, may be considered Guiano-Brazilian in origin. Haffer (1969) and Vanzolini and Williams (1970) offered convincing arguments supporting climatic cycles of wet-dry periods in the Amazon Basin in the Pleistocene. Dispersal into the Amazon Basin from southern Brazil during a dry period also may account for the disjunct occurrence of *M. moreirae* near Obidos, Pará, Brazil. I suspect that *Melanophryniscus* secondarily invaded the tropical and subtropical rain forests in southeastern Brazil and the subtropical forests on the eastern slope of the southern Andes in northeastern Argentina.

Dendrophryniscus was derived from the ancestral *Melanophryniscus* stock and has adapted to wet tropical forests. In southeastern Brazil one species has become a bromeliad inhabitant, while another and the species in the Amazon Basin are found on the forest floor. The ancestral form probably originated in the forests of the ancient Coastal Brazilian Shield. The striking differences among the species examined suggest that they have been isolated for a considerable period of time. The presence of another species of *Dendrophryniscus* in northeastern Brazil indicates a former connection between the eastern species along the coastal portions of the Brazilian Shield. They were probably connected to the form in the Amazon

Basin sometime in the Tertiary. Subsequent climatic shifts, similar to those discussed by Vanzolini and Williams (1970) and geologic changes have fragmented *Dendrophryniscus* into three or four isolated populations.

It appears that one of the major factors initially contributing to differentiation of the *Atelopus* line was the ability of the ancestors to utilize streams for breeding. As soon as the ancestral forms moved out of the lowlands and away from the primitive pond and still-water breeding sites and into the mountains and irregular terrain, they adapted to fast moving stream habitats. Thus an entire new adaptive zone became available. Behavioral modifications, including placing the eggs beneath rocks, and structural changes followed. Increased yolk content of each egg allowed for a longer developmental period of the tadpole within the egg but reduced the number of eggs per spawn. The larvae, however, were larger and stronger upon hatching and better able to maintain themselves in the fast moving water. In addition the larger, more advanced larvae were able to feed immediately on hatching and were not dependent on yolk material for food early in the free-swimming stage. Specialized larval adaptations, especially the sucking disc, were evolved in this fast stream habitat.

With the initial major uplifts of the Andes in Peru and Ecuador in the Late Cretaceous (Ham and Herrera, 1963) and in Colombia in Late Cretaceous and Paleocene (Jacobs, Bürgl and Conley, 1963) and of the mountains of northern Venezuela in the Eocene (Mencher, 1963), entire new areas became available to and were exploited by *Atelopus*. The ancestral stock probably came from southeastern portions of the Guiana Shield where the more primitive *Atelopus flavescens* is found today. However, it is possible that *Atelopus* initially invaded the montane habitat in the southern Andes and moved north along their eastern slope. It appears also that the higher elevations have been invaded several times. The presence of *Atelopus* in Central America is attributed to a northward movement following emergence of the Panamanian isthmus in the Pliocene (Lloyd, 1963).

The apparent close association of species of *Atelopus* with mountain streams has restricted species to particular drainage systems. The resulting isolation (drainage system and mountain top) probably accounts for the striking differences among many populations and probably has been an important factor contributing to speciation.

Very little can be said about the history of *Oreophrynella*. Apparently it was derived from

the same stock that gave rise to the other three genera but probably at a different time. It is a very specialized frog which is restricted to an ancient part of the Guiana Shield. Harrington (1962) indicated that this area has been a relatively stable land mass since the Triassic.

Mayr and Phelps (1967) discussed the relationships among the bird faunas of the tepuis of Venezuela. They mentioned that many authors attribute the avian distributional patterns to fragmentation of a once widespread avifauna in conjunction with the erosion and dissection of a former vast sandstone tableland, the Roraima formation, which covered more than a million square kilometers of the Guiana Shield. Mayr and Phelps pointed out that this plateau is much more ancient than its bird fauna and accordingly discredited the theory. However, this theory may explain the distribution of *Oreophrynella*, whose origin may extend well into the Early Tertiary and probably into the Cretaceous.

While this study has clarified many of the problems that previously existed, it has created, at least in my mind, several new problems and posed numerous questions. Many of these problems are concerned with the reproductive biology and the effectiveness of certain alleged premating isolating mechanisms. Some of my interpretations as well as possible explanations to several of the new problems suffer from a lack of knowledge of the biology of these frogs. Solutions and answers must wait until more information becomes available through extensive field work.

RESUMEN

Ranas Atelopodid son uno de los grupos más interesantes y diversos de la anura neotropical. El estado sistemático y la historia evolucionista de los géneros de esta familia han sido pobremente entendidos. La meta de este estudio era analizar los conocimientos disponibles de la morfología y biología de estas ranas para clarificar sus relaciones evolucionistas y su historia. El grupo incluye aproximadamente 40 especies de cuatro géneros: *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, y *Oreophrynella*. Los datos indican que *Brachycephalus*, un género originalmente incluido dentro la familia, no está estrictamente relacionado con los demás cuatro géneros. Sus relaciones serán discutidos en otra parte.

Espécimens representantes de todos los géneros y de la mayoría de las especies fueron estudiados. Datos respecto de la miología, la osteología, y morfología reproductiva fueron acumulados. Toda literatura disponible fue revisada y la infor-

mación pertinente fue asimilado como parte de este informe.

Una descripción detallada de la musculatura del muslo y de la mandíbula y la osteología de cada especie es presentado. Los cráneos, las cinturas pélvicas, y los aparatos hioideos son descritos y ilustrados. Componentes del oído, algunas aspectos de la morfología externa, la biología reproductiva, y la ecología son descritos.

Cada género es definido por 43 caracteres. Sus distribuciones geográficas son presentados en resumen y sus especies incluidas y referidas son mencionadas. *Atelopus minutus* Melin y *Atelopus proboscideus* Boulenger son puestos en el género *Dendrophryniscus*. *Atelopus rubriventris* Vellard es puesto en el género *Melanophryniscus*.

Los cuatro géneros son discutidos y sus estados característicos comparados. *Melanophryniscus* tiene el mayor número de características primitivas y el menor número de características avanzadas y es probablemente el más semejante a la cepa ancestral. *Atelopus*, también, tiene muchos características primitivas, pero tiene el mayor número de características avanzadas. *Atelopus* y *Melanophryniscus* fueron derivados del mismo linaje, pero *Atelopus* ha experimentado una radiación significativa al nivel específico y muestra varios adelantos no encontrados en los demás géneros. *Dendrophryniscus* fue derivado de la línea de *Melanophryniscus* y muestra una evolución paralela en algunas estados característicos con *Atelopus*. *Oreophrynella* tiene más estados avanzados característicos que *Melanophryniscus* o *Dendrophryniscus* y solamente uno menos que *Atelopus*. Sin embargo, *Oreophrynella* tiene el mayor número de estados únicos y el menor número de estados primitivos. Aparentemente *Oreophrynella* fue derivado desde la cepa ancestral a un tiempo distinto de la línea *Melanophryniscus-Atelopus-Dendrophryniscus* y posteriormente se ha hecho muy especializado.

Los mayores direcciones evolucionarias y los cambios de características morfológicas aparentemente son asociados con cambios en el mecanismo de locomoción; otras son el resultado de metamorfosis diferencial. Modificaciones biológicas asociados con la pérdida del aparato del oído medio y el desarrollo de coloración aposemático son importantes. El estado familiar del Atelopodidae es discutido y rechazado. Los géneros *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, y *Oreophrynella* son puestos en la familia Bufonidae, lo que es redefinido.

La cepa ancestral de la cual los cuatro géneros fueron derivados probablemente existió en Amé-

rica del Sur antes del comienzo del cenozoico. La cepa ancestral *Melanophryniscus-Dendrophryniscus-Atelopus* probablemente ocurrió en las sabanas o bosques deciduos del Brasil sureste. *Melanophryniscus* ha retenido muchas de las características ancestrales generalizadas y actualmente se encuentra en el mismo tipo general de ámbito natural. *Dendrophryniscus* fue derivado de la cepa de *Melanophryniscus* y fue adaptado a la selva húmeda tropical del este del Brasil y la cuenca Amazónica. *Atelopus* se ha adaptado al ámbito

natural a orillas del arroyo y se ha movido a las áreas montañosas que se hicieron disponibles con el levantamiento de los Andes en los finis del cretáceo y el comienzo del terciario. Este ámbito natural nuevo ha sido explotado con buen éxito por *Atelopus* y ha sido un factor mayor contribuyente a su radiación específica. *Oreophrynella* es una rana muy especializada que fue derivada de una cepa antigua de Bufonidae y que fue subsecuentemente restringida al Cerro Roraima un parte antigua del Escudo Guianico.

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