

EVOLUTIONARY RELATIONSHIPS AND OSTEOLOGY OF  
THE FROG FAMILY LEPTODACTYLIDAE

by

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Volume II

tongue large, rounded, posterior edge free; (45) toes fully webbed, outer metatarsal tubercle lacking, inner metatarsal tubercle not spade-like, digital tips narrow, first finger shorter than second; (46 - 48) (49) two adults examined were 63 and 64 mm. SVL; (50) tympanum absent; (51) fifth toe very broad, much broader than in any other leptodactylid.

Composition.-- monotypic.

Distribution.-- Known only from the Cordillera de Nehuelbuta, Mallew, Chile.

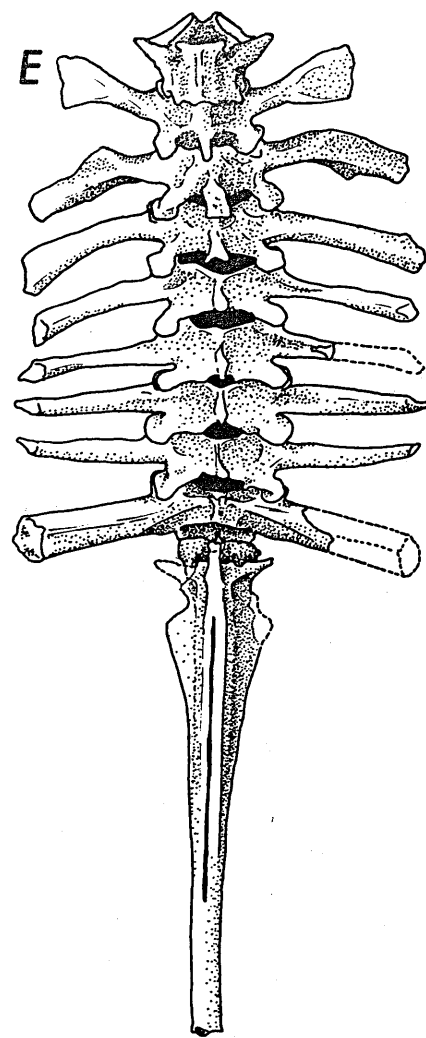
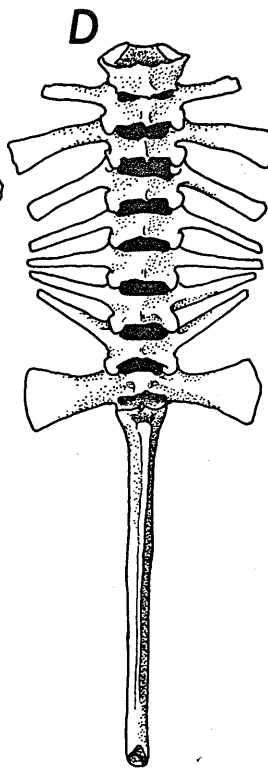
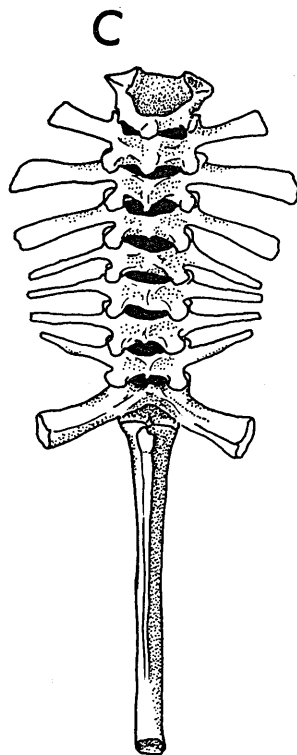
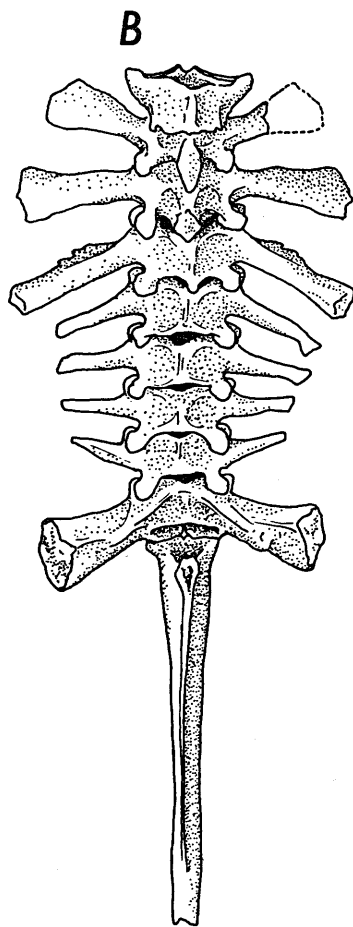
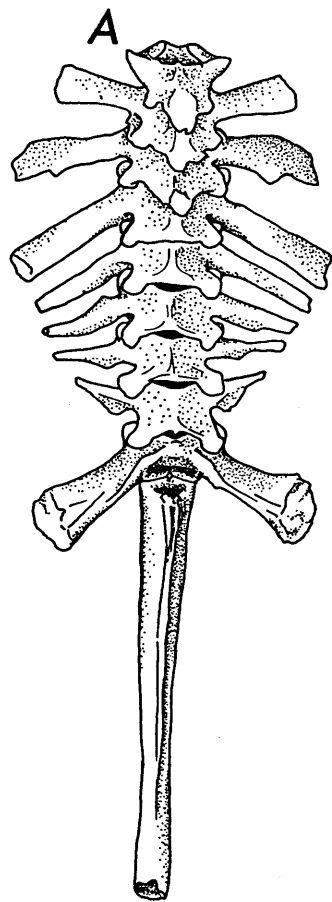
Remarks.-- The osteological characters (nos. 1 - 38) of Telmatobufo bullocki were studied by use of stereo-radiographs of the holotype and paratype. The observation of some characteristics is very difficult and the statements listed above are subject to reinterpretation. For example, the first two vertebrae appear to be fused; this may not be the case, but judging from prior experience with skeletons and radiographs, I feel the present interpretation is probably correct. Similar arguments and qualifications can be made for several other characteristics involving skull bones. The transverse process of the posterior presacral vertebrae of Telmatobufo are shortened as in Caudiverbera, Ceratophrys, Proceratophrys, and a few other Neotropical leptodactylid genera. Except for the dilated sacral diapophyses, the

vertebral column of Telmatobufo looks like that of Proceratophrys (Fig. 79). I consider Telmatobufo to be more closely related to Caudiverbera than to the other Telmatobiini. Caudiverbera and Telmatobufo share three characters which are not exhibited by the other Telmatobiini: shortened transverse processes of the posterior presacral vertebrae, vertical pupil, and absence of an outer metatarsal tubercle. The two genera differ in the casquing of the skull of Caudiverbera; the skull of Telmatobufo is identical, insofar as my observations will permit, with that of Telmatobius. In several respects Telmatobufo is intermediate between Neoprocoela and Telmatobius and fits the generalized pattern of Telmatobiini.

Schmidt (1952) suggested that Telmatobufo was closely allied to, but noticeably distinct from, Telmatobius. The only subsequent author to discuss the validity and relationships of Telmatobufo was Gallardo (1962, 1965), who suggested that Telmatobufo bullocki was identical with Aruncus valdivianus Philippi. He further suggested (1962) that Aruncus was not related to Telmatobius but to Calyptocephalella (= Caudiverbera) but did not substantiate his opinions with data.

Cei's (1958) reproductions of the long-lost and unpublished plates for Philippi's (1902) work provide much more evidence concerning the identities of the myriad of names proposed by Philippi than do Philippi's brief

Figure 79. Vertebral columns of five genera of the Telmatobiinae. (A) Proceratophrys cristiceps (KU 106273, x 3), (B) Odontophrynus cultripes (KU 92975, x 3), (C) Cycloramphus pinderi (KU 92807, x 3), (D) Thoropa miliaris (KU 92856, x 3), and (E) Batrachophrynus macrostomus (KU 96127, x 1.5).



descriptions. The plates provide adequate grounds for rejecting Gallardo's contention that Telmatobufo Schmidt is a synonym of Aruncus Philippi. The plate for Aruncus valdivianus (plate I in Cei, 1958) indicates that the frog had little, if any, webbing between the toes, whereas the specimens of Telmatobufo bullocki have fully webbed feet. The fingers of Aruncus are proportionately much longer than is the case for Telmatobufo. However, the most convincing data is the illustrated tympanum in Aruncus valdivianus and the absence of the tympanum in Telmatobufo bullocki. Cei's (1958) suggestion that the figures of Aruncus valdivianus represent a poor rendition of Bufo spinulosus is reasonable. Cei (1958) objected to the inclusion of Aruncus valdivianus in the synonymy of Bufo spinulosus because the figures are not sufficiently accurate to permit an assignment to subspecies, and the synonymy would affect the application of subspecific names. I suggest that Aruncus valdivianus Philippi, 1902, be considered a nomen dubium for the present.

Telmatobius Wiegmann, 1835

(Figs. 80-81)

Telmatobius Wiegmann, 1835, Nova Acta Acad. Leop.-carol, 17:262 [Type-species by monotypy, Telmatobius peruvianus Wiegmann, 1835].

Pseudobatrachus Peters, 1873, Mtber. k. Preuss. Akad.

Wiss., Berlin, p. 414 [Type-species by monotypy,  
Pseudobatrachus jelskii Peters, 1873].

Cophaeus Cope, 1889, Bull. U. S. Natl. Mus., 34:312, 381  
 [Apparently a replacement or substitute name for part  
 or all of Boulenger's (1882) Telmatobius, which Cope  
 considered not equal to Telmatobius of Wiegmann  
 (1835)].

Diagnostic definition.-- (3) transverse processes  
 of posterior presacral vertebrae not shortened; (5)  
 cervical and second vertebrae not fused; (6) cranial  
 bones not involved in dermostosis; (7) omosternum large;  
 (8) sacral diapophyses dilated; (9) maxillary arch toothed,  
 teeth pointed, pedicellate; maxillary arch toothless in  
 a few populations; (10) alary processes of premaxillae  
 directed posterodorsally, broad at base; (11) palatal  
 shelf of premaxilla narrow with relatively long palatal  
 process; (12) facial lobe of maxilla relatively deep,  
 not exostosed; (13) palatal shelf of maxilla relatively  
 narrow, pterygoid process lacking; (14) maxillary arch  
 complete in most species, quadratojugal lacking in  
 edentulous patagonicus; (15) nasals separated medially and  
 small in dentate species, larger and narrowly separated  
 in patagonicus; (16) nasals not in contact with maxillae or  
 pterygoids; (17) nasals widely separated from frontoparietals;  
 (18) frontoparietal fontanelle small, except in patagonicus

Figure 80. Dorsal and ventral views of skull of Telmatobius hautholi (KU 72879, x 7). Right septomaxilla lost in preparation.



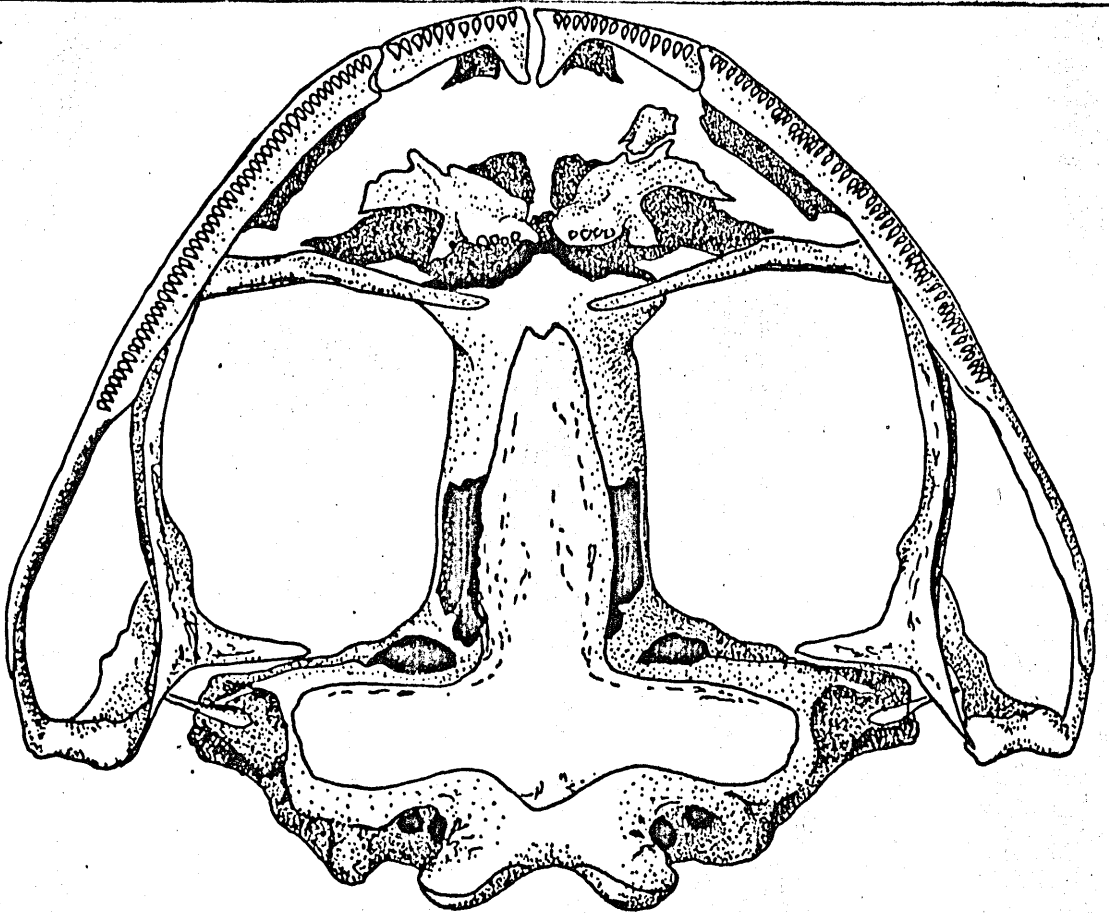
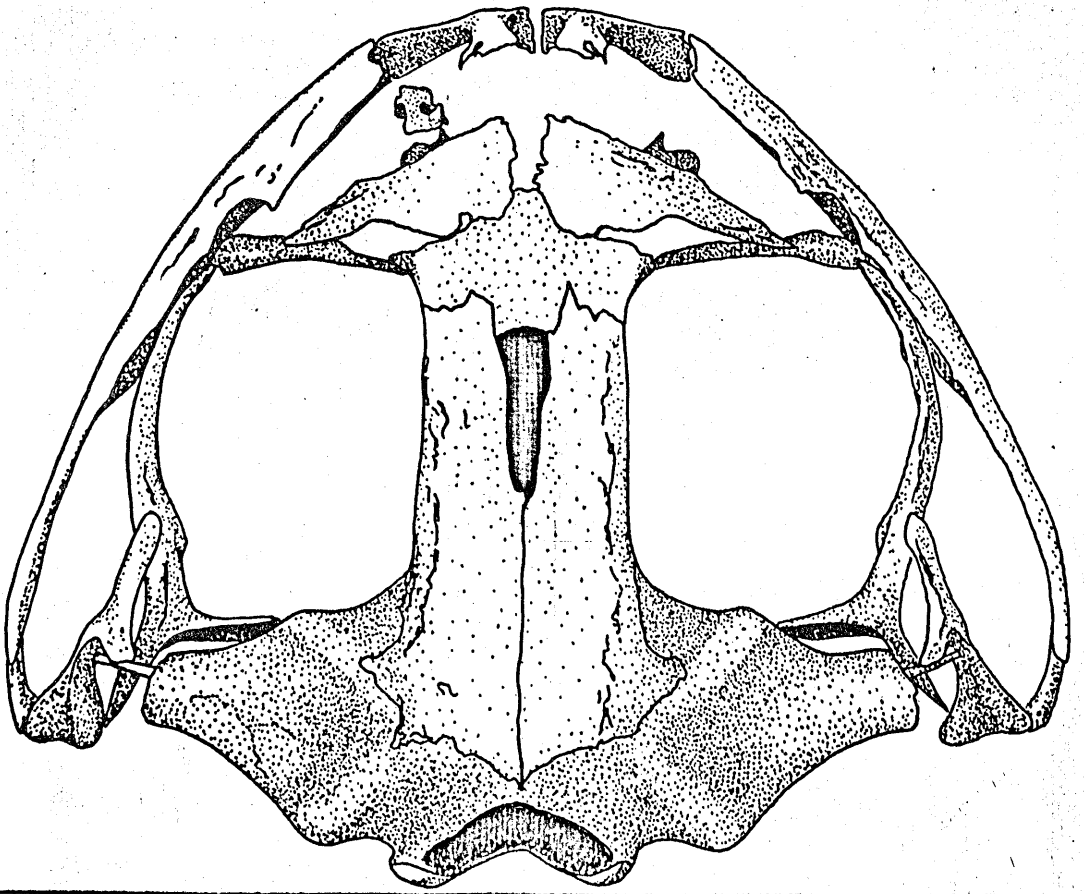
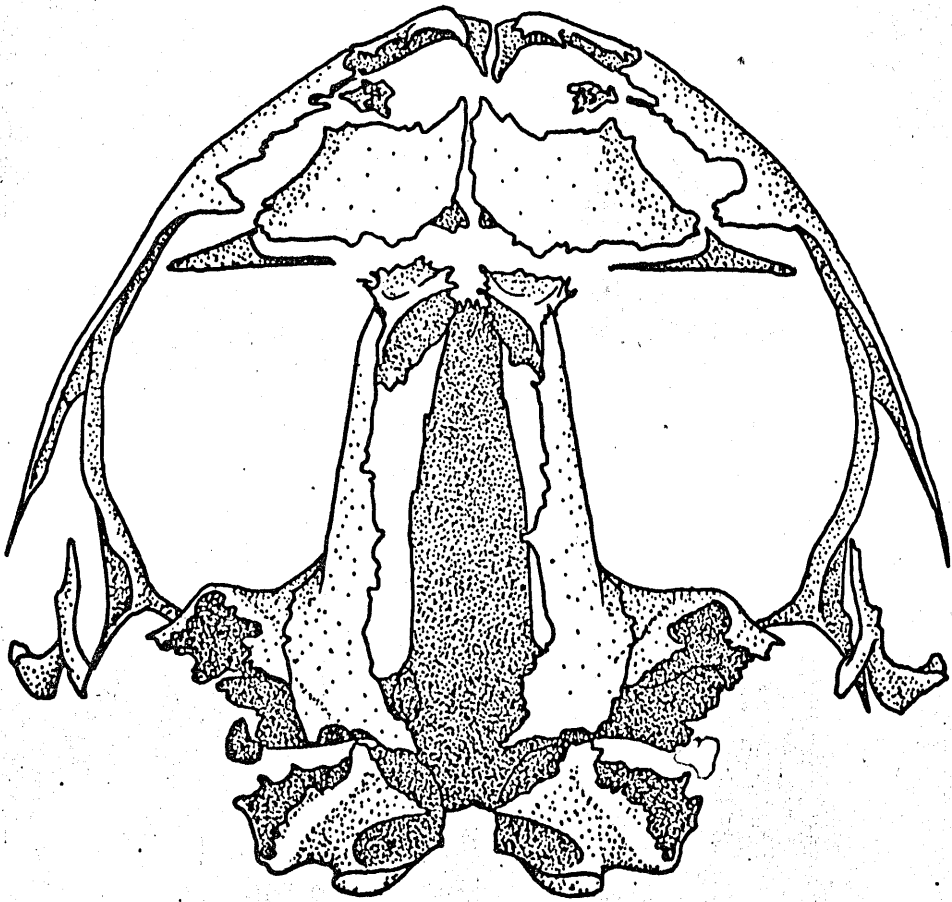
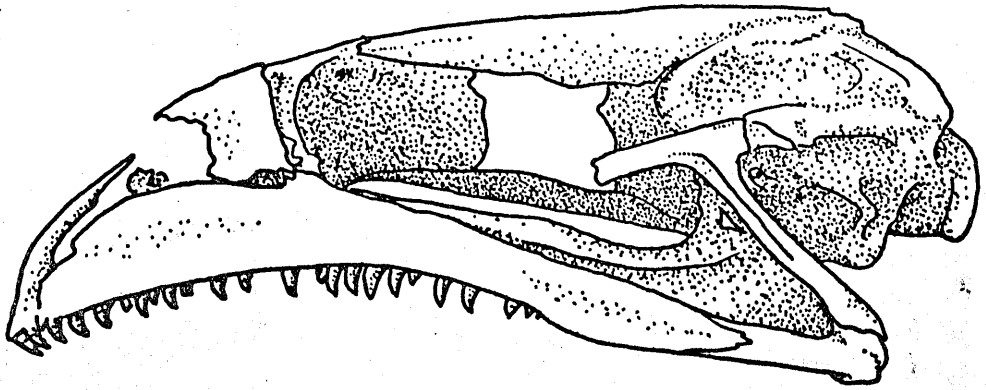


Figure 81. Lateral view of skull of Telmatobius marmoratus (UMMZ 68179, x 5.5) and dorsal view of skull of Telmatobius patagonicus (KU 80781, x 10).



in which it is large; (19) frontoparietals not or but slightly ornamented; (21) temporal arcade absent; (22) epiotic eminences well defined; (23) cristae paroticae short and stocky; carotid artery not enclosed in a canal, sometimes a shallow groove is present on the frontoparietal and otoccipital; (24) zygomatic ramus of squamosal relatively long, blunt, widely separated from maxilla; (25) otic ramus of squamosal very short, no otic plate; (26) squamosal-maxillary angle about  $40^{\circ}$ ; (27) columella present, absent in patagonicus; (28) prevomers present, usually toothed, sometimes edentate, entire, in contact medially or narrowly separated; (29) palatines long and narrow, narrowly separated medially; (30) sphenethmoid entire, extending anteriorly to posterior edge of nasals; (31) anterior ramus of parasphenoid relatively narrow, lacking median keel, extending anteriorly between palatines; (32) parasphenoid alae oriented at right angles to anterior ramus, not overlapped laterally by median rami of pterygoids; (33) pterygoids relatively small, anterior rami elongate, nearly reaching palatines; (34) occipital condyles relatively large, not stalked, narrowly separated medially; (37) alary processes of hyoid plate on narrow stalks; (40) m. depressor mandibulae in two slips; (41) pupil horizontal; (42) males lacking vocal sac; nuptial asperities or clusters of spines on thumb and

sometimes on chest; (43) body lacking glands; (44) tongue large, rounded, posterior edge free; (45) toes usually completely webbed, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged, digital tips narrow; (46) larvae with dextral vent, 2/3 tooth rows, labial papillae interrupted anteriorly; (49) adults to about 60 mm. SVL; (50) tympanum small or concealed.

Composition.-- Vellard (1951) recognized 19 species of the genus. Schmidt (1954a) recognized 21 and Vellard (1960) modified his earlier account and recognized 23 species. Batrachophrynus patagonicus is a species of Telmatobius and one additional species has been described since Vellard's last paper. Forty-nine populations of Telmatobius are presently afforded nomenclatorial recognition. The following species of Telmatobius are recognized; the number of subspecies is included in parentheses: albiventris (4), arequipensis (2), atacamensis, brevipes, brevirostris (3), cinereus, crawfordi (2), culeus (6), halli (2), hauthali (2), ignavus, intermedius, jelskii (4), laevis, marmoratus (7), montanus, niger, oxycephalus, patagonicus, peruvianus, praebasalticus, rimac (2), simonsi, vellardi, and verrucosus.

Distribution.-- South American Andes from southern Ecuador (1° S) to central Chile and Argentina (32° S). The greatest diversity occurs in southern Peru.

Remarks.-- As presently constituted, Telmatobius is one of the larger leptodactylid genera. Vellard (1951, 1953, 1955, 1960) placed the 23 species known to him in three species groups: peruvianus group (stream frogs), marmoratus group (primarily or totally aquatic frogs), and jelskii group (semiterrestrial frogs). However, several authors have pointed out that the closest relatives of some aquatic species are semiterrestrial species. Loss of the maxillary or prevomerine teeth has been a major taxonomic character in the study of the relationships of the frogs of this genus. Maxillary teeth are lost by some members of the peruvianus and marmoratus groups. Prevomerine teeth are lost by some populations of all species groups.

I have seen few skeletons of this genus, and therefore my characterization of it will probably undergo some alteration with the acquisition of additional material in the future. The paedomorphic T. patagonicus is strikingly different in cranial osteology (Fig. 81) from the other species I examined.

† Neoprocoela Schaeffer, 1949

Neoprocoela Schaeffer, 1949, Bull. Amer. Mus. Nat. Hist., 93:57 [Type-species by original designation, Neoprocoela edentatus Schaeffer, 1949 (= N. edentata), Lower Oligocene].

Schaeffer (1949) described and named a relatively well preserved bufonoid frog from the Lower Oligocene of Patagonia as a new genus and new species of Leptodactylidae. The fossil is edentate (as is reflected in Schaeffer's choice of a trivial name), has a moderately small frontoparietal fontanelle, and dilated sacral diapophyses. Schaeffer did not consider the fossil to be a bufonid because to do so "...would require the presence of the Bufonidae (sensu stricto) in South America by no later than the early Oligocene, an occurrence which is not supported by the known paleontological facts." Exactly what facts these were was not explained by Schaeffer. Instead, he assigned the fossil to the Leptodactylidae, and characterized it as having a number of primitive, criniid-like traits. Schaeffer suggested that Neoprocoela was related to Batrachophrynus and Telmatobius.

The discovery of a Miocene toad (Bufo marinus) from Colombia (Estes and Wassersug, 1963) clearly establishes the Bufonidae in South America from at least the Eocene because South America was isolated from Middle America between the Eocene and Pliocene (Lloyd, 1963). Therefore, Schaeffer's objections to placing Neoprocoela in the Bufonidae can be seriously questioned. Tihen (1962b) placed Neoprocoela in the synonymy of Bufo and considered the type-species as a species of the B. calamita group. Tihen associated the fossil with Bufo for the following

reasons: (1) in edentulous leptodactylids, the prevomers are greatly reduced in size, (2) the alary processes of leptodactylids are directed dorsally or laterally, not toward the midline as in Neoprocoela edentata and bufonids, (3) the sphenethmoid is entire in Neoprocoela, (4) the shape of the squamosal suggests a large squamosal-maxillary angle, (5) the broad nasals are in median contact, (6) there is a long maxillary-pterygoid contact, (7) the maxillae are very broad, (8) the atlantal cotyles are closely approximated ventrally, (9) the first transverse processes are directed anterolaterally and are expanded (= dilated), and (10) the sacral diapophyses are expanded (= dilated). Tihen cited two other characters of Neoprocoela which are uncommon in bufonids but characteristic of the Bufo calamita group--large frontoparietal fontanelle and very short otic ramus of the squamosal. Tihen argued that while each of the ten characteristics listed above can be demonstrated to occur in one or more leptodactylid groups, the simultaneous occurrence of all ten is not known for any leptodactylid, but is the case in Bufo. Tihen's "leptodactylid condition" for his comparison of Neoprocoela, leptodactylids, and bufonids, must have been based on the skeletons of some of the Australo-Papuan leptodactylids. Characters (3) and (5) of Neoporcoela are very much unlike the conditions seen in edentulous Australo-Papuan leptodactylids, but are



like the conditions seen in some edentulous Neotropical leptodactylids. With the exception of characters (1), (2), and (10), Neoprocoela agrees completely with Batrachophrynus. The fossil agrees with Batrachophrynus in the two characteristics cited by Tihen that are "unusual" for Bufo. The dilation of the sacral diapophyses of Neoprocoela is not as great as in Bufo. The sacral diapophyses are round in Batrachophrynus (Fig. 79). The dilation of the sacral diapophyses of Neoprocoela is no greater than that seen in Telmatobufo, a close relative of Batrachophrynus. The length of the transverse processes of the posterior presacral vertebrae is not evident in the single fossil of Neoprocoela; this character is very different in Batrachophrynus and the Bufo calamita group.

Tihen recorded the alary processes (ascending processes of Tihen) of the premaxillae as directed toward the midline in Neoprocoela. This is not a leptodactylid trait but clearly a bufonid trait. Perusal of Schaeffer's figures clearly indicates that the skull of Neoprocoela was crushed and distorted. The skull apparently was crushed from the left to the right side. The premaxillae are distorted with an anterior rotation at their median suture; this results in a deflection toward the midline of the alary processes. As in Batrachophrynus, the alary processes are long and thin.

The large prevomers of Neoprocoela readily distinguish it from Batrachophrynus, in which the prevomers are minute. In Caudiverbera, Telmatobius, and Telmatobufo, the prevomers are large and toothed. It is only logical to assume that the ancestral stock of Batrachophrynus had large and toothed prevomers. In the course of loss of the prevomers and prevomerine teeth, two patterns are observed. In one pattern, tooth loss occurs late; the prevomerine bones are reduced in size until only the dentigerous ramus and a small semicircle of bone surrounding the inner edge of the choana remains. The teeth and dentigerous ramus are then lost, in that order. This is the pattern seen in the Myobatrachinae. In the other pattern, the prevomer is not greatly reduced in size before the teeth are lost. The bone continues to be reduced in size subsequent to tooth loss. This pattern is seen in several genera of the Telmatobiinae, Leptodactylinae, and Elosiinae. Neoprocoela fits the intermediate condition between Telmatobufo and Batrachophrynus.

Neoprocoela is intermediate between Telmatobufo and Batrachophrynus in the shape of the sacral diapophyses and in shape of the cristae paroticae, as well as the size of the prevomers. Tihen also cited the "toad-like" body shape of Neoprocoela as an additional bufonid character. However, Telmatobufo is very toad-like even

in the possession of well defined parotoid glands.

Based on the skeletal data evident in the figures of Neoprocoela published by Schaeffer (1949) and Tihen (1962b), the following characteristics of my diagnostic definition can be stated: (2) vertebral shield probably absent; (4) cervical cotylar arrangement type II; (5) cervical and second vertebrae not fused; (6) skull bones not exostosed, therefore derm of head free; (8) sacral diapophyses dilated; (9) maxillary arch edentate; (10) alary processes of premaxilla narrow, directed posterodorsally; (11) palatal shelf of premaxilla very broad, slightly indented; (12) facial lobe of maxilla deep; (13) palatal shelf of maxilla broad with a well developed pterygoid process; (14) maxillary arch complete; (15) nasals large, in broad median contact; (16) nasals in contact with maxillae; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle of moderate size; (19) frontoparietals not ornamented; (21) temporal arcade lacking; (23) cristae paroticae moderately short, stocky; (24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; (25) otic ramus of squamosal very small, no otic plate; (28) prevomers large, edentate; (29) palatines elongate; (30) sphenethmoid large, entire; (32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid; (33) anterior rami of pterygoids elongate, in long contact with maxillae, reaching

palatines; (34) occipital condyles large, not stalked, narrowly separated medially; (36) terminal phalanx of one digit knobbed; (49) snout-coccyx length at least 66 mm. The single terminal phalanx could be of the thumb even if the frog had T-shaped terminal phalanges.

Batrachophrynus Peters, 1873

(Fig. 82)

Batrachophrynus Peters, 1873, Mtber. k. Preuss. Akad.

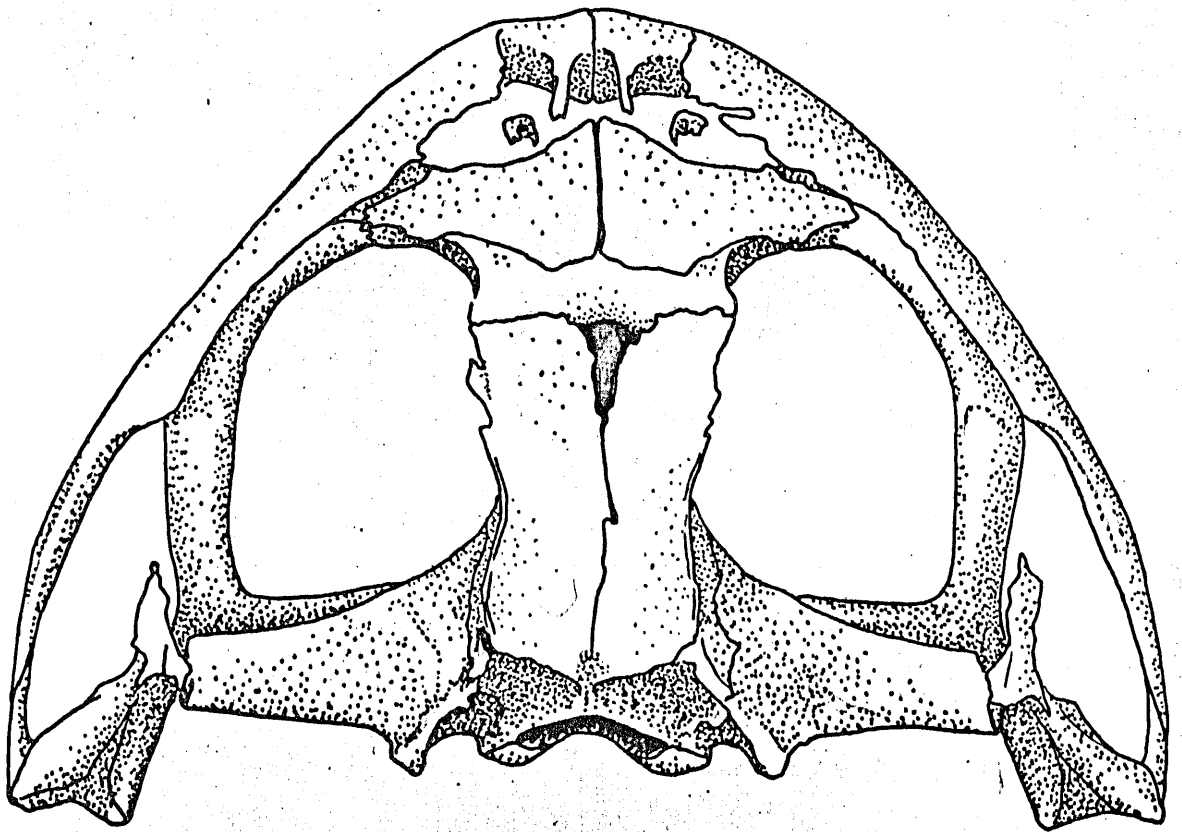
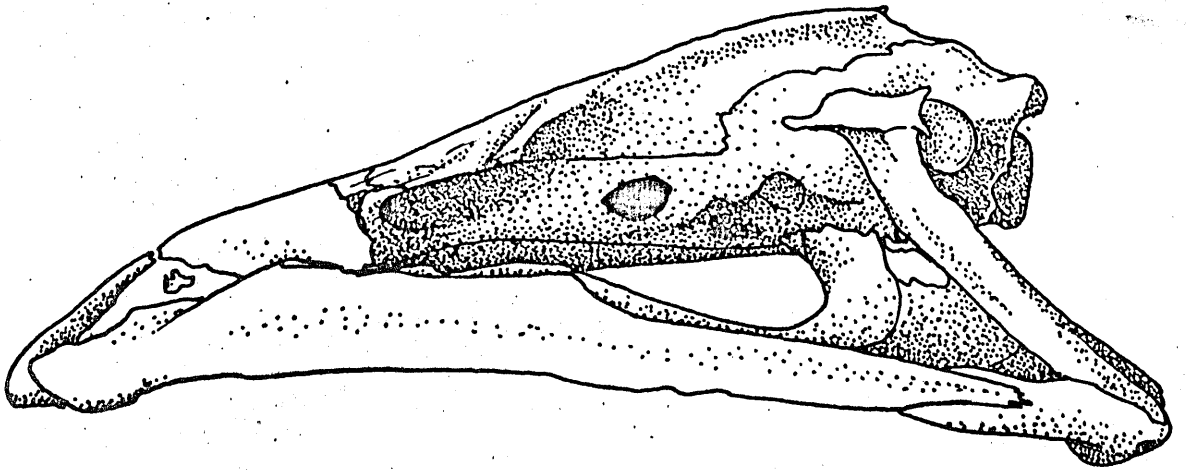
Wiss., Berlin [Type-species by present designation,

Batrachophrynus macrostomus Peters, 1873].

Diagnostic definition.-- (3) transverse processes of posterior presacral vertebrae oriented at right angles to sagittal line, as long as sacral diapophyses; (5) cervical and second vertebrae not fused; (6) cranial bones not dermostosed; (7) omosternum present, large; (8) sacral diapophyses round; (9) maxillary arch edentate; (10) alary processes of premaxillae narrow, directed posterodorsally; (11) palatal shelf of premaxilla very broad, slightly indented; (12) facial lobe of maxilla deep; (13) palatal shelf of premaxilla broad, pterygoid process relatively small; (15) nasals large, in broad median contact; (16) nasals in contact with maxillae and pterygoids; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle small; (19) frontoparietals not ornamented, except for a sharp shelf immediately

posterior to orbit; (21) temporal arcade lacking; (22) epiotic eminences large posteriorly, obsolete anteriorly; (23) cristae paroticae very long and narrow; carotid artery not enclosed in bony canal, frontoparietals sometimes having groove between ridge and epiotic eminence; (24) zygomatic ramus of squamosal short; (25) otic ramus of squamosal very short, no otic plate; (26) squamosal-maxillary angle  $35 - 40^{\circ}$ ; (27) columella present, thin; (28) prevomers small, edentate, only dentigerous ramus present; (29) palatines broad, widely separated medially, lacking odontoids; (30) sphenethmoid large, entire, extending anteriorly to front of nasals; (31) anterior ramus of parasphenoid broad, pointed, keeled medially, extending anteriorly between palatines; (32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid, broadly overlapped laterally by median rami of pterygoids; (33) pterygoids very large, anterior rami in long contact with maxillae, reaching palatines; (34) occipital condyles large, not stalked, narrowly separated medially; (37) alary processes of hyoid plate on narrow stalks; (40) m. depressor mandibulae in two slips; (41) pupil horizontal; (42) males apparently lacking nuptial asperities and vocal sac; (43) body lacking glands; (44) tongue large, completely adherent; (45) toes fully webbed, outer metatarsal tubercle present,

Figure 82. Lateral (x 3) and dorsal (x 2) views  
of skull of Batrachophrynus macrostomus (KU 96127).



inner metatarsal tubercle not enlarged, digital tips narrow, first finger longer than second; (46) larvae with dextral vent, 2/3 tooth rows, labial papillae interrupted anteriorly; (49) adult brachydactylus are 47 - 58 mm. SVL and macrostomus grows to 160 mm. SVL; (50) tympanum absent.

Composition.-- Two species are recognized, brachydactylus and macrostomus.

Distribution.-- Lago de Junín region in central Peru.

Remarks.-- Batrachophrynus and Telmatobius are usually considered to be very closely related and were separated solely on the basis of the presence (Telmatobius) or absence (Batrachophrynus) of maxillary and prevomerine teeth. Four populations of Telmatobius lack maxillary teeth (brevipalmatus, edentatus, intermedius, and patagonicus). The palatal shelf is broad in Batrachophrynus and narrow in Telmatobius, the prevomers are small and edentate in Batrachophrynus but usually are moderate-sized to large and toothed in Telmatobius regardless of whether there are teeth on the maxillary arch, and the posterior edge of the tongue is not free in Batrachophrynus. The distinctions between Batrachophrynus and Telmatobius are difficult to assess at present because so few species have been studied. The aquatic Telmatobius bear greater resemblance



in external characters to Batrachophrynus than to the semiterrestrial species Telmatobius.

Alsodini Mivart, 1869

Alsodina Mivart, 1869:290.

Cacotina Mivart, 1869:290.

Batrachylinae Gallardo, 1965:83.

Four genera are included in this Neotropical tribe--Batrachyla, Eupsophus, Hylorina, and Thoropa. The distribution of the group is only slightly more extensive than that of the Telmatobiini, in that one genus (Thoropa) is found in the mountains of southeastern Brasil. Eupsophus and Hylorina are closely related as are Batrachyla and Thoropa. However, the two generic pairs share few significant characters. The cervical cotylar arrangement is type II in Eupsophus and Hylorina, whereas it is type I in Batrachyla and Thoropa. All four genera have frontoparietal fontanelles, vertebral columns in which the transverse processes of all vertebrae (except 1 and 2) are as long as the sacral diapophyses, and slightly dilated sacral diapophyses. All four genera have free swimming tadpoles. The tadpoles of Batrachyla differ from those of the other genera in having an uninterrupted series of labial papillae. The tadpoles of Thoropa are greatly flattened and attenuate (Fig. 2) in an adaptation to torrential stream life. Amplexus is

inguinal in Batrachyla, but is axillary in Eupsophus and Hylorina; the amplexic position is not known for Thoropa. Eupsophus and Hylorina lay numerous small eggs in water, whereas Batrachyla lays fewer larger eggs in terrestrial sites. The eggs of Batrachyla hatch and the larvae live in the jelly mass until the mass is inundated. Thoropa has large eggs which are deposited on wet stones in situations where water trickles over stone ledges (Myers, 1946). Werner C. A. Bokermann (pers. comm.) suggested that the eggs are laid on the banks of the torrential streams inhabited by Thoropa.

The following diagnostic characteristics are uniform among the four genera of the group: (3) transverse processes of posterior presacral vertebrae long; (5) cervical and second vertebrae not fused; (6) cranial bones not involved in dermostosis; (7) omosternum present, moderately large; (8) sacral diapophyses somewhat dilated-- see Fig. 79; (9) maxillary arch toothed, teeth blunt, pedicellate; (12) facial lobe of maxilla deep, not exostosed; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle moderate-sized; (19) frontoparietals not ornamented; (20) frontoparietal not fused with proötic; (21) temporal arcade lacking; (37) alary processes of hyoid plate on narrow stalks; (42) males with nuptial asperities on thumb and sometimes second finger; some species of Eupsophus have cluster of asperities

on chest; (45) outer metatarsal tubercle present, inner metatarsal tubercle not enlarged or spade-like; (46) larvae with median vent.

The tribal name, Alsodini, is based on Alsodes Bell, 1843, which was recently shown to be a synonym of Eupsophus (Lynch, 1968b). The heterogeneity of the tribe and the mosaic of primitive characteristics exhibited by the four included genera suggest that the Alsodini might be best regarded as a suprageneric grade between the primitive Telmatobiini and the advanced Eleutherodactylini.

Eupsophus Fitzinger, 1843

(Fig. 83)

Eupsophus Fitzinger, 1843, Syst. Rept., p. 31 [Type-species by original designation, Cystignathus roseus Duméril and Bibron, 1841].

Hammatodactylus Fitzinger, 1843, Syst. Rept., p. 31 [Type-species by original designation, Cystignathus nodosus Duméril and Bibron, 1841].

Borborocoetes Bell, 1843, Zool. Voy. Beagle, Reptiles, 5:34 [Type-species by present designation, Borborocoetes grayi Bell, 1843; preoccupied by Borborocoetes Schoenherr, 1842 (Insecta: Coleoptera)].

Alsodes Bell, 1843, Ibid., 5:34 [Type-species by monotypy, Alsodes monticola Bell, 1843].

Eusophus Cope, 1865, Rev. Nat. Hist., 5:113 [Emendation (?) of Eupsophus Fitzinger, 1843].

Borborocaetes Cope, 1866, J. Acad. Nat. Sci. Philadelphia, (2)6:94 [Emendation of Borborocoetes Bell, 1843, hence taking same type-species].

Cacotus Günther, 1868, Proc. Zool. Soc. London, 1868:482 [Type-species by monotypy, Cacotus maculatus Günther, 1868].

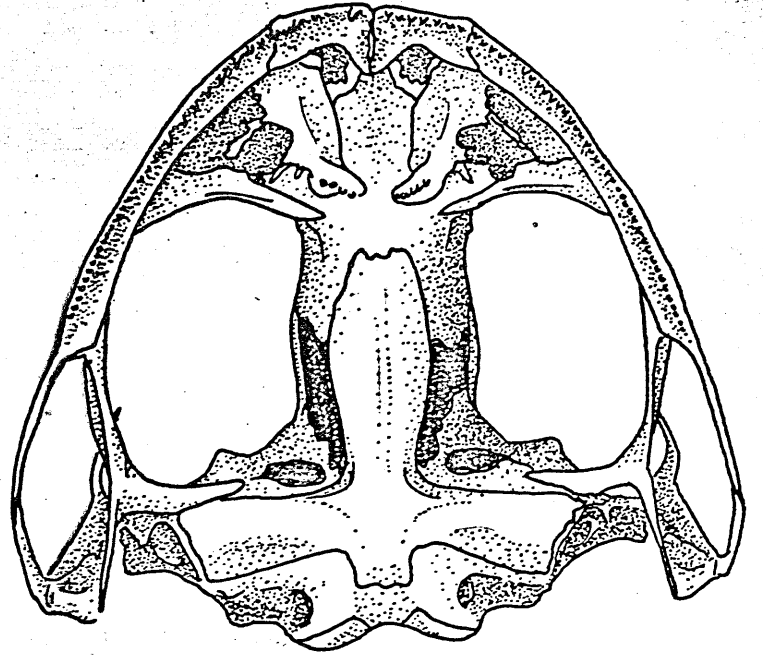
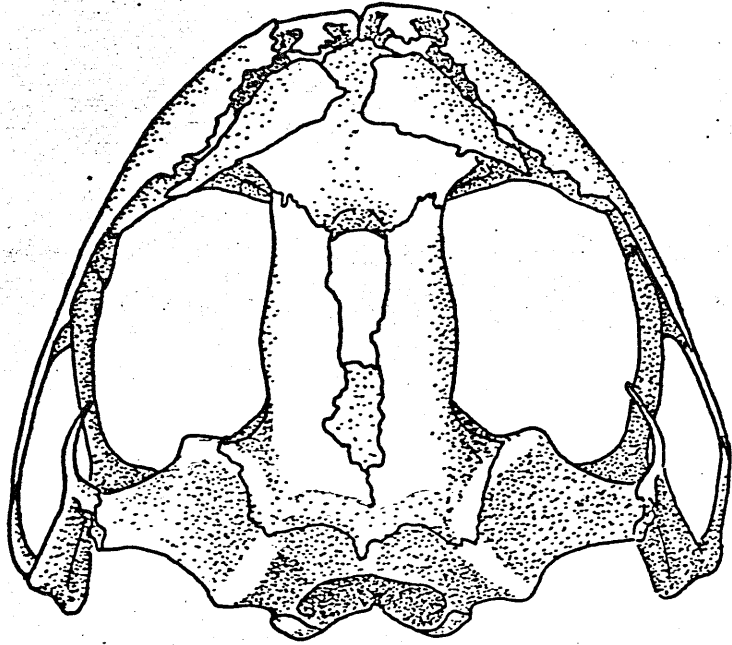
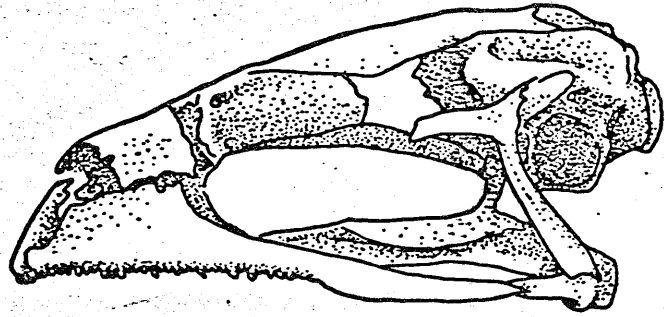
Phrynopus Peters, 1873, Mtber. k. Preuss. Akad. Wiss., Berlin, 1873:416 [Type-species by monotypy, Phrynopus peruanus Peters, 1873].

Borborocoetea Strand, 1928, Ark. Naturgesch., 92A:55 [Replacement name for Borborocoetes Bell, 1843 (preoccupied), hence taking same type-species].

Diagnostic definition.-- (4) cervical cotylar arrangement type II; (10) alary processes of premaxillae directed posterodorsally, moderately wide at base; (11) palatal shelf of premaxilla relatively deep, palatal process elongate; (13) palatal shelf of maxilla of moderate width, pterygoid process moderately large; (14) maxillary arch complete, quadratojugal present; (15) nasals small, widely separated medially; (16) nasals in broad contact with maxillae, not in contact with pterygoids; (22) epiotic eminences prominent; (23) cristae paroticae relatively broad, elongate; carotid artery passes dorsal

to skull bones; (24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; (25) otic ramus of squamosal as long as zygomatic ramus, expanded medially into small otic plate; (26) squamosal-maxillary angle  $50 - 55^{\circ}$ ; (27) columella present or absent; (28) prevomers moderate-sized, separated medially, entire, toothed except in juninensis; (29) palatines broad, widely separated medially, bearing odontoid ridges; (30) sphenethmoid entire, extending anteriorly to anterior edge of nasals; (31) anterior ramus of parasphenoid broad, short, keeled medially; (32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid, broadly overlapped laterally by median rami of pterygoids; (33) pterygoids moderate-sized, anterior rami in long contact with maxillae, reaching palatines; (34) occipital condyles large, not stalked, narrowly separated medially; (36) terminal phalanges knobbed; (40) m. depressor mandibulae in two slips except in juninensis which has only the pars tympanicus; (41) pupil horizontal; (42) males with median subgular vocal sac or none; (43) body lacking glands or having extensive, diffuse glandular areas over dorsum; (44) tongue large, round, posterior edge free; (45) toes lacking webbing or fringing to two-thirds webbed; (46) larvae with 2/3 tooth rows, labial papillae interrupted anteriorly; (47) amplexus axillary; (48) eggs small and numerous,

Figure 83. Lateral, dorsal, and ventral views  
of skull of Eupsophus roseus (AMNH 22104, x 7).



laid in gelatinous masses in ponds; (49) males 32 - 80, females 32 - 60 mm. SVL; (50) tympanum visible externally, concealed, or absent.

Composition.-- Revisionary studies of the Argentine and Chilean species are available (Cei, 1962a, Grandison, 1961, and Gallardo, 1962). As a result of these studies and my own (Lynch, 1969a), eight species of the genus are presently recognized: illotus, juninensis, monticola, nodosus, peruanus, roseus, septentrionalis, and vertebralis. The status of the genus in Peru is poorly known.

Distribution.-- The Andes of southern Ecuador to Argentina and Chile; between 4° and 50° S latitude in western South America.

Remarks.-- Boulenger (1882) combined a large number of genera and species into Borborocoetes Bell (= Eupsophus) in his synopsis of living amphibians. While most of his generic groupings were a vast improvement over the previous classifications, Borborocoetes was a notable exception. He included a variety of unrelated groups in Borborocoetes. The Borborocoetes of Boulenger and Noble is best described as a grade (in the sense of Huxley, 1958). All of the species included are members of the Telmatobiinae, and according to the present classification belong to the genera Batrachyla, Eleutherodactylus, Eupsophus, Ischnocnema, Niceforonia, Thoropa, and Zachaenus.



The Chilean and Argentine species of Eupsophus were studied in detail by Cei (1960, 1962a, and 1962b) and Grandison (1961), but they confused one species of Batrachyla with Eupsophus (taeniatus). Cei (1962a) and Grandison (1961) divided Eupsophus into three species groups--nodosus group, peruanus group, and roseus group. These authors also recognized a monotypic taeniatus group, which is here included in Batrachyla. Three species of the genus (juninensis, monticola, and septentrionalis) have lost the columella. These species also lack tympanic annuli. The tympanic annulus is very small in two other species of the genus, illotus and nodosus, and is concealed beneath the skin. In peruanus, roseus, and vertebralis, the columella is normal-sized and the tympanic annulus is visible externally.

Schaeffer (1949) described, but did not name, a fossil frog from the Lower Oligocene of Chubut, Argentina, and referred it to Eupsophus. The nasals of the fossil are apparently in median contact, unlike the condition seen in the living species of the genus. The fossil could equally well be a species of Telmatobius, were it not for the fact that the frontoparietal fontanelle is moderately large, not small. The middle ear was not preserved.

Hylorina Bell, 1843

(Fig. 84)

Hylorina Bell, 1843, Zool. Voy. Beagle, Reptiles, 5:44

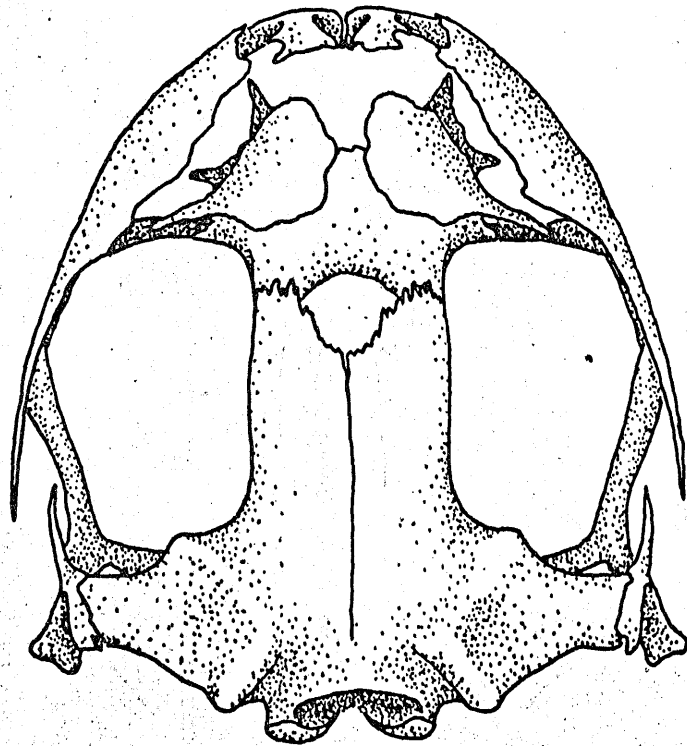
[Type-species by monotypy, Hylorina sylvatica Bell, 1843].

Hylorhina Agassiz, 1846, Nomencl. Zool., index:190

[Emendation of Hylorina Bell, 1843, hence taking same type-species].

Diagnostic definition.-- (4) cervical cotylar arrangement type II; (10) alary processes of premaxillae directed dorsally, wide at base; (11) palatal shelf of premaxilla narrow, palatal process relatively small; (13) palatal shelf of maxilla narrow, pterygoid process minute; (14) maxillary arch incomplete, quadratojugal absent, replaced by ligamentous sheath; (15) nasals moderate sized, widely separated medially; (16) nasals in tenuous contact with maxillae, not in contact with pterygoids; (22) epiotic eminences moderately well defined; (23) cristae paroticae short, stocky; carotid artery passes dorsal to skull bones; (24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; (25) otic ramus of squamosal moderately long, shorter than zygomatic ramus, expanded medially into small otic plate; (26) (27) columella present; (28) prevomers moderately large, entire, narrowly separated medially, toothed; (29) palatines broad, widely separated medially, no odontoid ridges; (30) sphenethmoid entire, extending anteriorly to middle of nasals; (31) anterior ramus of parasphenoid

Figure 84. Dorsal view of skull of Hylorina sylvatica (FMNH 7102, x 8) as interpreted from stereo-radiographs and limited dissection.



broad, short, not keeled medially; (32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; (33) pterygoids small, anterior rami short, extending to middle of orbit; (34) occipital condyles moderately large, not stalked, narrowly separated medially; (36) terminal phalanges knobbed, elongate; (40) m. depressor mandibulae in two slips; (41) pupil vertical; (42) males with median subgular vocal sac; (43) body with glandular dorsolateral folds; (44) tongue large, rounded, posterior edge free; (45) toes lacking webbing or lateral fringes, digital tips narrow, first finger longer than second; (46) larvae with 2/2 tooth rows, labial papillae interrupted anteriorly; (47) amplexus axillary; (48) eggs small, numerous, laid in gelatinous masses at bases of plants in water; (49) males 50 - 60, females 60 - 68 mm. SVL; (50) tympanum visible externally; (51) digits extremely long, phalangeal formulae not increased.

Composition.-- monotypic.

Distribution.-- Central Chile.

Remarks.-- Because Hylorina is uncommon, the genus was studied with the aid of stereo-radiographs. Hylorina has been considered generically distinct since Bell's description of the type-species. In part the distinction stemmed from erroneous data provided by Boulenger (1882), who reported the sternum as bony. The genus Hylorina is

very distinctive even though the sternum is a cartilaginous plate which tends to calcify in old adults. The combination of vertical pupil, free toes, greatly elongated digits, externally visible tympanum, and teeth on maxillary arch and prevomerine dentigerous processes immediately distinguishes Hylorina from all other frog genera. In spite of the distinctiveness of Hylorina, its skeletal morphology allies it with Eupsophus. The data on breeding biology reported by Barrio (1967b) provide additional distinction for Hylorina, but also point out the similarity between Eupsophus and Hylorina.

Batrachyla Bell, 1843

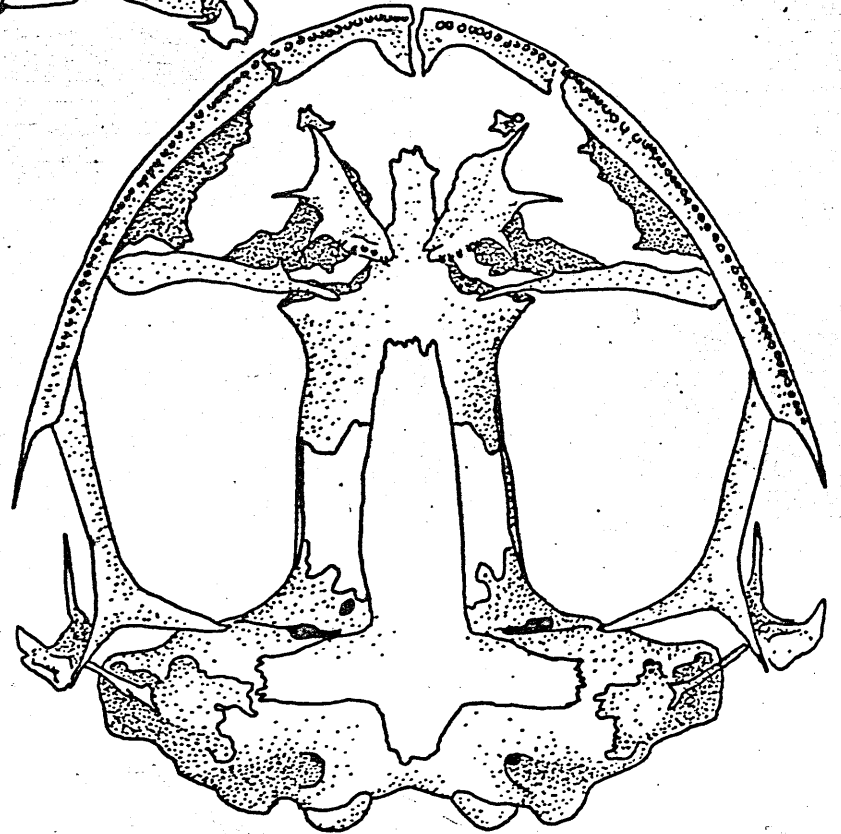
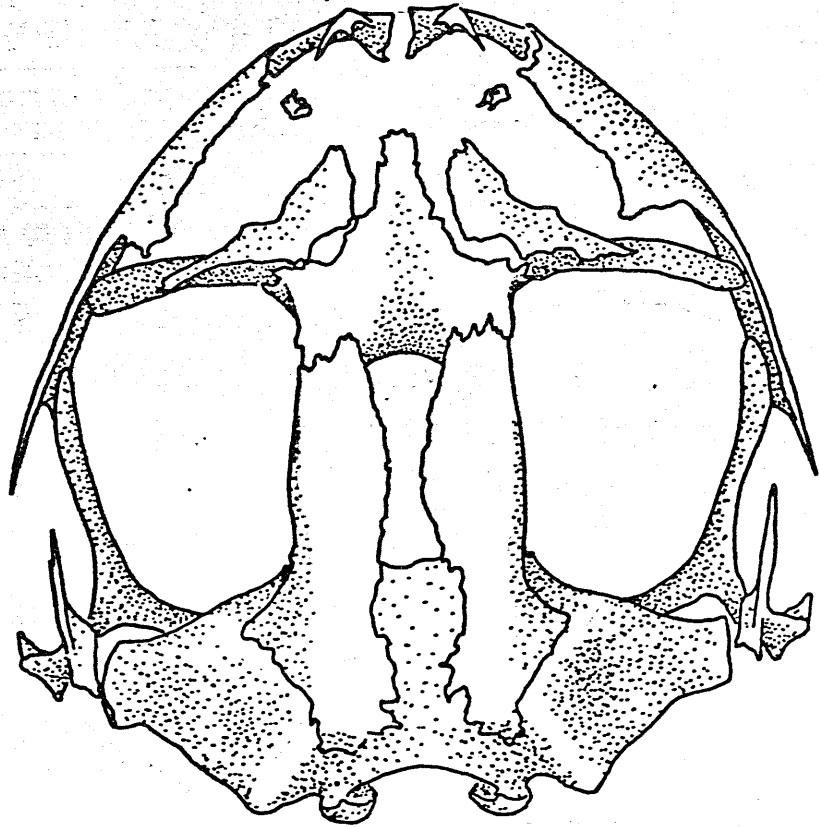
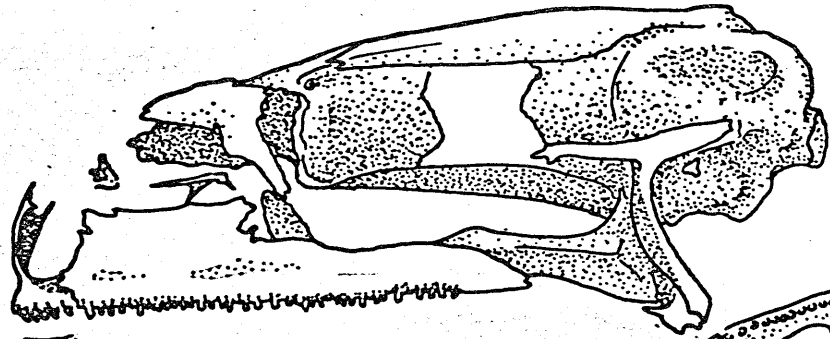
(Fig. 85)

Batrachyla Bell, 1843, Zool. Voy. Beagle, Reptiles, 5:43

[Type-species by monotypy, Batrachyla leptopus Bell, 1843].

Diagnostic definition.-- (4) cervical cotylar arrangement type I; (10) alary processes of premaxillae directed dorsally and somewhat laterally, moderately wide at base; (11) palatal shelf of premaxilla very narrow, palatal process relatively large; (13) palatal shelf of maxilla narrow, pterygoid process lacking; (14) maxillary arch incomplete, quadratojugal absent; (15) nasals widely separated medially, relatively small; (16) nasals separated from maxillae and pterygoids; (22) epiotic eminences

Figure 85. Lateral, dorsal, and ventral views of skull of Batrachyla leptopus (UMMZ S-2246, x 10).





obsolete; (23) cristae paroticae stocky, relatively long; carotid artery passes dorsal to skull bones; (24) zygomatic ramus of squamosal elongate, widely separated from maxilla; (25) otic ramus of squamosal moderately long, expanding medially into small otic plate; (26) squamosal-maxillary angle about  $60^{\circ}$ ; (27) columella present; (28) prevomers relatively small, entire, separated medially, toothed; (29) palatines curved, narrow, widely separated medially; (30) sphenethmoid entire, extending anteriorly to a point anterior to nasals; (31) anterior ramus of parasphenoid broad, short, lacking median keel; (32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid, not overlapped by median rami of pterygoids; (33) pterygoids small, thin, anterior rami short, not extending beyond middle of orbits; (34) occipital condyles small, not stalked, widely separated medially; (36) terminal phalanges T-shaped; (40) m. depressor mandibulae in two slips; (41) pupil horizontal; (42) males with median subgular vocal sac; (43) body lacking glands; (44) tongue moderately large, posterior one-third free; (45) toes lacking web or lateral fringes, digital tips bulbous, somewhat dilated, first finger shorter than second; (46) larvae with  $2/3$  tooth rows, labial papillae not interrupted about mouth; (47) amplexus inguinal; (48) eggs relatively few, large,

laid in terrestrial situations, tadpoles become aquatic after nest is inundated; (49) adults 27 - 40 mm. SVL; (50) tympanum visible externally.

Composition.-- Barrio (1967a) recognized two species (antartandica and leptopus) of Batrachyla. Lynch (1969a) demonstrated that Eupsophus taeniatus belongs to the genus Batrachyla.

Distribution.-- Chile and adjacent Argentina between 32° and 50° S latitude.

Remarks.-- Boulenger (1882) and Myers (1962) considered Batrachyla synonymous with Eleutherodactylus (Hylodes Fitzinger, 1843, in the case of Boulenger). Both authors were under the mistaken impression that the two genera did not differ in significant characters. The two differ as follows (the condition in Eleutherodactylus is enclosed in parentheses): quadratojugal absent (present), frontoparietal fontanelle present (absent), nasals small and widely separated medially (large and in median contact), sacral diapophyses dilated (rounded), males with nuptial asperities on thumb (lacking nuptial asperities), aquatic tadpoles (development direct--no tadpole stage), and amplexus inguinal (axillary). The breeding biology of Batrachyla is decidedly more primitive than that of Eleutherodactylus but approaches the condition of the latter in that the eggs are relatively large, few in number, and laid in moist terrestrial situations (Barrio,

1967a, and Cei, 1962a). In contrast to the eleutherodactyline pattern, tadpoles emerge when the egg hatches and development proceeds in the typical anuran manner.

Thoropa Cope, 1865

(Fig. 86)

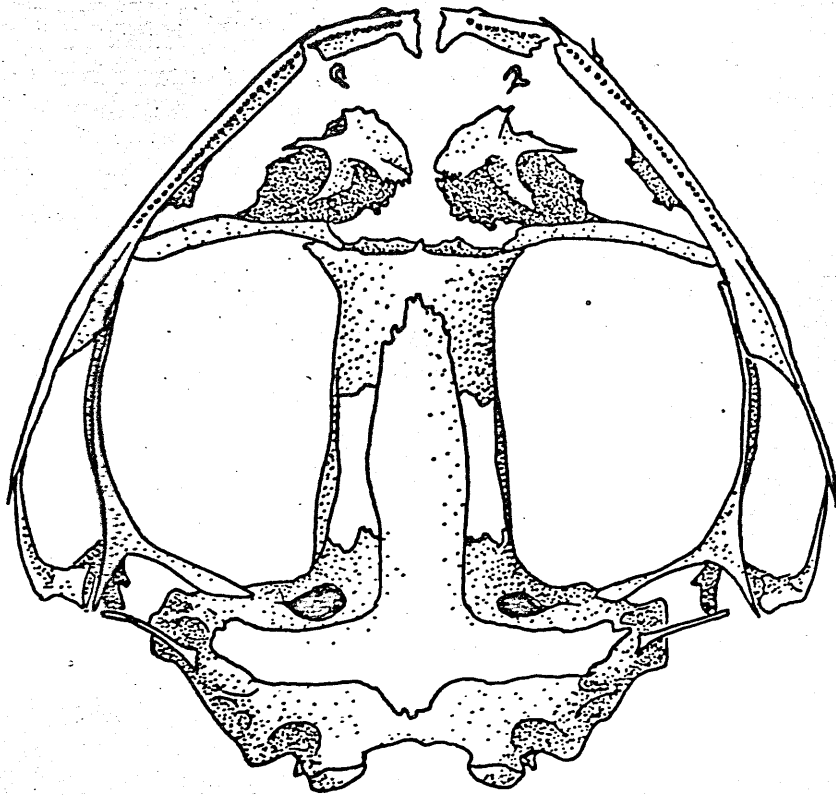
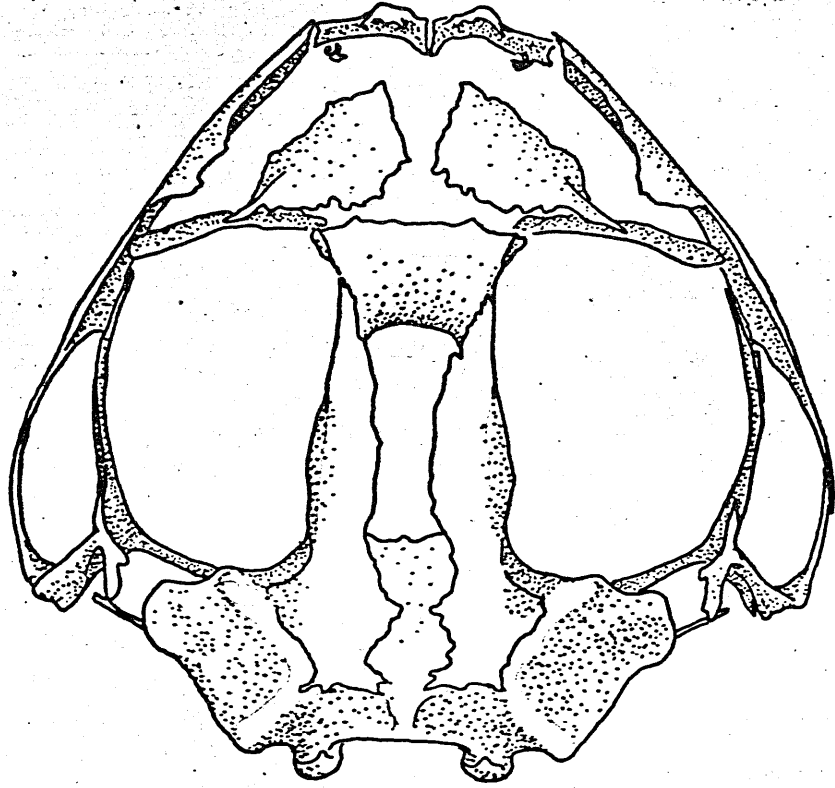
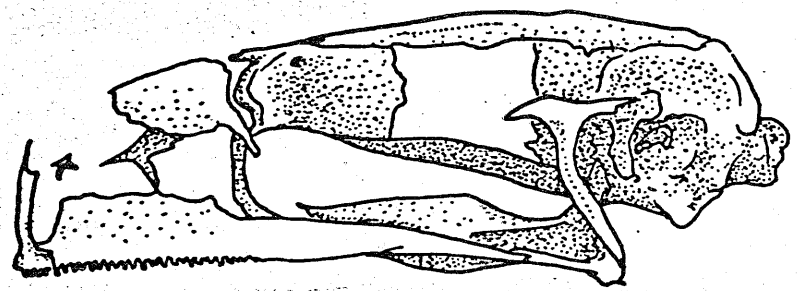
Thoropa Cope, 1865, Rev. Nat. Hist., 5:110 [Type-species by monotypy, Cystignathus missiessii Eydoux and Souleyet, 1842].

Ololygon Fitzinger (1843) is often cited as an older generic name for Thoropa. The type-species of Ololygon is Hyla strigilata Spix, 1824 (by original designation of Fitzinger, 1843). Therefore, Ololygon Fitzinger is a synonym of Hyla Laurenti, 1768.

Diagnostic definition.-- (4) cervical cotylar arrangement type I; (10) alary processes of premaxillae directed dorsally and slightly anteriorly, relatively narrow at base; (11) palatal shelf of premaxilla very narrow with elongate palatal process; (13) palatal shelf of maxilla broad, pterygoid process present; (14) maxillary arch complete, quadratojugal present; (15) nasals relatively large with moderately long maxillary processes, separated medially; (16) nasals not in contact with maxillae or pterygoids; (22) epiotic eminences relatively well defined; (23) cristae paroticae long and

narrow in miliaris, short and relatively stocky in lutzi and petropolitanus; carotid artery passes dorsal to skull bones; (24) zygomatic ramus of squamosal relatively short; (25) otic ramus of squamosal moderately long, no otic plate; (26) squamosal-maxillary angle 50 - 70°; (27) columella present; (28) prevomers relatively small, entire, separated medially, toothed; (29) palatines long and narrow, expanded laterally, separated medially; (30) sphenethmoid entire, extending anteriorly to posterior edge of nasals or not reaching nasals; (31) anterior ramus of parasphenoid broad, keeled medially, extending anteriorly to prevomers; (32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid, relatively short, not overlapped laterally by median rami of pterygoids; (33) pterygoids large, anterior rami in long contact with maxillae, not reaching palatines; (34) occipital condyles large in miliaris, small in lutzi and petropolitanus, not stalked, moderately to widely separated medially; (36) terminal phalanges T-shaped; (40) m. depressor mandibulae in two slips; (41) pupil horizontal; (42) males with median subgular vocal sac; (43) body lacking glands; (44) tongue large, oval, posterior edge free; (45) toes lacking webbing, bearing lateral fringes, digital tips bulbous, somewhat dilated, first finger shorter than second; (46) larvae with 2/3 tooth rows, labial papillae broadly interrupted anteriorly; (47) (48) eggs large, few in

Figure 86. Lateral, dorsal, and ventral views of skull of Thoropa lutzi (KU 92850, x 8).



number, laid in lotic situations; (49) males 19 - 78, females 24 - 70 mm. SVL; (50) tympanum visible externally; (51) tadpoles with greatly flattened and attenuate bodies and tails.

Composition.-- Three species were recognized in the revision by Bokermann (1965): lutzi, miliaris, and petropolitanus.

Distribution.-- Mountains of southeastern Brasil between 12° and 30° S latitude.

Remarks.-- Thoropa is least different from Batrachyla, although most authors have considered it inseparable from Eupsophus. Gallardo (1965) and Lynch (1969a) demonstrated the distinctiveness of these two genera. Lutz (1954) suggested that Thoropa was closely related to Cycloramphus. Thoropa and Cycloramphus belong to different tribes; this distinction is supported by osteological, non-osteological, and behavioral and larvae data.

#### Odontophrynini New Tribe

Two genera are included in this tribe--Odontophrynus and Proceratophrys. (the nominal genus Macrogenioglottus is inseparable from Odontophrynus). Proceratophrys is the generic name used herein for the group previously called Stombus. The members of this tribe bear considerable external resemblance to the Ceratophryinae, especially

Ceratophrys. The ilia of the Odontophrynini (Fig. 38) are nearly identical to those of the Ceratophryinae, but the two groups differ in many ways (see subfamily characters for Ceratophryinae and Telmatobiinae). The Odontophrynini are distributed in non-forested and some forested habitats in Argentina, Paraguay, Uruguay, and along the eastern edge of Brasil to Estado de Ceará. Like the other primitive Telmatobiinae, the Odontophrynini have an aquatic stage in the life history, and amplexus is axillary. The following diagnostic characteristics are the same in both genera: (3) transverse processes of posterior presacral vertebrae short; (5) cervical and second vertebrae free; (6) cranial bones not involved in dermostosis; (7) omosternum lacking; (9) maxillary arch toothed, teeth blunt, pedicellate; (11) palatal shelf of premaxilla broad, weakly notched, palatal process large; (12) facial lobe of maxilla deep; (14) maxillary arch complete; (16) nasals in contact with maxillae and pterygoids; (18) frontoparietal fontanelle lacking; (20) frontoparietals not fused with proötics; (21) temporal arcade lacking; (22) epiotic eminences prominent; (23) cristae paroticae long and narrow; carotid artery passes dorsal to skull bones; (27) columella present; (28) prevomers relatively small, entire, toothed, narrowly separated medially; (29) palatines large, narrowly separated medially, bearing odontoid ridge, expanded laterally; (30) sphenethmoid large, entire, extending



anteriorly to front edge of nasals; (31) anterior ramus of parasphenoid narrow, pointed, not keeled; (32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; (33) pterygoids large, anterior rami long, in broad sutural contact with maxillae, maxillary process of nasals, and palatines; (36) terminal phalanges knobbed; (37) alary processes of hyoid plate on narrow stalks; (40) m. depressor mandibulae in two slips; (41) pupil horizontal; (42) males with median, subgular vocal sac; (44) tongue large, round, posterior edge free; (46) larvae with median vent, 2/3 tooth rows, and labial papillae broadly interrupted anteriorly; (47) amplexus axillary; (48) eggs small, numerous, laid in gelatinous masses in ponds; (50) tympanum concealed.

The pectoral girdle is not as massive as in the Telmatobiini, and the omosternum has been lost in the Odontophrynini. The occipital condyles are more widely separated in Odontophrynus than in Proceratophrys (Figs. 87 - 88). The cervical cotylar pattern of both genera is type II, although the cotyles are more widely spaced in Odontophrynus (Fig. 79). In several character complexes, the Odontophrynini are intermediate between the Ceratophryinae and the Telmatobiini, but they also bear some resemblance to the Eleutherodactylini.

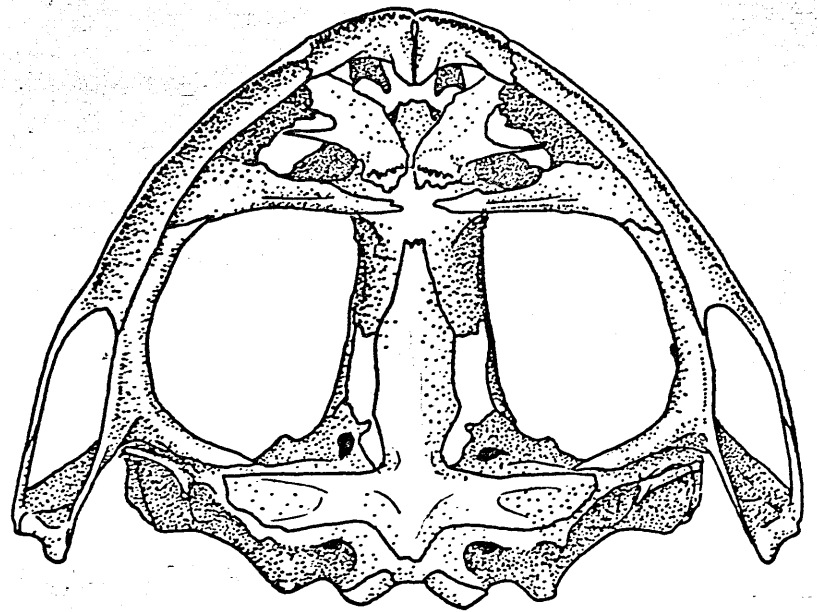
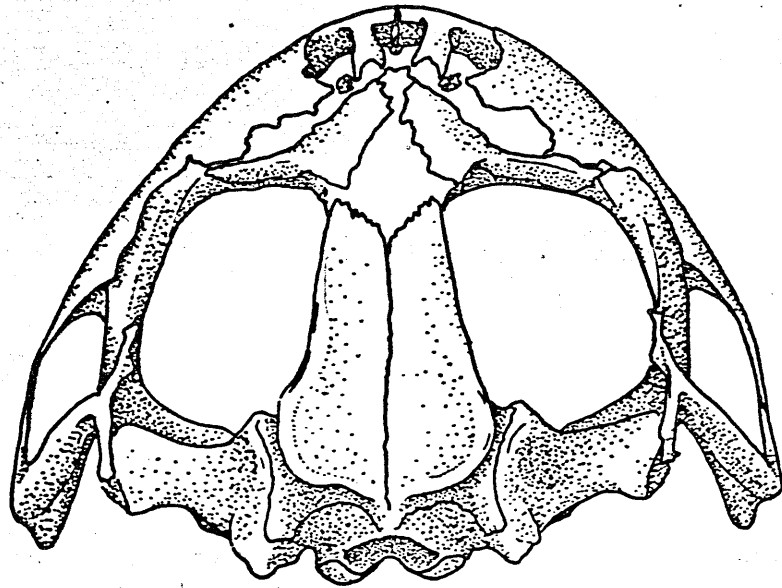
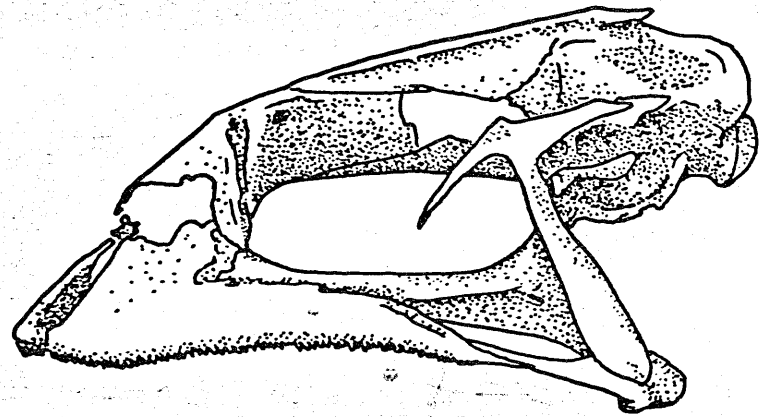
Odontophrynus Reinhardt and Lütken, 1862

(Fig. 87)

Odontophrynus Reinhardt and Lütken, 1862, Vid. Meddel.Naturh. Foren., 13:159 [Type-species by monotypy,  
Odontophrynus cultripes Reinhardt and Lütken, 1862].Macrogenioglottus Carvalho, 1946, Bol. Mus. Rio de  
Janeiro, (new ser.) 73:1 [Type-species by original  
designation, Macrogenioglottus alipioi Carvalho, 1946].

Diagnostic definition.-- (4) cervical cotylar arrangement type II, but cotyles well separated medially; (8) sacral diapophyses slightly dilated; (10) alary processes of premaxillae directed posterodorsally, long, relatively narrow at base; (13) palatal shelf of maxilla broad, pterygoid process small or lacking; (14) maxillae not expanded posteriorly; (15) nasals relatively large, keeled, narrowly separated anteriorly; (17) nasals not in contact with frontoparietals; (19) frontoparietals not ornamented except for ridge around posterior half of the braincase roof; (24) zygomatic ramus of squamosal long, tapering, widely separated from maxilla; (25) otic ramus of squamosal long, expanded medially into narrow otic plate; (26) squamosal-maxillary angle 50 - 55°; (34) occipital condyles large, not stalked, median separation moderate; (42) males with nuptial asperities on thumb; (43) parotoid and/or temporal or tibial glands present; (45) toes about one-half webbed, outer metatarsal tubercle

Figure 87. Lateral, dorsal, and ventral views of skull of Odontophrynus carvalhoi (KU 100441, x 5).



present, inner metatarsal tubercle enlarged and spade-like, digital tips narrow, relatively few supernumerary tubercles on plantar surface, first finger longer than second; (49) males 30 - 60, females 34 - 70 mm. SVL.

Composition.-- Savage and Cei (1965) recognized four species (americanus, carvalhoi, cultripes, and occidentalis). The type species of Macrogenioglottus, Odontophrynus alipioi (Carvalho) [new combination] is here added to the genus.

Distribution.-- Semi-arid and arid non-forested habitats of northern Argentina, southern Bolivia and Paraguay, Uruguay, and along the coastal provinces of southeastern and eastern Brasil to Bahía.

Remarks.-- Carvalho (1946) named Macrogenioglottus alipioi on the basis of two specimens from Bahía, Brasil. The genus was distinguished from all others on the basis of the greatly enlarged m. genioglottus, slightly dilated sacral diapophyses, short coccyx, and slightly different positions of the prevomerine dentigerous processes. The myological distinction between Macrogenioglottus and Odontophrynus remains valid, but with the description of O. carvalhoi (Savage and Cei, 1965), the other differences between the two genera were mitigated. The architecture of the temporal region of alipioi was figured by Limeses (1965) and is like that of other species of Odontophrynus. Savage and Cei (1965) recognized two groups in

Odontophrynus, one for cultripes and occidentalis, and another for americanus and carvalhoi. Odontophrynus alipioi belongs to the latter group and seems closely related to carvalhoi. The two species share many characteristics but differ (insofar as is known at present) in some body proportions, color pattern, and colors in life.

Odontophrynus alipioi has been collected recently near São Paulo (W. C. A. Bokermann, pers. comm.).

Boulenger (1882) confused Odontophrynus with Ceratophrys, Lepidobatrachus, and Proceratophrys. The ceratophryine leptodactylids are readily separated from the two telmatobiline genera in that the derm of the head is fused with the skull bones and a dermostosed vertebral shield is present in the Ceratophryinae. In addition, the Ceratophryinae have non-pedicellate teeth whereas all other leptodactylids (if dentate) have pedicellate teeth. Odontophrynus and Proceratophrys, especially those of the bigibbosa group, are somewhat difficult to separate on external characters alone. The thenar surfaces of Proceratophrys are covered with numerous conical supernumerary tubercles, whereas the thenar surfaces of Odontophrynus lack supernumerary tubercles or have relatively few, non-conical supernumerary tubercles. Some, but not all, species of Odontophrynus have body glands (parotoid, temporal, or tibial), whereas no species of Proceratophrys has glands. Osteologically, the two genera

are readily separated. Proceratophrys has a complete post-orbital bridge (squamosal only), and Odontophrynus has a "normal" squamosal. Proceratophrys has extensive exostosis of the frontoparietal bones and Odontophrynus has no exostosis of the frontoparietals but does have a ridge around the posterior half of the frontoparietal shelf.

Proceratophrys Miranda-Ribeiro, 1920

(Fig. 88)

Proceratophrys Miranda-Ribeiro, 1920, Rev. Mus. Paulista

12:301 [Type-species by monotypy, Ceratophrys bigibbosa Peters, 1872].

Diagnostic definition.-- (4) cervical cotylar arrangement type II, cotyles closely approximated; (8) sacral diapophyses rounded; (10) alary processes of premaxillae long, strongly directed posterodorsally, except in bigibbosa group, relatively narrow at base; (13) palatal shelf of maxilla broad, pterygoid process prominent; (14) maxillae slightly expanded posteriorly; (15) nasals relatively narrow, keeled, separated medially (boiei group) or in contact (bigibbosa group) medially; (17) nasals in contact with frontoparietals; (19) frontoparietals bear lateral crests which meet posteriorly; frontoparietal crests are heavily exostosed posteriorly in oristiceps and probably in bigibbosa; (24) zygomatic ramus of squamosal broad and

elongate, in sutural contact with maxilla, weakly exostosed; (25) otic ramus of squamosal large, exostosed, expanded medially into relatively large otic plate; (26) squamosal-maxillary angle  $40 - 50^{\circ}$ ; (34) occipital condyles large, not stalked, closely juxtaposed; (42) males lacking nuptial asperities on thumb; (43) body lacking glands; (45) toes free of webbing, usually with lateral fringes, outer metatarsal tubercle present, inner metatarsal tubercle small or enlarged and spade-like, digital tips narrow, numerous conical supernumerary thenar and plantar tubercles, first finger longer than second; (49) adults 30 - 95 mm. SVL.

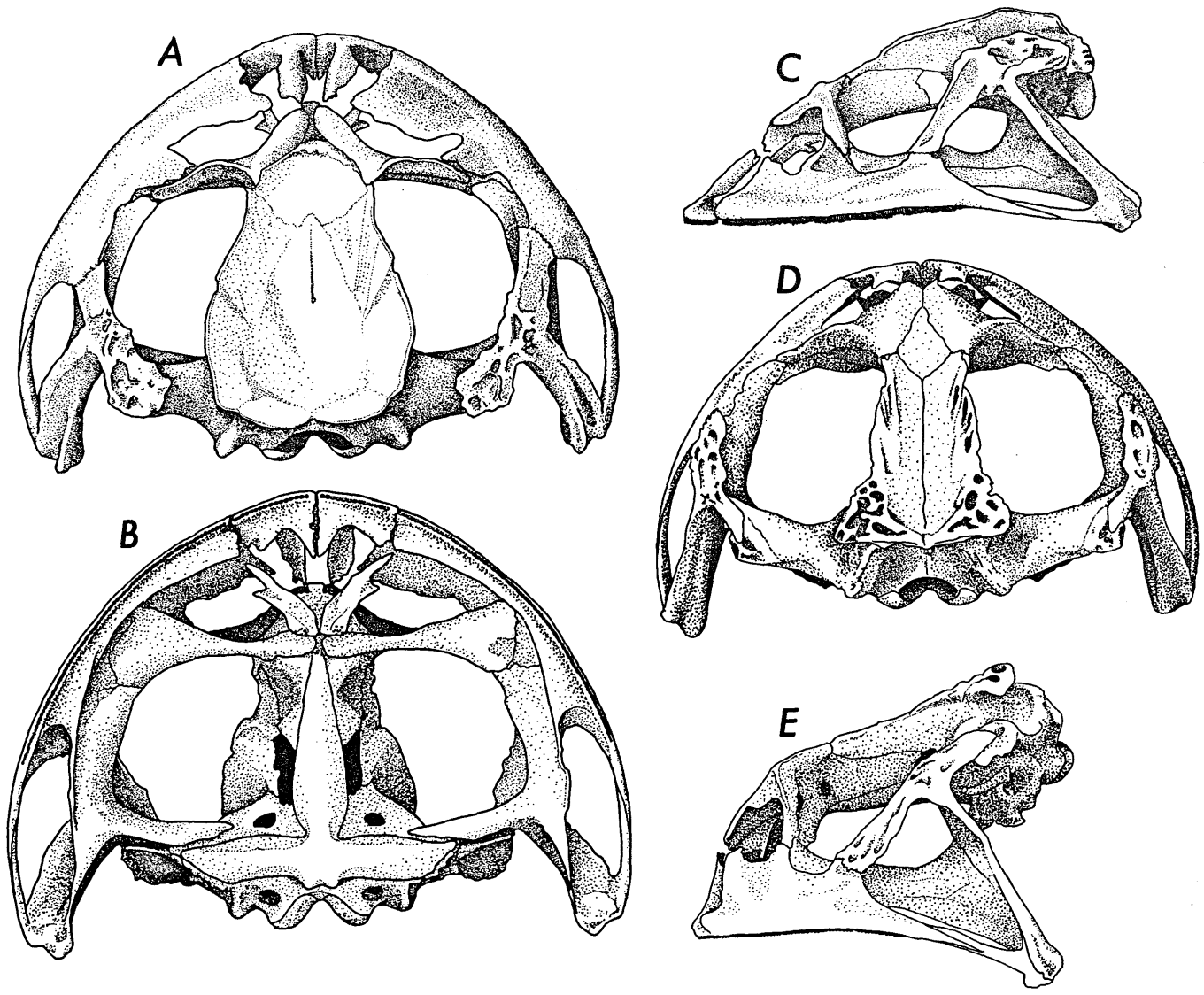
Composition.-- Eight of the nominal species listed as Ceratophrys by Gorham (1966) belong to this genus: appendiculata, bigibbosa, boiei, cristiceps, fryi, goyanus, renalis, and schirchi. Gorham (1966) did not list Stombus melanopogon Miranda-Ribeiro, 1926. Bokermann (1966) considered boiei, melanopogon, renalis, and schirchi synonymous and used boiei, the oldest name. He also considered goyanus a synonym of cristiceps.

Distribution.-- The lowland zone east of the Brazilian Highlands from Fortaleza (Ceará) to Santa Catarina, Brasil, and adjacent Misiones Province, Argentina.

Remarks.-- Almost all of the literature pertaining to species of this genus has accumulated under the generic name Stombus, a synonym of Ceratophrys (see pp. 376-78).



Figure 88. (A-C) Dorsal, ventral and lateral views of skull of Proceratophrys boiei (KU 93076) and (D-E) dorsal and lateral views of skull of P. cristiceps (KU 106273). All x 3.



Reig and his students have consistently argued that Stombus (auctorum) is generically distinct, but they have also repeatedly questioned the generic position of cristiceps. I include cristiceps in the genus Proceratophrys and consider bigibbosa its closest relative; this arrangement is similar to that used by Reig in that cristiceps is not considered especially closely related to appendiculata, boiei, and fryi. The differences between bigibbosa and cristiceps on the one hand, and appendiculata, boiei, and fryi on the other, are not of the magnitude I would use at the generic level. The five species form a group on the basis of the thenar and plantar tubercle arrangement, body shape, and the architecture of the temporal region. The two species groups differ in head shape and the correlated and underlying cranial architecture (snout is elongate and sloping in boiei group, blunt and short in bigibbosa group) and in the development of cranial exostosis (Fig. 88). The differences in musculature that Limeses (1964, 1965) cited as suggestive of separate genera are trivial differences; greater ranges of variation occur within Odontophrynus and several other frog genera. The species of the bigibbosa group are less unlike Odontophrynus in external features than are the species of the boiei group. In the boiei group, the eyelids are provided with elongate "horns", whereas in the bigibbosa group, the eyelid has only a few large tubercles.

## Grypiscini Mivart, 1869

Grypiscina Mivart, 1869:295.

Cyclorhamphinae Lutz, 1954:175.

Cycloramphiinae: Gallardo, 1965:84.

Three genera are included in this tribe--

Crossodactylodes, Cycloramphus, and Zachaenus. The nominal genus Craspedoglossa is here considered to be a synonym of Zachaenus. The tribe name is based on Grypiscus Cope, a synonym of Cycloramphus Tschudi. At first glance, this group seems to be highly heterogeneous, especially when one considers the supposed relationships of the leptodactylid genera as recognized by herpetologists in the 1910 - 1930 period when the following genera (all of this group) were recognized: Craspedoglossa, Cycloramphus, Grypiscus, Iliodiscus, Oocormus, and Zachaenus.

Miranda-Ribeiro (1926), Lutz (1954), and Cochran (1955) considered Zachaenus to be closely related to Geratophrys. Oocormus was often recognized even by Lutz after she pointed out that it was a synonym of Zachaenus (1944).

Various authors including Noble (1931) suggested that Cycloramphus was closely related to Telmatobius. Cycloramphus, Iliodiscus, and Grypiscus were usually considered valid until Bokermann (1951) pointed out that they were not generically distinct. Lutz (1954) included only Cyclorhamphus (sic) and Thoropa in the subfamily, Lutz and Carvalho (1958) considered Paratelmatobius to be a

generic link between Cycloramphus and Batrachophrynus and Telmatobius, and Gallardo (1965) placed Craspedoglossus (sic), Cycloramphus, Holoaden, and Zachaenus in the subfamily Cycloramphiinae. All of these authors used labile characters (head shape and toe webbing) to define their groupings. Most of the genera that have been considered related to Cycloramphus are burrowing frogs and have long, flat snouts.

The following diagnostic characteristics are the same in the included genera: (3) transverse processes of posterior presacral vertebrae not shortened; (4) cervical cotylar arrangement type I; (5) cervical and second vertebrae free; (6) cranial bones not involved in dermostosis; (9) maxillary arch toothed, teeth blunt, pedicellate; (12) facial lobe of maxilla deep, not exostosed; (14) maxillary arch complete, maxilla expanded posteriorly, quadratojugal deep; (15) nasals relatively large, in broad median contact; (17) nasals in contact with frontoparietals; (18) frontoparietal fontanelle lacking; (20) frontoparietal not fused to proötic; (21) temporal arcade lacking; (23) cristae paroticae very short, stocky; carotid artery passes dorsal to skull bones; (24) zygomatic ramus of squamosal attenuate, curved, widely separated from maxilla; (25) otic ramus of squamosal long, curved medially and expanded medially to form otic plate which rests on crista parotica; (34) occipital

condyles relatively small, not stalked, widely separated medially; (37) alary processes of hyoid plate on narrow stalks; (40) m. depressor mandibulae in two slips; (41) pupil horizontal; (47) amplexus axillary.

The developmental pattern of Cycloramphus and Zachaenus is intermediate between the typical pattern of an aquatic tadpole and the eleutherodactyline pattern of direct development (Lutz, 1944). The eggs are deposited in terrestrial situations (usually in very wet leaves on the forest floor) and the tadpole hatches and lives in the moist, decomposing gelatinous mass. The tadpoles can survive in an aquatic medium but do not feed (Lutz, 1944). Crossodactylodes lays only a few large eggs in bromeliads and the tadpole develops in the moist axillae of the bromeliads (W. O. A. Bokermann, pers. comm.).

Holoaden, Paratelmatoobius, and Thoropa do not agree with the diagnostic characteristics listed above and are included in other groups; Holoaden is in the Eleutherodactylini, Paratelmatoobius in the Leptodactylinae, and Thoropa in the Alsodini.

The three genera of the tribe occur in forested mountane areas in southeastern Brasil and Uruguay. Two of the species presently placed in Zachaenus (roseus and sawayae) are not members of that genus. Their status is discussed in the account of Zachaenus.

Crossodactylodes Cochran, 1938

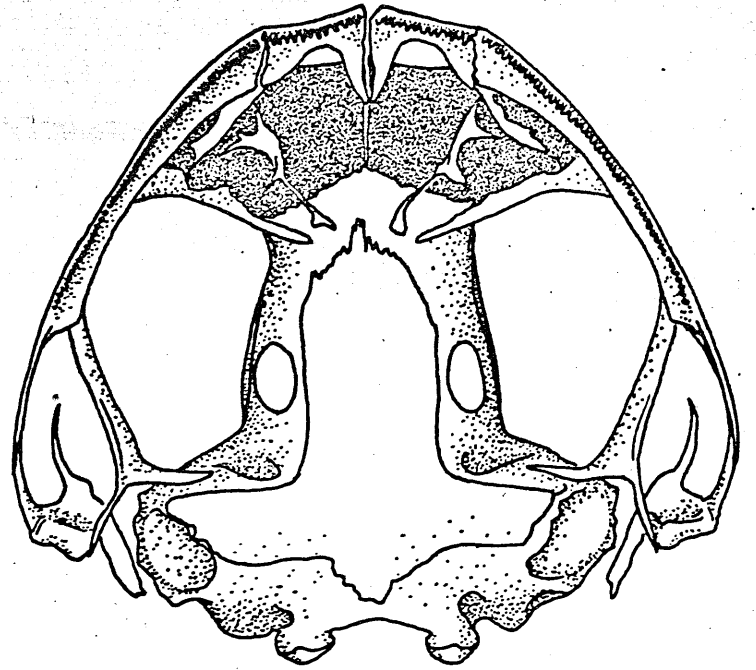
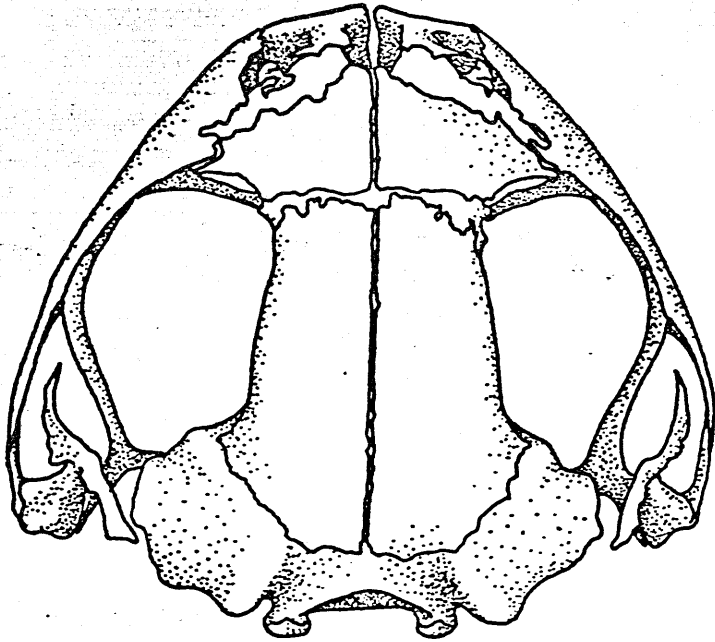
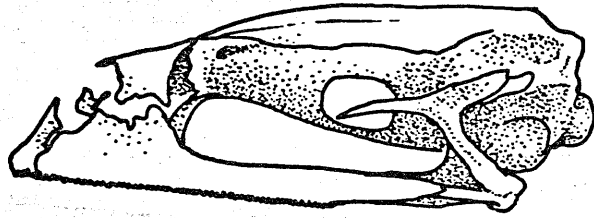
(Fig. 89)

Crossodactylodes Cochran, 1938, Proc. Biol. Soc. Washington, 51:41 [Type-species by original designation, Crossodactylodes pintoi Cochran, 1938].

Diagnostic definition.-- (7) omosternum relatively small; (8) sacral diapophyses dilated; (10) alary processes of premaxillae directed posterodorsally, broad at base; (11) palatal shelf of premaxilla relatively broad, broadest laterally, with long palatal process; (13) palatal shelf of maxilla broad anteriorly, narrow over most of its length, pterygoid process lacking; (16) nasals in tenuous contact with maxillae, not in contact with pterygoids; (17) nasals in tenuous contact with frontoparietals, narrowly separated from frontoparietals; (19) frontoparietals not ornamented, lacking sagittal crest; (22) epiotic eminences obsolete; (26) squamosal-maxillary angle about  $45^{\circ}$ ; (27) columella absent; (28) prevomers small, edentate, dentigerous rami almost completely lost, widely separated medially; (29) palatines narrow, widely separated medially, lacking odontoid ridges; (30) sphenethmoid entire, extending anteriorly beneath nasals; (31) anterior ramus of parasphenoid broad, not keeled; (32) parasphenoid alae oriented at right angles to anterior ramus, narrowly overlapped laterally by median rami of pterygoids; (33) pterygoids relatively small,

Figure 89. Lateral, dorsal, and ventral views of skull of Crossodactylodes pinto (paratype, USNM 120611, x 13).





anterior rami extending to middle of orbit, ventral pterygoid flange small; (36) terminal phalanges Y-shaped, lateral processes long and slender; (37 - 39) (42) males with median subgular vocal sac; males with cluster of spines on thumb; (43) body lacking glands; (44) tongue oval, posterior one-third free, non-boletoid; (45) toes not webbed, lacking lateral fringes, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged and spade-like, digital tips enlarged into pads, first finger shorter than second; (46) tadpoles semi-aquatic; (48) eggs large, few in number, deposited in terrestrial bromeliads; (49) males 15 - 17.5 mm. SVL; (50) tympanum absent (not hidden as stated by Cochran, 1938, 1955).

Composition.-- monotypic.

Distribution.-- The Coastal Ranges of Guanabara and Espírito Santo, Brasil.

Remarks.-- Cochran (1938, 1955) considered Crossodactylodes to be related to Crossodactylus (Elosiinae). She based her opinion on the presence of a cluster of spines on the thumbs of the males of both genera and the erroneous opinion that both genera have dermal glands on the top of each digital pad. Cochran noted that when the digital tips of Crossodactylodes were dried out, a weak furrow appeared in the center of the digital pad; she considered this condition a precursor of the condition

seen in elosines (distinct dermal glandular pads). The apparent glands observed by Cochran are an artifact resulting from the presence of Y-shaped terminal phalanges. Cochran pointed out that the two genera shared the loss of prevomerine teeth; the prevomerine bones are much smaller in Crossodactylodes than in Crossodactylus, which usually has larger prevomerine dentigerous processes and rarely prevomerine teeth.

The architecture of the temporal region and the size of the roofing bones of Crossodactylodes are like the condition seen in Cycloramphus and Zachaenus. The other cranial characters of Crossodactylodes are not contrary to the conditions which obtain in Cycloramphus and Zachaenus, although Crossodactylodes is separable from these two genera by many skull characters. The data on breeding biology were provided by Werner Bokermann (in litt.) and suggest that Crossodactylodes is more closely related to Cycloramphus and Zachaenus than to the Eleutherodactylini, which it resembles in many osteological features.

Cycloramphus Tschudi, 1838

(Fig. 90)

Cycloramphus Tschudi, 1838, *Classif. Batr.*, p. 81

[Type-species by monotypy, Cycloramphus fuliginosus Tschudi, 1838].

Cyclorhamphus Agassiz, 1846, *Nomencl. Zool.*, index, p. 110

[Emendation of Cycloramphus Tschudi, 1838, hence taking same type-species].

Pithecoposis Günther, 1859, Cat. Bat. Sal. British Mus., p. 22 [Type-species by monotypy, Pithecoposis fuliginosus (Tschudi, 1838)].

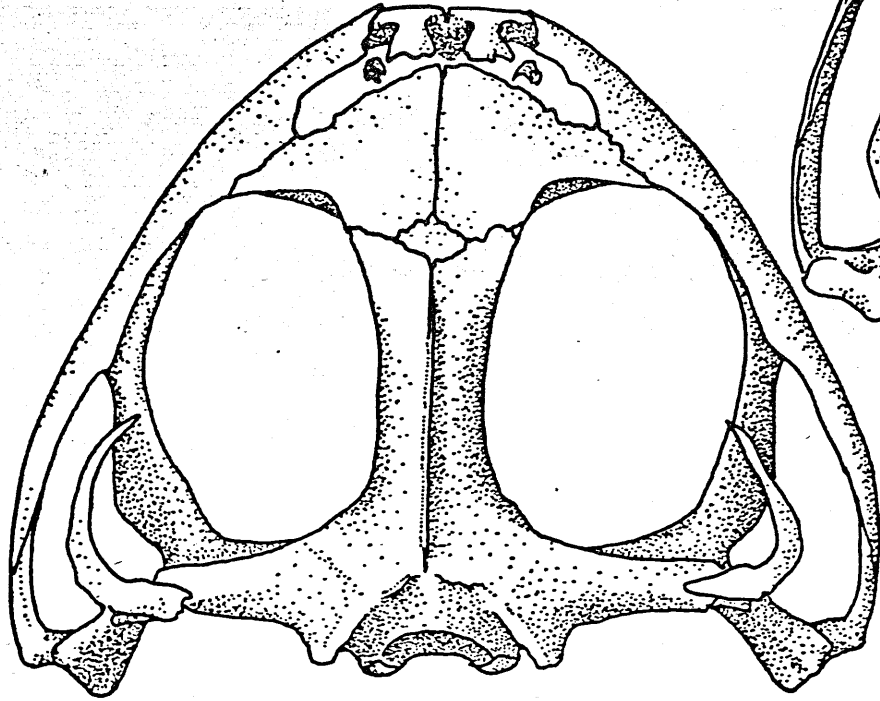
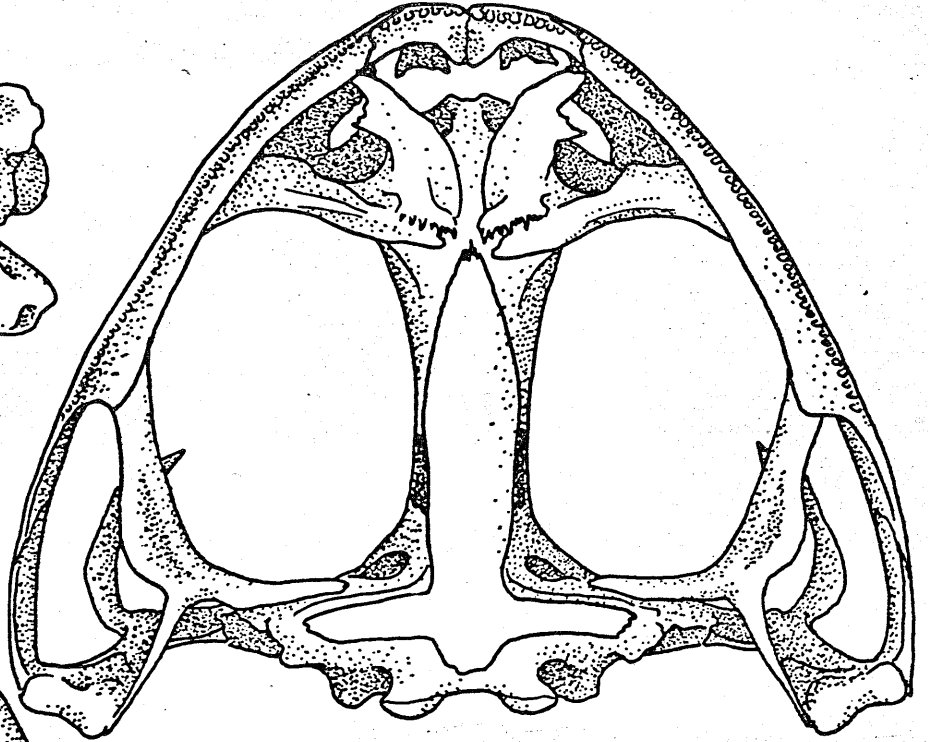
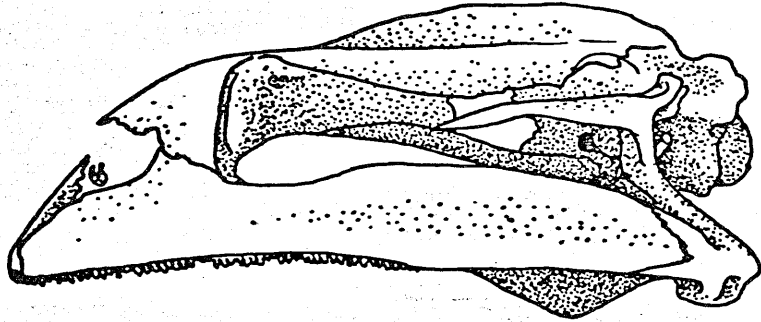
Grypiscus Cope, 1867, J. Acad. Nat. Sci. Philadelphia, (2) 6:206 [Type-species by monotypy, Grypiscus umbrinus Cope, 1867].

Iliodiscus Miranda-Ribeiro, 1920, Rev. Mus. Paulista, 12:267 [Type-species by subsequent designation (Bokermann, 1951), Telmatobius brasiliensis Steindachner, 1864; his designation is hereby rejected (see "Remarks") and the type-species is here designated as Iliodiscus dubius Miranda-Ribeiro, 1920].

Niedenis Ahl, 1923, Zool. Anz., 58:107 [Type-species by monotypy, Niedenis spinulifer Ahl, 1923].

Diagnostic definition.-- (7) omosternum moderate-sized; (8) sacral diapophyses rounded to very slightly dilated; (10) alary processes of premaxillae directed posterodorsally, relatively broad at base; (11) palatal shelf of premaxilla of moderate depth, not notched, palatal process short; (13) palatal shelf of maxilla relatively narrow, pterygoid process large; (16) nasals in contact with maxillae, not with pterygoids; (19) frontoparietals not ornamented, bearing large sagittal crest; (22) epiotic eminences prominent posteriorly, obsolete anteriorly; (26)

Figure 90. Lateral, dorsal, and ventral views of skull of Cycloramphus eleutherodactylus (KU 92785, x 6).



squamosal-maxillary angle less than  $43^{\circ}$ , measurement difficult because of curvature of both elements; (27) columella present; (28) prevomers present, entire, moderately large, toothed, separated medially; (29) palatines broad, widely separated medially, bearing small odontoid ridges; (30) sphenethmoid entire, extending anteriorly beneath nasals, not visible dorsally or only a small area visible between junctions of nasals and frontoparietals; (31) anterior ramus of parasphenoid broad, not keeled; (32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped by median rami of pterygoids; (33) pterygoids relatively small, anterior rami extending to middle of orbit, pterygoids bearing large ventral flange--cf. Fig. 25; (36) terminal phalanges knobbed; (42) males with median subgular vocal sac; males lacking nuptial asperities except for C. ohausi which has a cluster of spines on each thumb; (43) inguinal glands present; (44) tongue large, round, semi-boletoid; (45) toes free of webbing, bearing lateral fringes, or partly to fully webbed, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged and spade-like, digital tips narrow, first finger not longer than second; (46) larvae with very brief tadpole stage, semi-aquatic, vent median, 1/1 tooth rows, labial papillae broadly interrupted anteriorly; (48) eggs laid in moist terrestrial situations, hatch near end of larval period, eggs large, few in number (Lutz, 1929); (49) adults

30 - 55 mm. SVL; (50) tympanum concealed.

Composition.-- Seven to nine species are recognized depending on the author. Gorham (1966) listed eight species--asper, diringshofeni, eleutherodactylus, fuliginosus, granulosus, neglectus, ohausi, and umbrinus, whereas Bokermann (1966) recognized boulengeri, dubius, and pinderi as valid (which Gorham considered synonyms of other names) and placed umbrinus in the synonymy of fuliginosus. The most recent revision of the genus is that of Bokermann (1951), although Cochran (1955) studied a large part of the genus. In view of the differences of opinion as to how many, and which, species are valid, a thorough generic review is desirable.

Distribution.-- Forested habitats in southeastern Brasil.

Remarks.-- Within comparatively recent times (Miranda-Ribeiro, 1926, Noble, 1931), the genus Cycloramphus was divided into three genera (Cycloramphus, Grypiscus, and Iliodiscus). Bokermann (1951) and Cochran (1955) combined the three into a single genus. Cochran (1955) suggested that the genus is heterogeneous because C. ohausi mitigates some of the differences between Ceratophrys, Cycloramphus, and Crossodactylus. Her statements reflect a philosophy of single-character classification and do not accurately indicate the homogeneity of the genus Cycloramphus.



The generic partitioning of Cycloramphus was based on the variation in webbing of the toes and Cope's argument that the presence of pseudoteeth on the lower jaw of umbrinus justified generic distinction. I have not observed odontoids on the lower jaw of any species of the genus, although Noble (1922) figured a serrate lower jaw of a cotype of umbrinus. Six species of the genus (asper, diringshoefensi, dubius, eleutherodactylus, granulosus, and pinderi) lack webbing or lateral fringes on the toes; three species (boulengeri, fuliginosus, and neglectus) have one-half to fully webbed toes. The two groups are bridged by ohausi which has basal webbing and lateral fringes on the toes. The basal webbing probably is best regarded as the broadened junction of the fringes. I consider the lack of webbing to be primitive, because the allied Zachaenus lacks webbing.

Bokermann (1951) designated Telmatobius brasiliensis Steindachner (= Cycloramphus fuliginosus) as the type-species of Iliodiscus Miranda-Ribeiro, 1920. This action rendered Iliodiscus a strict synonym of Cycloramphus. However, Miranda-Ribeiro (1920) placed the webless species of Cycloramphus in Iliodiscus; Telmatobius brasiliensis was included in Cycloramphus, not Iliodiscus, and therefore cannot be considered for subsequent designation as the type-species of Iliodiscus. Accordingly, Bokermann's (1951) restriction is hereby rejected. Miranda-Ribeiro

(1920) included four nominal species in Iliodiscus (dubius, eleutherodactylus, pinderi, and semipalmatus). Gorham (1966) listed dubius as the type-species. I designate I. dubius Miranda-Ribeiro, 1920, as the type-species of Iliodiscus Miranda-Ribeiro, 1920.

Zachaenus Cope, 1866

(Figs. 91-93)

Zachaenus Cope, 1866, J. Acad. Nat. Sci. Philadelphia, 6:94 [Type-species by original designation, Cystignathus parvulus Girard, 1854].

Oocormus Boulenger, 1905, Ann. Mag. Nat. Hist., (7)16:181 [Type-species by monotypy, Oocormus microps Boulenger, 1905].

Craspedoglossa L. Müller, 1922, Blatter Aquar. Terr., 33:167 [Type-species by monotypy, Craspedoglossa sanctaecatharinae L. Müller, 1922].

Diagnostic definition.-- (7) omosternum relatively large; (8) sacral diapophyses rounded; (10) alary processes of premaxillae directed sharply posterodorsally, relatively broad at base; (11) palatal shelf of maxilla relatively deep, not notched, palatal process moderate-sized; (13) palatal shelf of maxilla of moderate width, pterygoid process lacking; (16) nasals in contact with maxillae, not with pterygoids; (19) frontoparietals not ornamented except for prominent sagittal crest and supraorbital processes; (22) epiotic eminences obsolete; (26)

squamosal-maxillary angle about  $45^{\circ}$ ; (27) columella present; (28) prevomers relatively large, entire, toothed, narrowly separated medially; (29) palatines slender, widely separated medially, no odontoid ridges; (30) sphenethmoid entire, usually not visible dorsally; (31) anterior ramus of parasphenoid narrow, not keeled; (32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; (33) pterygoids relatively small, anterior rami extending to middle of orbit, large ventral flange; (36) terminal phalanges knobbed; (42) males with median subgular vocal sac; males lacking nuptial asperities; (43) body lacking glands; (44) tongue round, semi-boletoid; (45) toes lacking webbing and lateral fringes, outer metatarsal tubercle present, inner metatarsal tubercle enlarged, not spade-like, digital tips narrow, first finger as long as second; (46) development abbreviated, tadpole semi-aquatic, vent median, 1/1 tooth rows, labial papillae broadly interrupted anteriorly (Lutz, 1944); (48) eggs large, few in number, deposited in moist, terrestrial situation, larvae hatch and remain in gelatinous mass until metamorphosis; (49) adults less than 30 mm. SVL; (50) tympanum concealed.

Composition.-- The nominal species of Craspedoglossa (bolitoglossa, sanctaecatharinae, and stejnegeri) and of Zachaeus (parvulus, roseus, and sawayae). Bokermann (1966)

Figure 91. Dorsal, lateral, and ventral views of skull of Zachaenus parvulus (KU 107090, x 12).

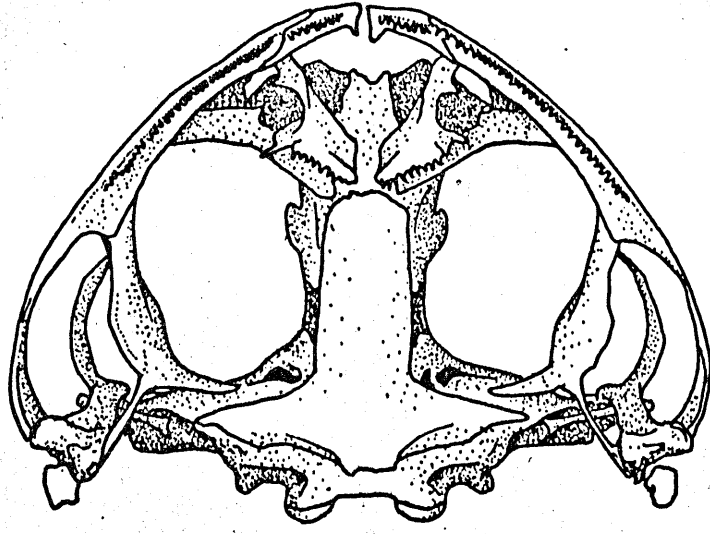
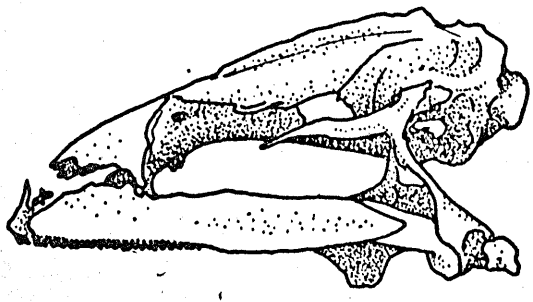
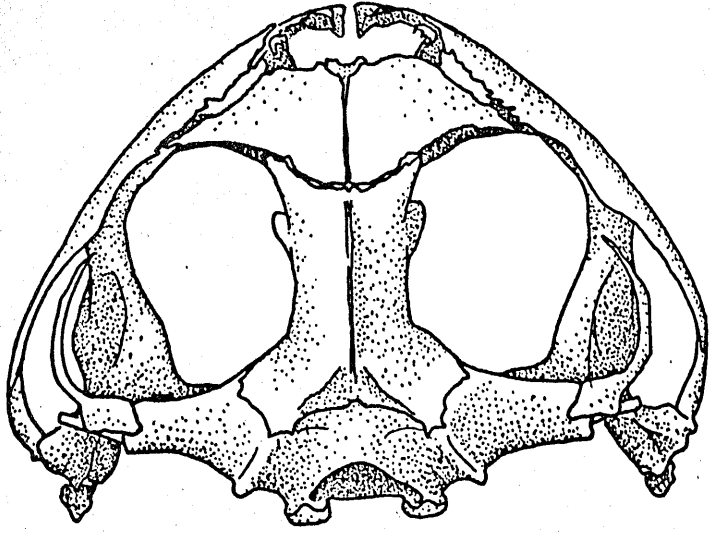


Figure 92. Dorsal, lateral, and ventral views  
of skull of Zachaenus stejnegeri (KU 92742, x 12).

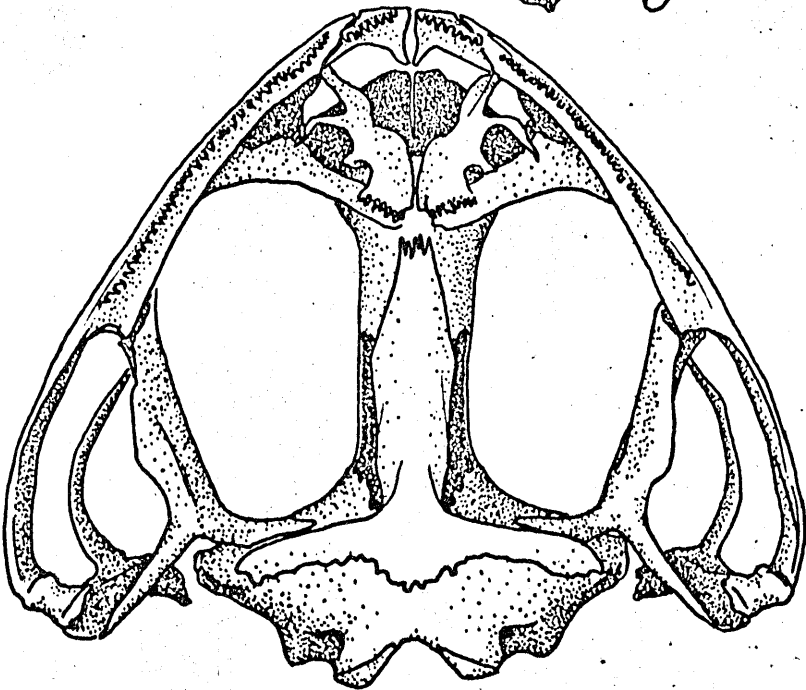
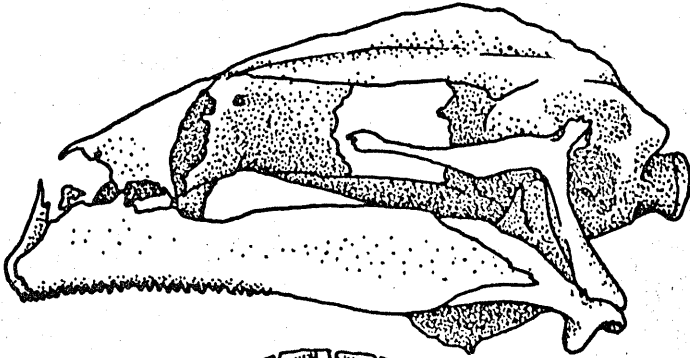
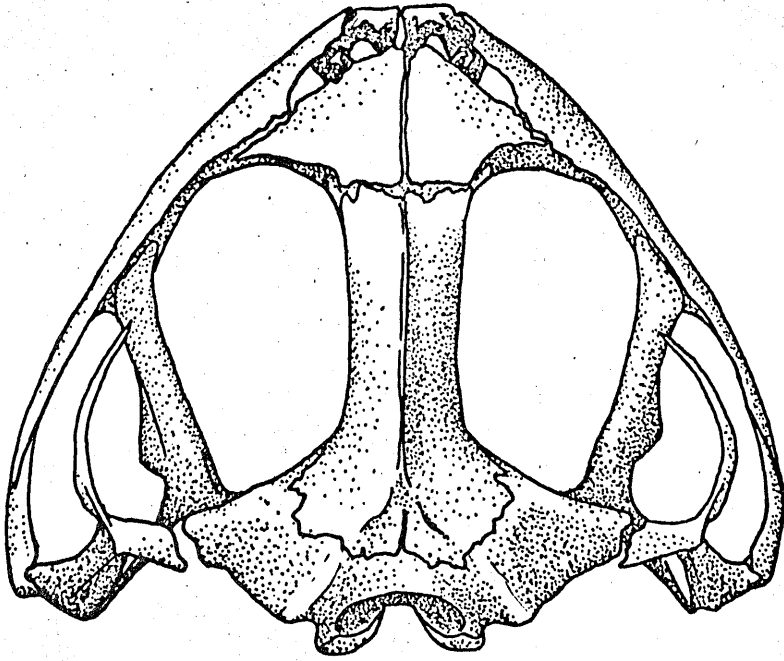
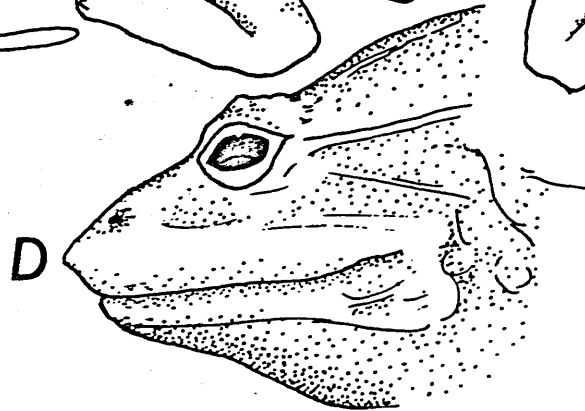
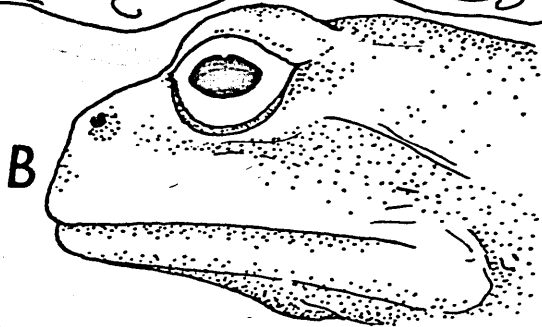
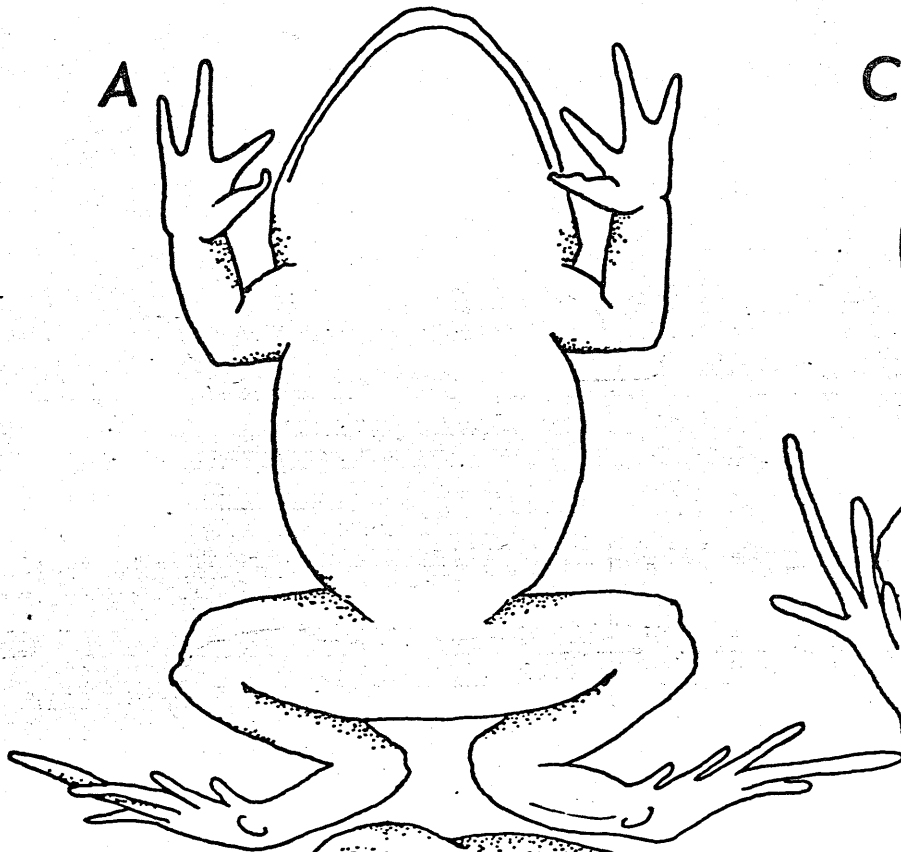


Figure 93. Body outlines and sides of heads of  
(A-B) Zachaenus stejnegeri (KU 92744) and (C-D) Z.  
parvulus (KU 93078). All x 3.5.





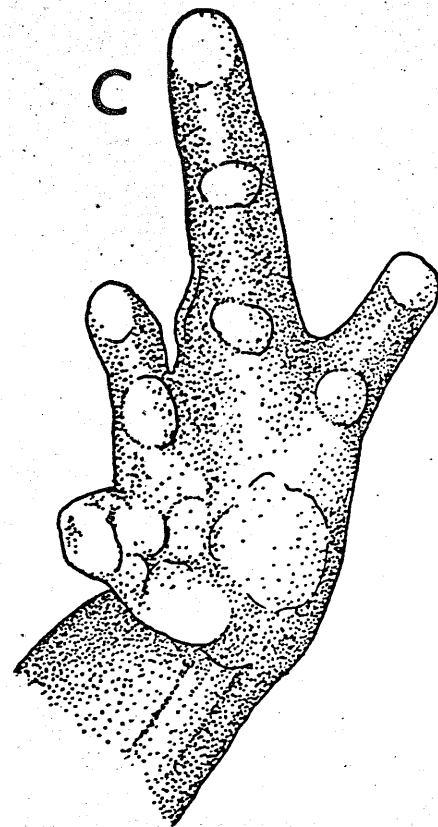
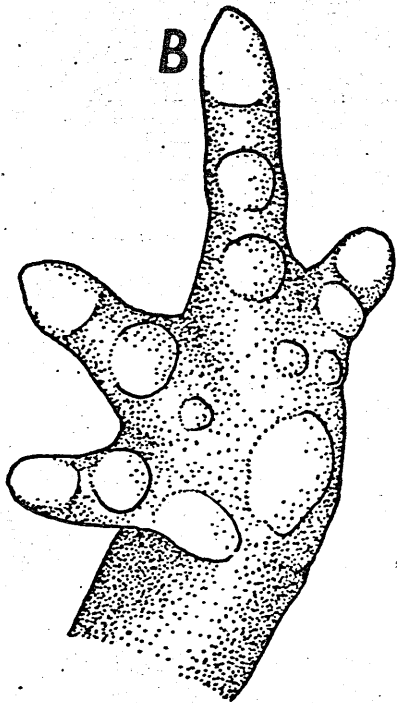
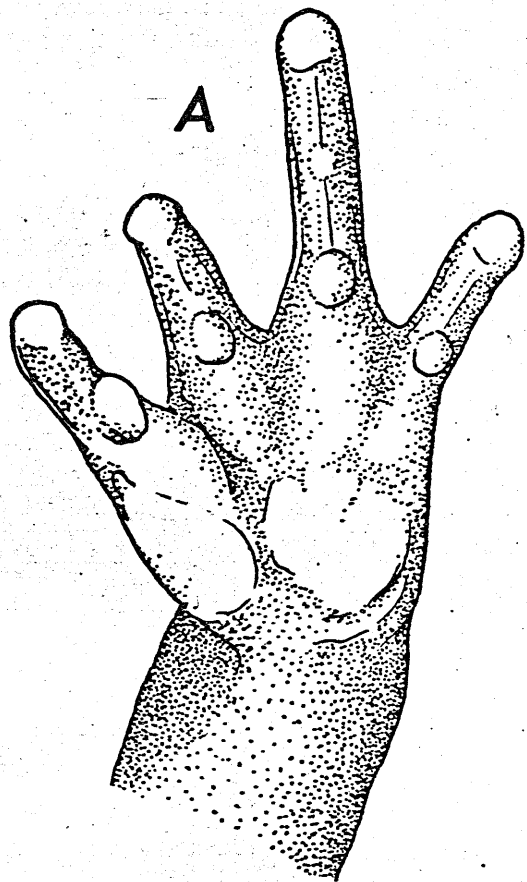
considered sanctaecatharinae to be a synonym of bolitoglossus. I do not consider roseus or sawayae members of this genus (see Remarks).

Distribution.-- Southern and southeastern Brasil.

Remarks.-- Lutz (1944) demonstrated that Oocormus microps is a synonym of Zachaenus parvulus. Parker (1926) noted the striking similarities in color pattern and proportions between Oocormus microps (= Zachaenus parvulus) and Sminthillus brasiliensis (= Euparkerella), which occur sympatrically in southeastern Brasil. Boulenger (1905) confused them and included Euparkerella in the syntypic series of Oocormus microps as juvenile specimens. The two genera belong to different tribes and can be distinguished externally only by the shape and lengths of the fingers and toes (Fig. 94).

Craspedoglossa is here placed in the synonymy of Zachaenus for the first time. Cochran (1955) pointed out that the two nominal genera might be best combined but separated them on the basis of the axillary patagium of Zachaenus (see Fig. 93). Telmatobufo is the only other leptodactylid with an axillary patagium, although the loose, "baggy" skin of Batrachophrynus and the strictly aquatic Telmatobius produces a poorly defined patagium. The snout is more sloping in Zachaenus parvulus than in Craspedoglossa (sensu strictu). The axillary patagium is used as a species-group character in other groups of frogs

Figure 94. Hands of three frogs of the Telmatobiinae.  
(A) Zachaenus parvulus (KU 93078, x 12), (B) Euparkerella  
brasiliensis (KU 112370, x 25), and (C) Scythrophrys  
sawayae (USNM 125530, x 25).



(for example, the Hyla marmorata and H. godmani groups), and is best regarded as a species-group character here as well. In all other characters used in the generic diagnoses, Craspedoglossa and Zachaenus are identical.

Cope (1890) named a second species of the genus (roseus) based on a single specimen from Port Otway, Patagonia; the unique holotype is now a macerated heap of fragments (Cochran, 1955, 1961b). The original description includes several points that clearly disassociate roseus from Zachaenus (tympanum visible, tongue not boletoid, prevomerine dentigerous processes small and round, outer metatarsal tubercle lacking, and toes fringed). The osteological data provided by Cope (nasals small, widely separated medially, and frontoparietals complete, i.e., no fontanelle) and those observed by me (pterygoid lacking ventral flange, zygomatic ramus of squamosal short and straight otic ramus of squamosal not curved medially but expanded medially into small otic plate) clearly disassociate roseus from Zachaenus. Unfortunately, the present data are insufficient for generic assignment. Zachaenus roseus Cope is tentatively considered a species inquirenda in the family Leptodaactylidae, probably in the Telmatobiinae.

Cochran (1953) named a single specimen of a frog from Paraná, Brasil, as a third species of Zachaenus (sawayae). The species is clearly not a Zachaenus, although its relationships are not apparent; only the holotype is

known, and no osteological observations can be made.

Zachaenus sawayae is considered by me to be the type-species of a new genus of the Telmatobiinae; the tribal relationships are not apparent. The new genus is named at the end of the Telmatobiinae account (p. 554-56).

#### Eleutherodactylini Lutz, 1954

Eleutherodactylinae Lutz, 1954:175.

Lutz (1954) proposed this subfamily for the inclusion of Eleutherodactylus alone; as was the case with the Cyclorhamphinae, she did not provide any diagnostic statements for the new group. Gallardo (1965) included Basanitia, Otenocranius, Eleutherodactylus, Microbatrachylus, and Syrrhophus in the Eleutherodactylinae. I include the following genera in the tribe Eleutherodactylini: Amblyphrynus, Eleutherodactylus, Euparkerella, Holoaden, Hylactophryne, Ischnocnema, Niceforonia, Sminthillus, Syrrhophus, and Tomodactylus. The nominal genera Basanitia, Noblella, Phrynanodus, and Trachyphrynus are considered to be synonyms of Eleutherodactylus (Lynch, 1968c, 1968d). The nominal genera Noblella Barbour and Pseudohyla Andersson are considered to be synonyms of Eleutherodactylus (see below).

The following diagnostic characteristics are the same in all of the included genera: (3) transverse processes of posterior presacral vertebrae not shortened;

(4) cervical cotylar arrangement type I; (5) cervical and second vertebrae not fused; (8) sacral diapophyses rounded; (9) maxillary arch usually toothed, if toothed, teeth blunt, pedicellate; (14) maxillary arch complete, maxillae tapering posteriorly, quadratojugal shallow; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle usually absent; (21) temporal arcade lacking; (23) carotid artery passes dorsal to skull bones; (41) pupil horizontal; (42) males lacking nuptial asperities; (45) outer metatarsal tubercle present, inner metatarsal tubercle not spade-like; (46) development direct in known species; (47) amplexus axillary in known species; (48) eggs relatively large, few in number, deposited in terrestrial situations, bromeliads, etc., in all known species.

Except for the nature of the T-shaped terminal phalanges, the skeleton of the eleutherodactylines is relatively generalized. The sternum is cartilaginous, an omosternum is usually present and relatively large, the cervical cotyles are widely separated medially, the transverse processes of the presacral vertebrae are neither greatly expanded nor shortened, the sacral diapophyses are rounded or only slightly dilated, the ilia are of the leptodactylinae type, all cranial bones are present although a few species have lost the prevomerine bones or

the columellae. The cranial bones are not dermostosed but exostosis is developed in several groups. The nasals are large and usually in median contact, and the frontoparietal fontanelle is rarely developed. There is considerable variation in the size and shape of the zygomatic ramus of the squamosal among the genera and species of this tribe, and most of the variation is observed within Eleutherodactylus.

Morphologically, the tribe Eleutherodactylini is difficult to define. The relationships of ten genera I include in this tribe are not entirely obvious. The definition of the group rests solely on the mode of reproduction, and the included genera are judged to be related because the various sections of the tribe can be tied together through the use of several different character complexes. Species of the following genera are known to lay terrestrial eggs and to lack a free tadpole stage: Eleutherodactylus, Holoaden, Hylactophryne, Sminthillus, Syrrhophus, and Tomodactylus. Euparkerella and Niceforonia probably lay large terrestrial eggs, judging from the size of mature eggs and the oviducts. Reproductive data are not available for Amblyphrynus and Ischnocnema. Females of the latter genus have moderately large, unpigmented eggs, but the eggs are not so large as to be suggestive of direct development. However, the eggs of Ischnocnema are no smaller than those of Eleutherodactylus



maussi, which exhibits direct development (Heatwole, 1962). Eleutherodactylus, Sminthillus, Syrrhophus, and Tomodactylus have broadly T-shaped terminal phalanges. The terminal phalanges of Euparkerella are broad and small, but could not be accurately described as T-shaped. The terminal phalanges of the other five genera (Amblyphrynus, Holoaden, Hylactophryne, Ischnocnema, and Niceforonia) of the tribe are knobbed. Amblyphrynus bears considerable resemblance to the Eleutherodactylus cornutus group and differs only in the nature of the terminal phalanges. Hylactophryne and Ischnocnema bear considerable resemblance to one another and to the Eleutherodactylus binotatus and guentheri groups; these genera also differ only in the nature of the terminal phalanges. Niceforonia is superficially similar to Eupsophus and to the Eleutherodactylus unistrigatus complex (several species groups are involved). Niceforonia differs from Eupsophus in several osteological characters as well as in reproductive pattern, but differs from the Eleutherodactylus unistrigatus complex only in the nature of the terminal phalanges. Holoaden is not obviously related to any group of Eleutherodactylus, but is osteologically similar to Niceforonia.

Amblyphrynus Cochran and Goin, 1961

Amblyphrynus Cochran and Goin, 1961, *Fieldiana, Zool.*, 39:543

[Type-species by original designation, Amblyphrynus ingeri Cochran and Goin, 1961].

Diagnostic definition.-- (7) omosternum present; (9) maxillary arch toothed; (10) alary processes of premaxillae directed posterodorsally; (11) (12) facial lobe of maxilla deep, not exostosed; (13) (15) nasals large, in broad median contact; (16) nasals in tenuous contact with maxillae, not in contact with pterygoids; (19) frontoparietal bears large, well defined, exostosed, lateral crests; (20) (22) epiotic eminences obsolete; (23) cristae paroticae long, narrow; (24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; (25) otic ramus of squamosal short, not expanded medially into otic plate; (26) (27) columella present; (28) prevomers large, entire, toothed, in median contact; (29) palatines large, narrowly separated medially; (30) sphenethmoid entire, extending anteriorly beneath nasals; (31) anterior ramus of parasphenoid broad, not keeled, pointed anteriorly; (32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; (33) pterygoids of moderate size, lacking ventral flange, anterior rami not reaching palatines, median rami long; (34) occipital condyles large, not stalked, widely separated medially; (36) terminal phalanges knobbed; (37 - 40) (42) (43) body lacking glands; (44) tongue large, round, posterior edge free; (45) toes free of webbing,

digital tips narrow; (46 - 48) (49) the two known specimens are 51.5 and 83.0 mm. SVL; (50) tympanum visible externally.

Composition.-- Monotypic.

Distribution.-- Known from two localities in the Andes of central Colombia (850 - 2350 meters). Peracca's (1914) record of an Eleutherodactylus cornutus from the highlands in Departamento Antioquia, Colombia, may refer to this species.

Remarks.-- Cochran and Goin (1961) suggested that Amblyphrynus is a member of the "broad-headed leptodactylid" group which includes the ceratophryine genera, Proceratophrys, and Zachaenus. They suggested that Amblyphrynus was probably most closely related to Zachaenus. The resemblance between these two genera is spurious. This association can only be made by comparison of description of characters and will not bear up against specimen comparison or the additional osteological characteristics. The suggestion that this species is allied with the ceratophryine leptodactylids is contradicted by the lack of morphological agreement between the two groups. The ceratophryines have large, casqued skulls with extensive dermostosis and exostosis, a distinctly different type of cervical-occipital articulation, non-pedicellate teeth, expanded transverse processes of the anterior presacral vertebrae and shortened transverse processes of the posterior presacral vertebrae, and a dermostosed vertebral shield.

In many respects, Amblyphrynus resembles the large-headed frogs of the Eleutherodactylus cornutus group. The holotype of Amblyphrynus ingeri was first reported by Dunn (1944) as an Eleutherodactylus cornutus. The only characteristic separating these two groups is the nature of the terminal phalanges. When additional specimens of A. ingeri become available an effort must be made to determine if the terminal phalanges of the hind feet are knobbed or T-shaped. As pointed out previously, the terminal phalanges of the fingers may be knobbed and those of the toes T-shaped. This pattern is observed in several groups of Eleutherodactylus.

The only specimens of this species available were studied through the use of stereo-radiographs.

Eleutherodactylus Duméril and Bibron, 1841

(Figs. 95-99)

Cornufer Tschudi, 1838, *Classif. Batr.*, p. 28 [Type-species by monotypy, Cornufer unicolor Tschudi, 1838 (= Eleutherodactylus inoptatus)]. Suppression of Tschudi's names was requested by Zweifel (1966)].

Eleutherodactylus Duméril and Bibron, 1841, *Erp. gén.*, 8:620 [Type-species by monotypy, Hylodes martinicensis Tschudi, 1838. Myers (1962) listed the type-species designation as by original designation. The name Eleutherodactylus was included in the synonymy of

Hylodes martinicensis by Duméril and Bibron (1841). Apparently they had planned to use the generic name in their Érpetologie générale until Tschudi (1838) named their martinicensis in the genus Hylodes].

Hylodes Fitzinger (non Hylodes Fitzinger, 1826), 1843, Syst. Rep., p. 31 [Type-species by original designation, Hylodes martinicensis Tschudi, 1838].

Euhyas Fitzinger, 1843, Ibid., p. 31 [Type-species by original designation, Hylodes ricordii Duméril and Bibron, 1841].

Craugastor Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, p. 153 [Type-species by subsequent designation (Dunn and Dunn, 1940), Hylodes fitzingeri O. Schmidt, 1858].

Strabomantis W. Peters, 1863, Mtber. k. Preuss. Akad. Wiss., Berlin, p. 405 [Type-species by monotypy, Strabomantis biporcatus W. Peters, 1863].

Leiyla Keferstein, 1868, Ark. Naturges., 34:296 [Type-species by monotypy, Leiyla guentherii Keferstein, 1868].

Liyla Cope, 1870, Proc. Amer. Philos. Soc., 11:160 [Emendation of Leiyla Keferstein, 1868].

Limnophys Jiménez de la Espada, 1870, J. Sci. Math., Phys. Nat. Lisboa, 3:59 [Type-species by subsequent designation (Myers, 1962), Limnophys cornutus Jiménez de la Espada, 1870].

Pristimantis Jiménez de la Espada, 1870, Ibid., 3:61

[Type-species by monotypy, Pristimantis galdi Jiménez de la Espada, 1870].

Cyclocephalus Jiménez de la Espada, 1875, Vert. Viaje

Pacif., Batr., pl. 3 [Type-species by monotypy,

Cyclocephalus lacrimosus Jiménez de la Espada, 1875].

Hypodictyon Cope, 1885, Proc. Amer. Philos. Soc., 22:383

[Type-species by original designation, Phyllobates ridens Cope, 1866].

Liohyla Cope, 1894, Ibid., 31:335 [Emendation of Leiyla

Keferstein, 1868].

Basanitia Miranda-Ribeiro, 1923, Rev. Mus. Paulista,

13:851 [Type-species by monotypy, Basanitia lactea Miranda-Ribeiro, 1923].

Noblella Barbour, 1930, Zoologica, 11:81 [Type-species

by original designation, Sminthillus peruvianus Noble, 1921].

Phrynanodus Ahl, 1933, Zool. Anz., 104:29 [Type-species

by monotypy, Phrynanodus nanus Ahl, 1933].

Teletrema Miranda-Ribeiro, 1937, O Campo (Rio de Janeiro),

8 (89):67 [Type-species by monotypy, Teletrema heterodactylum Miranda-Ribeiro, 1937].

Microbatrachylus Taylor, 1940, Univ. Kansas Sci. Bull.,

26:499 [Type-species by original designation,

Eleutherodactylus hobartsmithi Taylor, 1936].

Otenocranius Melin, 1941, Medd. Göteborgs Mus. Zool. Avd., 88:49 [Type-species by subsequent designation (Myers, 1962), Limnophys cornutus Jiménez de la Espada, 1870].

Pseudohyla Andersson, 1945, Ark. Zool., 37A:86 [Type-species by monotypy, Pseudohyla nigrogrisea Andersson, 1945].

Trachyphrynus Goin and Cochran, 1963, Proc. California Acad. Sci., 31:502 [Type-species by original designation, Trachyphrynus myersi Goin and Cochran, 1963].

Diagnostic definition.-- (7) omosternum usually present, small, medium-sized, or large, long and narrow or relatively broad, absent in at least one species--E. ruthae; (9) maxillary arch toothed; (10) alary processes of premaxillae relatively broad at base, direction variable--dorsal, dorsolateral, or posterodorsal; (11) palatal shelf of premaxilla deep, usually deeply dissected; (12) facial lobe of maxilla deep, usually not exostosed; (13) palatal shelf of maxilla broad, usually with prominent pterygoid process; (15) nasals large, in broad median contact, narrowly separated in some species; (16) nasals not in contact with pterygoids, sometimes in contact with maxillae; (18) frontoparietal fontanelle absent in adults except in E. palmeri and E. whympersi; (19) frontoparietals not ornamented in most species groups, but bearing lateral crests in biporcatus, cornutus, galdi, and unistrigatus complexes; (20) frontoparietals fused with prootics or

Figure 95. Lateral and dorsal views of skull of  
Eleutherodactylus sulcatus (KU 100355, x 8).



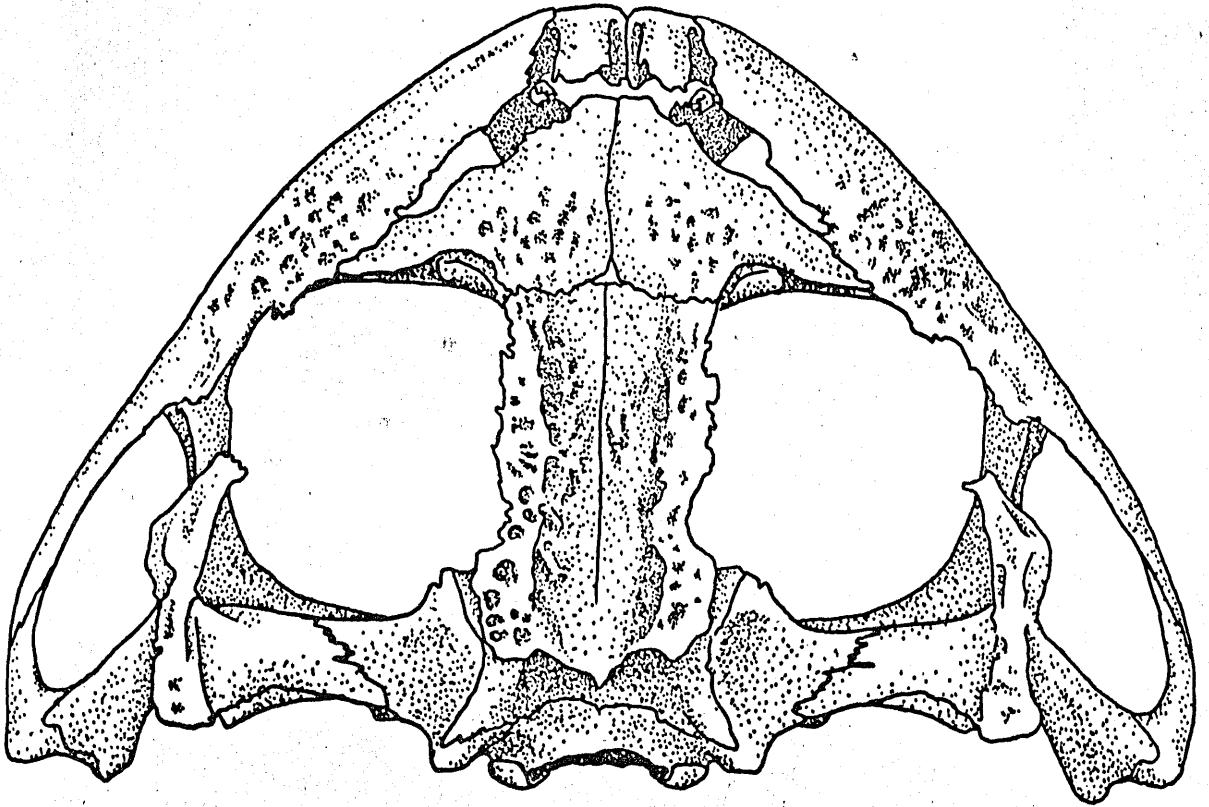
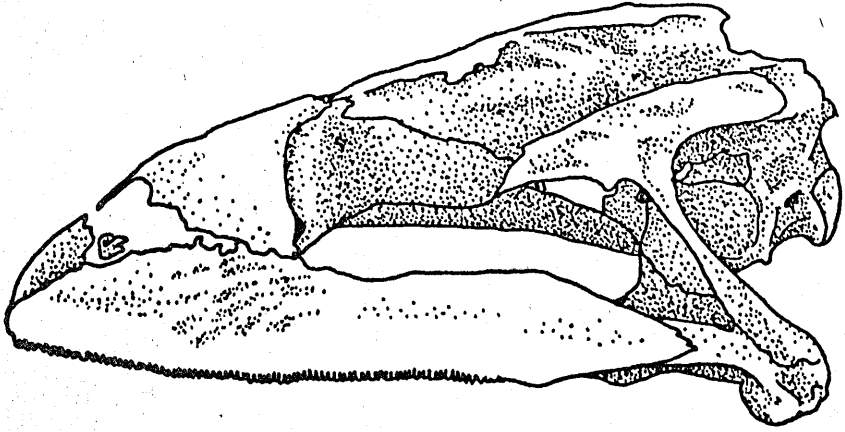
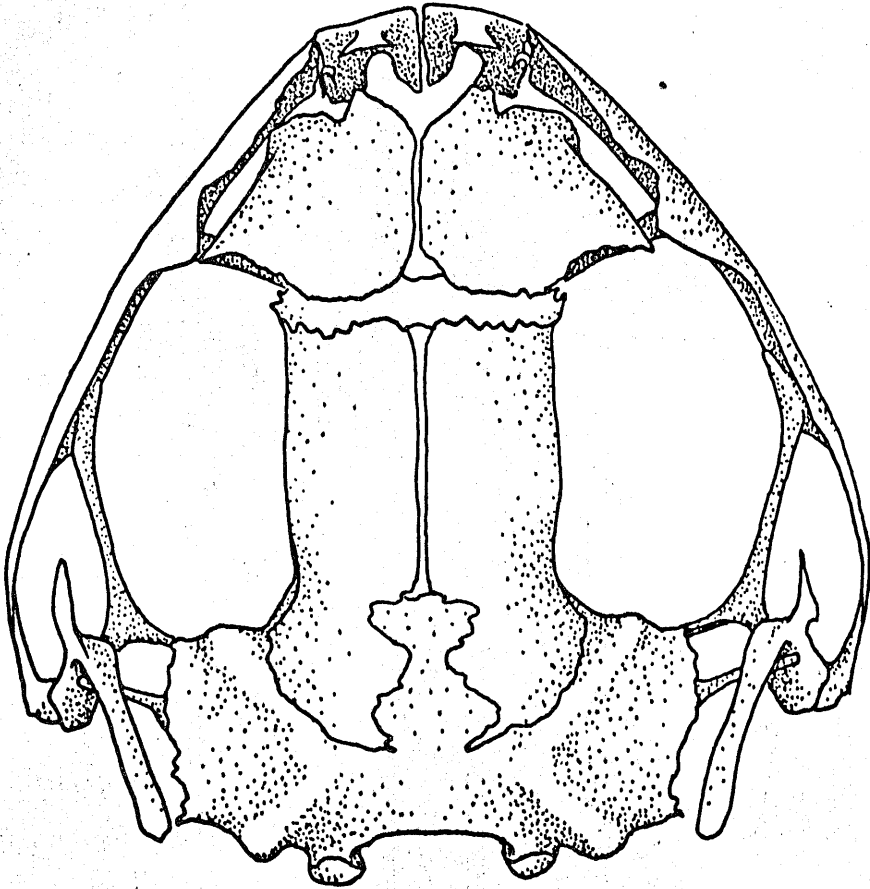
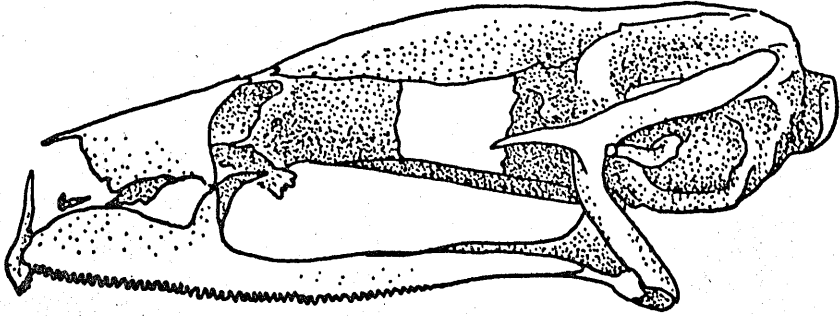


Figure 96. Lateral and dorsal views of skull  
of Eleutherodactylus diastema (KU 68263, x 12).



not. The bones are fused in most species in the West Indies and northern Andes, free in other groups; (22) epiotic eminences prominent to obsolete--group variable; (23) cristae paroticae short and stocky to long and narrow; (24) zygomatic ramus of squamosal short to long, sometimes knobbed, in contact with maxilla in one species (ruthae); (25) otic ramus of squamosal short to long, usually forming a small otic plate, ornamented in a few species groups--notably the galdi group; (26) squamosal-maxillary angle  $44 - 67^{\circ}$ , most  $50 - 60^{\circ}$ ; (27) columella present; (28) prevomers nearly always toothed, entire, narrowly separated medially to broadly separated medially; (29) palatines long, usually expanded laterally, relatively widely separated medially, no odontoid ridges; (30) sphenethmoid entire, extending anteriorly beneath nasals variable distance; (31) anterior ramus of parasphenoid narrow to broad, relatively long, nearly reaching prevomers, not keeled medially; (32) parasphenoid alae in two patterns: 1. alae deflected posteriorly, short, not overlapped laterally by median rami of pterygoids, and 2. alae oriented at right angles to anterior ramus, rarely deflected posteriorly, long, broadly overlapped by median rami of pterygoids. The first pattern is seen in West Indian species and some Andean species, whereas the second is seen in Central American and lowland South American species; (33) pterygoids slender to relatively massive, lacking

Figure 97. Dorsal views of the skulls of Eleutherodactylus conspicillatus (KU 108988, x 8) and E. planirostris (KU 92656, x 8). Arrows point to prevomerine teeth which are visible in dorsal view.

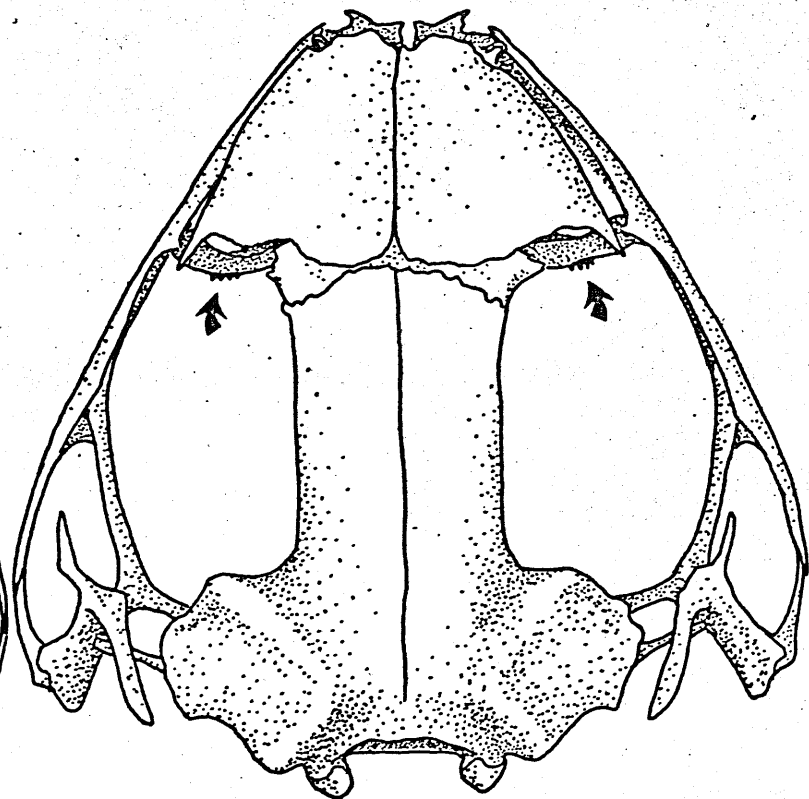
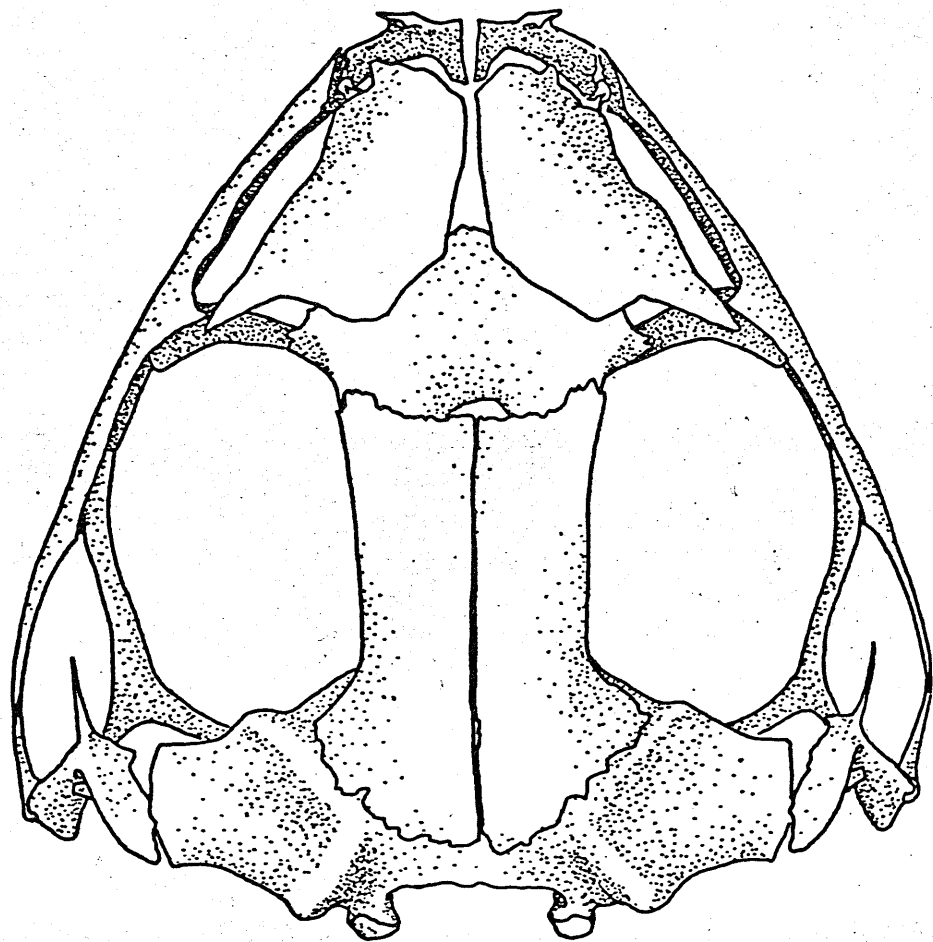
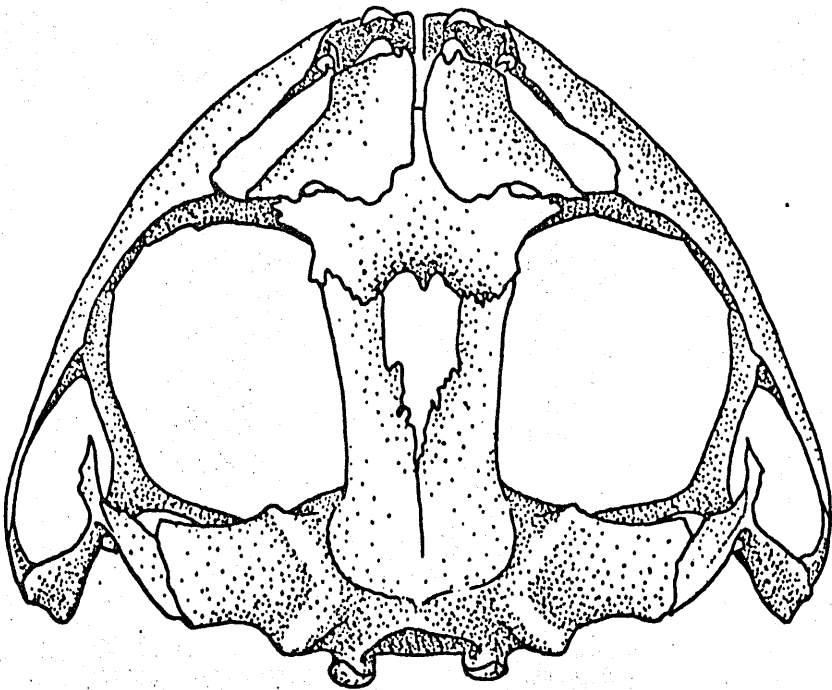
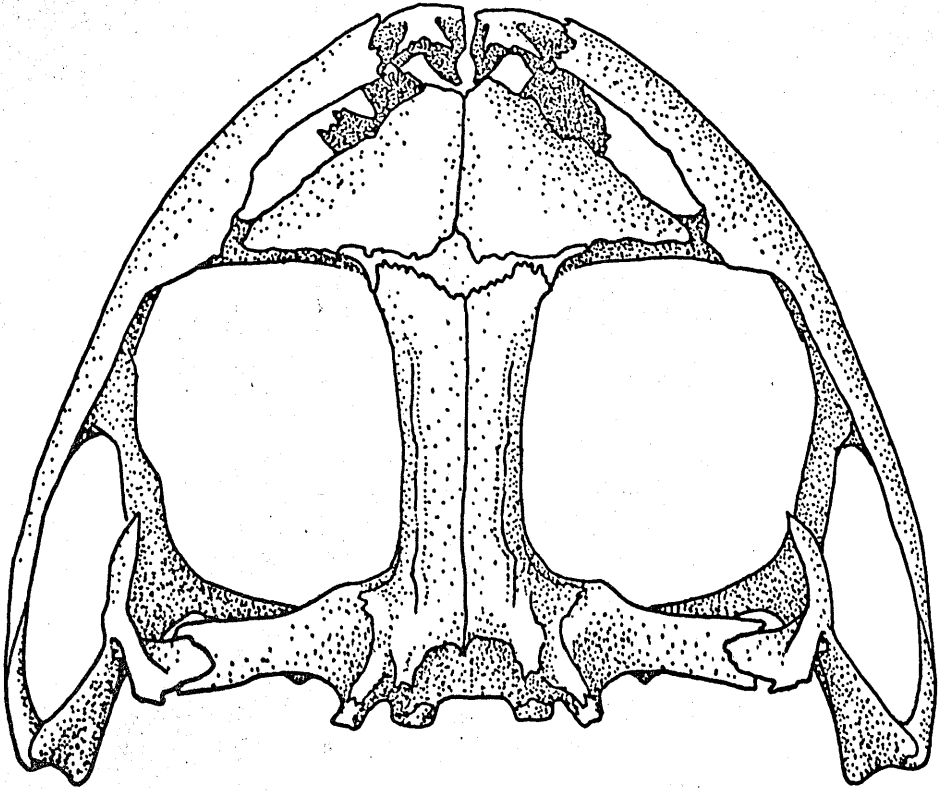


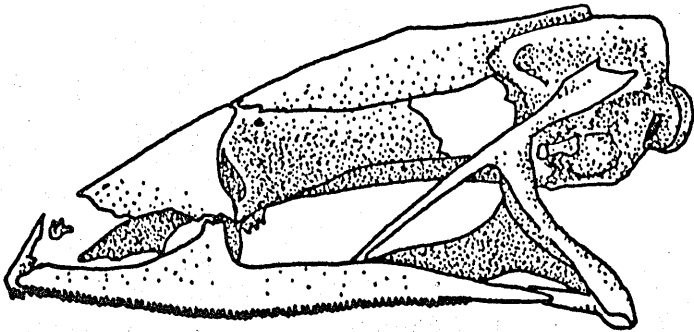
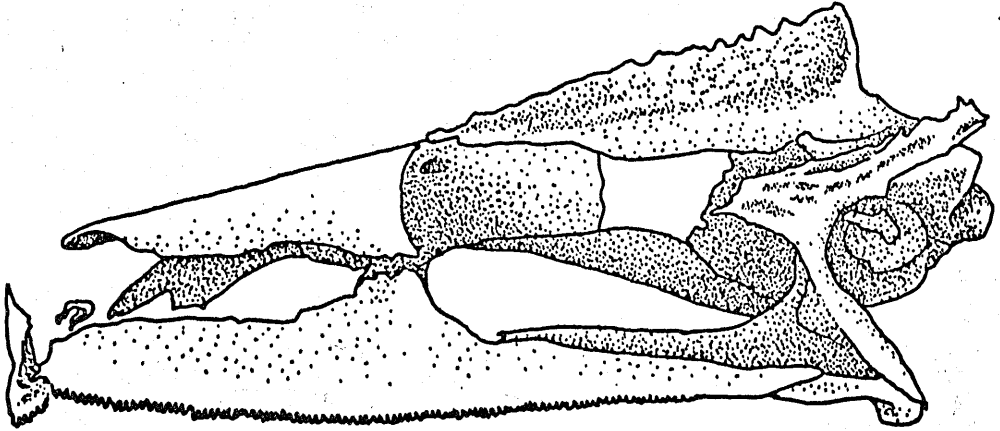
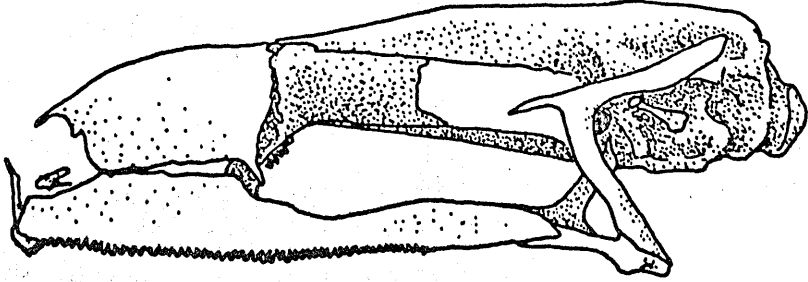
Figure 98. Dorsal views of skulls of  
Eleutherodactylus bufoniformis (KU 80621, x 4)  
and E. palmeri (KU 110923, x 6)..





ventral flange, anterior rami relatively short, not reaching palatines, median rami short to long, straight or bent; (34) occipital condyles relatively small, stalked or not, widely separated medially; (36) terminal phalanges nearly always clearly T-shaped, inner phalanges usually knobbed, terminal phalanges of toes more T-shaped than those of fingers; presence of T-shaped terminal phalanx is expressed externally by the presence of a terminal transverse groove across the tip of the digital pad; (37) alary processes of hyoid plate on narrow stalks; (40) m. depressor mandibulae in one slip in E. galdi, in one slip with separation into two slips dorsally in species of biporcatus and cornutus groups, or in two large slips in most species; (42) males with single subgular vocal sac or none, internal or external; (43) glands on body usually absent, those present are usually loosely organized inguinal glands; (44) tongue long and narrow to large and round, posterior edge usually free; (45) toes free of webbing to nearly fully webbed; when webbing is present, it is indicative of a close association with streams; webbing is greatest in anomalus, karlschmidti, punctariolus, and raniformis, although several species of the rugulosus group in Central America have the toes one-half webbed; digits usually bear large pads; (49) adults range from 12 - 100+ mm. SVL; (50) tympanum absent in anotis, concealed in many species, visible externally

Figure 99. Lateral views of skulls of Eleutherodactylus. (A) planirostris (KU 92656, x 8), (B) galdi (USNM field GOV 8944, x 8), and (C) ruthae (AS 4237, x 4).



in most species.

Composition.-- Gorham (1966) listed nearly 300 species in the most recent compilation of names in the genus. Albert Schwartz informed me that there are 100 species in the West Indies (including Trinidad). My own estimate is that the genus contains about 400 species, many yet unnamed.

Distribution.-- Sinaloa and Tamaulipas, México (but not on the Mexican Plateau) southward and eastward throughout Middle America to northern Argentina and southern Brasil; all West Indian islands; introduced into Florida.

Remarks.-- Myers (1962) discussed the generic synonymy of this genus and included most of the generic synonyms listed above as well as Syrrhophus and Lithodytes in the synonymy of Eleutherodactylus. Microbatrachylus was synonymized by Lynch (1965), and he later (1968c, 1968d) considered Basanitia, Phrynanodus, and Trachyphrynus inseparable from Eleutherodactylus.

Two generic synonyms are added at this time: Noblella Barbour and Pseudohyla Andersson. Noble (1921) named Sminthillus peruvianus on the basis of several specimens of a minute frog with an anterior epicoracoidal fusion (the distinguishing character of the genus). At the time of the description of peruvianus, the genus Sminthillus was known only from Cuba, but with the description of a species from southeastern Brasil by Parker (1926),

it began to appear that Sminthillus was a widespread, Neotropical genus of small frogs. Noble (1926b, 1931) suggested that Sminthillus was derived from Eleutherodactylus or Syrrhophus but placed it in another family (Brachycephalidae). Griffiths (1959) placed each of the three species of Sminthillus in a separate genus, utilizing Barbour's (1930) Noblella for peruviana. Barbour (1930) proposed Noblella for peruviana because the Cuban species was geographically remote from the two South American species and because he believed Sminthillus to be a Phyllobates (Dendrobatidae). Griffiths offered a new generic name, Euparkerella, for the Brazilian species. Euparkerella, while here retained as an eleutherodactyline, is very distinct from all other genera of the tribe and subfamily. Sminthillus is retained as a genus of eleutherodactylines on less secure grounds--the maxillary teeth are absent. Noblella peruviana, on the other hand, has maxillary teeth, although it apparently has no prevomers. The single specimen of this species available to me cannot be generically separated from Eleutherodactylus; an epicoracoidal bridge is not, in my opinion, sufficient basis for the maintenance of an otherwise undefinable generic group (see discussion on p. 180). Noblella therefore is placed in the synonymy of Eleutherodactylus. This action creates one minor problem--Noble's peruvianus was proposed in 1921, but Melin (1941) proposed a Hylodes

peruvianus which becomes a secondary homonym of Noble's name. Rather than propose a replacement name for a probably invalid species, I suggest that Melin's name be kept in mind by the person who eventually studies the conspicillatus group in the Amazon Basin of Peru.

Andersson (1945) proposed Pseudohyla as a hylid genus, but having studied the holotype of P. nigrogrisea, I do not consider the genus separable from Eleutherodactylus. Eleutherodactylus nigrogriseus (New Combination) is a small species of the genus and has been found in the valley of the Río Pastaza and on the slopes of the Cordillera Dué in eastern Ecuador.

The genus Eleutherodactylus is a large and unwieldy one, although Hyla and possibly Rana are more unwieldy at present. In contrast to the latter two genera (and perhaps to the opinions of several herpetologists) the genus Eleutherodactylus is marked by considerable homogeneity. There is a large range of sizes among the species; most species lack webbing between the toes but some have it, including one species with fully webbed feet (E. karlschmidti). Exostosis of the cranial bones is developed in several species groups but in general the phenomenon is an uncommon trait in the genus. Some species have minute digital pads and only small lateral projections of the terminal phalanges on the hands, but all species have moderate to large T-shaped terminal phalanges on

the toes (see pp. 209 - 18 for further discussion).

Three characters exhibit especially interesting variation in Eleutherodactylus--(1) fusion of the frontoparietal and otoccipital bones; (2) degree of overlap of the parasphenoid alae and median rami of the pterygoids; and (3) median separation of the prevomers. On the basis of the variation in these characters, the species of the West Indies and parts of the Andean system form one group and the species of México, Central America, and lowland South America form a second group. These characters are discussed below.

Baldauf and Tanzer (1965) improved our knowledge of leptodactylid skulls with the description of the cranium of Syrrhophus marnockii. In this work they pointed out the fusion of the frontoparietal and proötic in this species. These bones are fused in all species of Syrrhophus and Tomodactylus, whereas they are not fused in the Eleutherodactylus of México and Middle America. Although fewer than one-third of the species of Eleutherodactylus have been studied for this character, I feel that I have checked a sufficiently representative sample in that I have examined species from all parts of the range of the genus. Fusion of the frontoparietal and proötic (otoccipital, since the proötic is usually fused with the exoccipital) occurs in the species of the

genus found in the West Indies from Bermuda and the Bahamas (and Florida) to Trinidad. The species of the Hispaniolan inoptatus group (inoptatus and ruthae examined) as well as the Puerto Rican karlschmidti apparently have the two bones free. At least some (perhaps all) of the species of the Andean groups exhibit fusion of these bones. No species was examined from the Andes south of Ecuador. All species of the genera Syrrhophus and Tomodactylus as well as Sminthillus exhibit the fusion. No species of Eleutherodactylus in México or Central America normally exhibits frontoparietal-proötic fusion (see below), nor do species of the genus found in Chococoan Colombia and Ecuador. Insofar as I am aware, no species found in the Amazon Basin exhibits the fusion nor do the representatives of the genus in southeastern Brasil.

Some variability was noted. One specimen of E. fitzingeri (JDL S-407) exhibited fusion of the frontoparietal and otoccipital bones whereas the other nine specimens examined did not. One of three specimens of E. chloronotus examined exhibited the fusion. Two of the 19 specimens of E. curtipes examined did not exhibit fusion of these bones; both were small specimens, suggesting that the fusion is an ontogenetic phenomenon. In the cases of the first two species, I regard the fusion as aberrant. In each instance, the frontoparietals, nasals, prevomers, and



parasphenoid were bound to the sphenethmoid and otoccipitals with no apparent sutures. This suggests that the fusion in these cases resulted from extensive calcification rather than osteological fusion.

The degree of overlap between the median rami of the pterygoids and parasphenoid alae follows the same pattern as the frontoparietal-proötic fusion with some departure. The median pterygoid rami of the rhodopis group of Eleutherodactylus are short and bent so that there is no actual contact between the pterygoid and parasphenoid, but the median ramus of the pterygoid abuts against the otic capsule just above the parasphenoid ala. In the majority of species of the genus, the median ramus is broadly in contact with the anterior edge of the parasphenoid ala or the median ramus is shortened and may or may not reach the otic capsule and does not reach the shortened parasphenoid ala. In those species with a pterygoid-parasphenoid overlap, the frontoparietals and proötic bones are free. The members of the rhodopis complex of Eleutherodactylus have the bent pterygoid and hence do not have a typical pterygoid-parasphenoid overlap but because the median rami of the pterygoids are proportionately long, these species are included in the same complex as those species with a broad overlap of the parasphenoid alae and median pterygoid rami. In the rhodopis complex the frontoparietal and proötic bones are

not fused. Those species with a very short median ramus on the pterygoid and no pterygoid-parasphenoid overlap also exhibit the fused frontoparietal-proötic. For purposes of further discussion, these two major groups are here termed the Alpha and Beta groups of Eleutherodactylus. Members of the Alpha group (fused frontoparietal-proötic, non-overlap between pterygoids and parasphenoid alae) usually have relatively widely separated prevomers, whereas the Beta group frogs (frontoparietal and proötic not fused, pterygoids overlap parasphenoid alae) usually have the prevomers in contact or only narrowly separated.

I submit that the two divisions, Alpha and Beta, are natural divisions within the genus Eleutherodactylus and not simply a chaotic array of species exhibiting two osteological patterns. I borrowed the terminology of Etheridge (1960) for the major divisions since at this time I am not willing to afford the two divisions nomenclatorial recognition and prefer the informal divisional names. This course is taken because only a relatively small part of the genus has been surveyed, and many species could not be assigned to subgenus were nomenclatorial assignments made. If the two divisions were afforded nomenclatorial status, the Alpha group would be the subgenus Eleutherodactylus and the Beta group would take the name Craugastor.

Several osteological features seem to lend themselves well to the possible use of skeletal morphology in the assessment of species group relationships within the genus Eleutherodactylus. The degree of median separation of the prevomers has potential in that it varies concordantly with several other osteological traits (the development of cranial crests, shape of the rami of the squamosal, and size and shape of the nasal bones). Among the West Indian species of the genus, the species groups have long been based at least in part on the length of the prevomerine dentigerous processes, and I would expect this character complex to be of at least some value, although its use is greatly hampered by the occasional loss of dentigerous processes in several groups of the genus. I have not attempted to divide the species of the genus into species groups, because I have not studied all species of the genus and I cannot rely upon the literature for many characters that I regard as of potential importance. A study of the osteology of the genus Eleutherodactylus is envisioned, but prior to its initiation considerable research must be done in straightening out many nomenclatorial entanglements, the description of many more species, and synonymizing of many names.

Euparkerella Griffiths, 1959

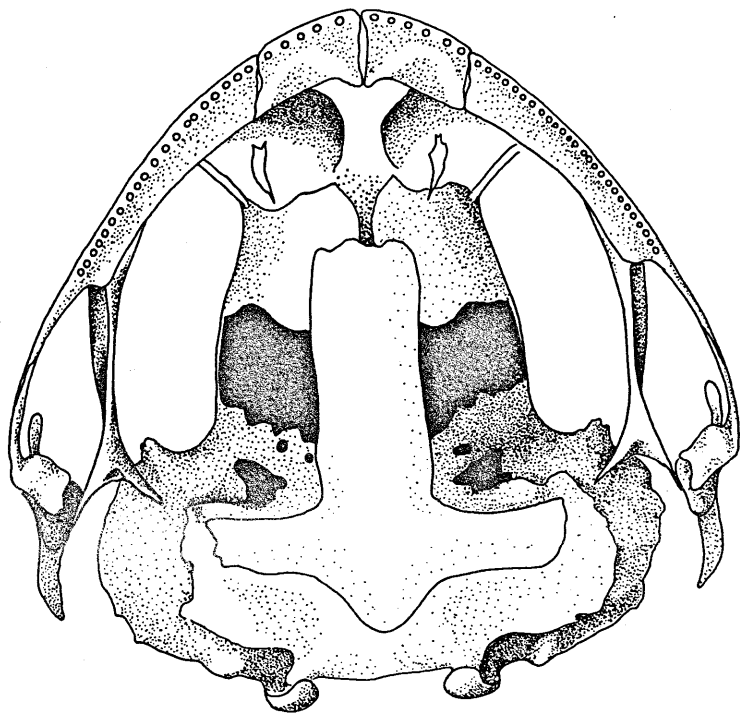
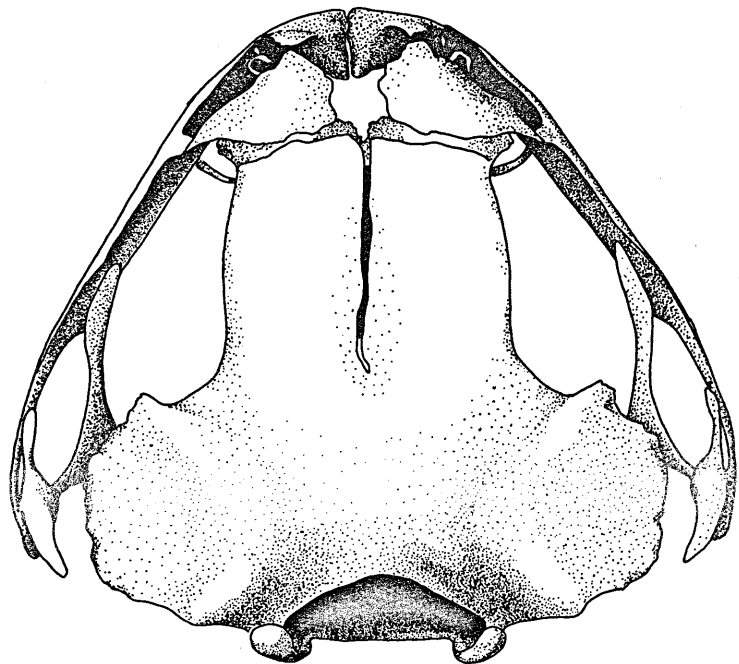
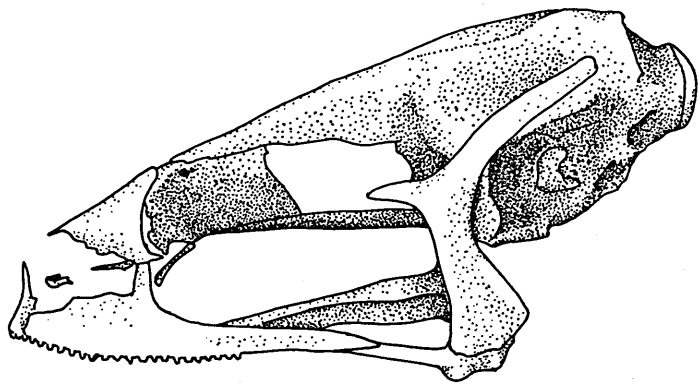
(Fig. 100)

Euparkerella Griffiths, 1959, Proc. Zool. Soc. London,

132:477 [Type-species by original designation,  
Sminthillus brasiliensis Parker, 1926].

Diagnostic definition.-- (7) omosternum present, small; (9) maxillary arch toothed; (10) alary processes of premaxillae directed posterodorsally, broad at base; (11) palatal shelf of premaxilla very broad, not notched, palatal process minute; (12) facial lobe of maxilla shallow; (13) palatal shelf of maxilla broad, tapering posteriorly, no pterygoid process; (15) nasals small, moderate median separation; (16) nasals in contact with maxillae, separated from pterygoids; (19) frontoparietals not ornamented; (20) frontoparietal fused to proötic; (22) epiotic eminences small; (23) cristae paroticae very broad, stocky; (24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; (25) otic ramus of squamosal elongate, not expanded medially into otic plate; (26) squamosal-maxillary angle about  $60^{\circ}$ ; (27) columella absent; (28) prevomers reduced to minute slivers, widely separated medially, edentate, dentigerous rami lost; (29) palatines very slender, reduced in size, widely separated medially; (30) sphenethmoid divided, extending anteriorly under posterior edge of nasals; (31) anterior ramus of parasphenoid very broad, not keeled medially; (32) parasphenoid alae oriented at right angles to anterior ramus, short, not overlapped by median rami of pterygoids; (33) pterygoids relatively small, anterior rami long, not

Figure 100. Lateral, dorsal, and ventral views  
of skull of Euparkerella brasiliensis (KU 93192, x 7.5)



reaching palatines; (34) occipital condyles small, stalked, widely separated medially; (36) terminal phalanges short and broad, bearing small hook-like lateral processes; (37) alary processes lacking on hyoid plate; (40) m. depressor mandibulae in two slips; (42) males with median subgular vocal sac; (43) body lacking glands; (44) tongue large, not notched, posterior edge free; (45) toes lacking webbing, digital tips pointed, not dilated, fingers and toes short; (46 - 48) (49) adults small, less than 20 mm. SVL; (50) tympanum absent.

Composition.-- Monotypic.

Distribution.-- Known only from the Serra dos Orgãos, state of Guanabara, Brasil.

Remarks.-- Parker (1926) named Sminthillus brasiliensis on the basis of the "juvenile" cotypes of Boulenger's Oocormus microps (= Zachaenus parvulus). Noble examined Parker's drawings of the pectoral girdle of brasiliensis and agreed with Parker that the species fit the characteristics of Sminthillus. At that time, Sminthillus comprised three species--one Cuban, one Peruvian, and one Brazilian. Griffiths (1959) argued that if all three species were independent derivatives of Eleutherodactylus, then each belongs to a separate genus. His solution was to place each in a monotypic genus. Griffiths proposed Euparkerella for the Brazilian species but did not provide diagnostic

statements for the genus. Euparkerella is very distinctive in its osteology. In external morphology, Euparkerella is superficially very similar to Zachaenus parvulus. These two species live in the same habitat (leaf litter) in southeastern Brasil and are frequently collected syntopically. The coloration of the two species is nearly identical. Euparkerella brasiliensis and Zachaenus parvulus differ in adult size and the length of the fingers (Fig. 94).

The skeleton of Euparkerella does not bear any close resemblance to that of any other leptodactylid genus, although the squamosal architecture, lack of columellae, and shape of the hyoid plate of Euparkerella suggest a relationship to the genus Holoaden. The terminal phalanges of Euparkerella are unique in the shape of the lateral expansions (Figs. 43 - 44). The digits are not pad-like and lack the terminal transverse groove that is found on the digital tips of Eleutherodactylus, Syrrhophus, Sminthillus, and Tomodactylus. The frontoparietal and proötic fusion of Euparkerella is suggestive of a relationship with the Alpha division of Eleutherodactylus. At present, I regard the relationships of Euparkerella as obscure but feel that the genus is probably more closely related to Holoaden than to either division of Eleutherodactylus.



Holoaden Miranda-Ribeiro, 1920

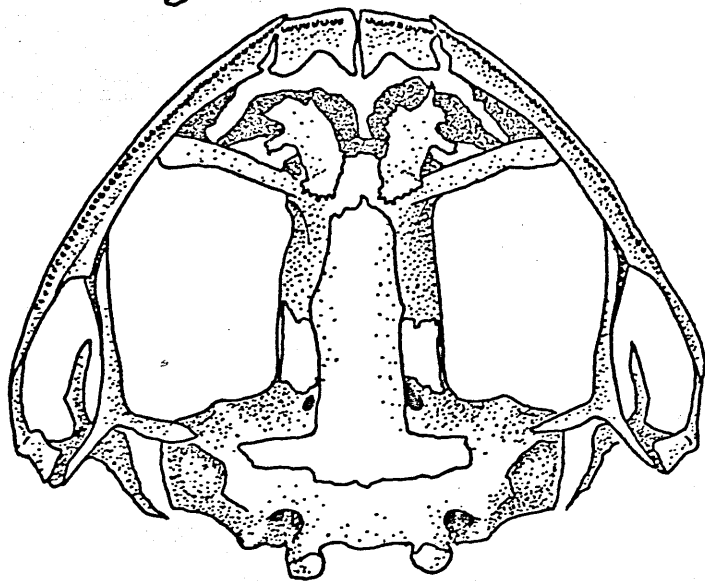
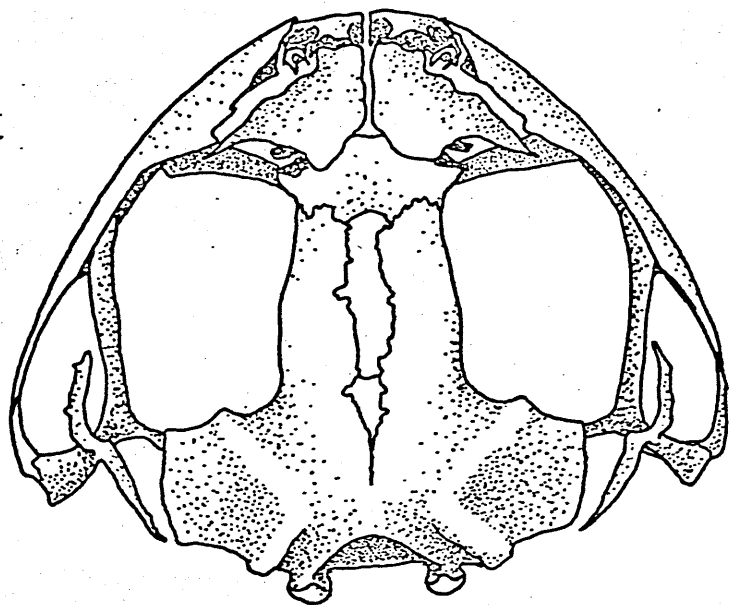
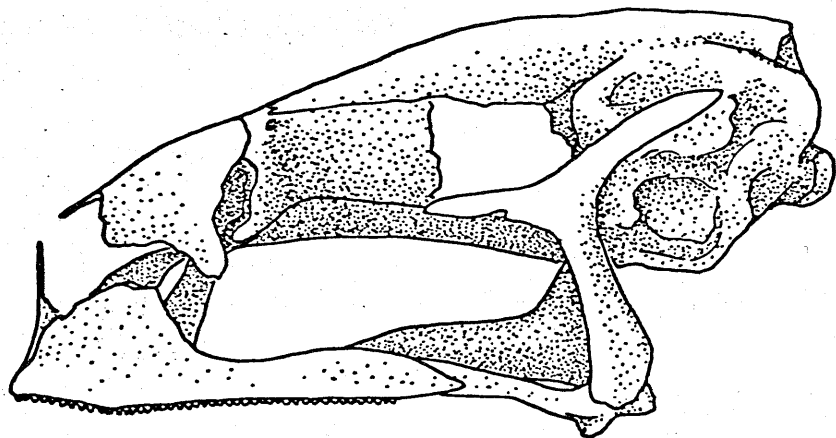
(Fig. 101)

Holoaden Miranda-Ribeiro, 1920, Rev. Mus. Paulista, 12:319

[Type-species by monotypy, Holoaden luederwaldti  
Miranda-Ribeiro, 1920].

Diagnostic definition.-- (7) omosternum moderate-sized;  
(9) maxillary arch toothed; (10) alary processes of  
premaxillae directed dorsally, moderately wide at base;  
(11) palatal shelf of premaxilla broad, slightly indented;  
(12) facial lobe of maxilla relatively shallow, not  
exostosed; (13) palatal shelf of maxilla of moderate  
width, no distinct pterygoid process; (15) nasals moderate-sized,  
narrowly separated medially; (16) nasals separated from  
maxillae and pterygoids; (18) frontoparietal fontanelle  
moderate-sized; (19) frontoparietals not ornamented;  
(20) frontoparietals not fused with proötics; (22)  
epiotic eminences small; (23) cristae paroticae short,  
stocky; (24) zygomatic ramus of squamosal moderately  
long, widely separated from maxilla; (25) otic ramus of  
squamosal long, not expanded medially into otic plate;  
(26) squamosal-maxillary angle about  $65^{\circ}$ ; (27) columella  
absent; (28) prevomers entire, toothed, separated medially;  
(29) palatines narrow, elongate, separated medially; (30)  
sphenethmoid entire, extending anteriorly beneath posterior  
edge of nasals; (31) anterior ramus of parasphenoid  
moderately broad, not keeled medially; (32) parasphenoid

Figure 101. Lateral (x 12), dorsal (x 6) and ventral (x 6) views of skull of Holoaden bradei (KU 107087).



alae oriented at right angles to anterior ramus, widely separated from median rami of pterygoids; (33) pterygoids slender, anterior rami long, nearly reaching palatines; (34) occipital condyles small, not stalked, widely separated medially; (36) terminal phalanges knobbed; (37) hyoid plate lacking alary processes; (40) m. depressor mandibulae in two slips; (42) males lacking vocal sac; (43) entire skin glandular forming large, indefinite parotoid, flank, and inguinal glands and a large glandular mass on the thighs; (44) tongue oval, not notched, posterior one-half free; (45) toes free of webbing, digital tips narrow; (49) adults small, 20 - 48 mm. SVL; (50) tympanum absent.

Composition.-- Two species are presently known (bradei and luederwaldti).

Distribution.-- The coastal Serras of southeastern Brasil.

Remarks.-- Miranda-Ribeiro (1920, 1926) included Holoaden in the Telmatobiidae with Acris, Iliodiscus, and Telmatobius. He considered the Telmatobiidae to be intermediate between the Hylidae and Leptodactylidae. Lutz (1958) considered Holoaden a member of a generic cline (Cycloramphus-Craspedoglossa-Holoaden) but did not place the genus in the Cycloramphinae. Holoaden is superficially similar to Zachaenus stejnegeri (Craspedoglossa auctorum) but differs in several osteological characters. Holoaden and Euparkerella lack alary processes on the hyoid plate

and differ from all other leptodactylids except Limnomedusa and Sminthillus in this character. Holoaden is osteologically similar to the Andean Niceforonia. This similarity may reflect a faunal relationship between the Brazilian highlands and the Andes or may reflect convergence in the arrangement of the skull bones resulting from adaptation to burrowing. In osteological and external characters, Holoaden does not seem especially closely related to any other genus included in the Eleutherodactylini except Euparkerella.

Hylactophryne Lynch, 1968

(Figs. 102-03)

Hylactophryne Lynch, 1968, Univ. Kansas Publs. Mus. Nat. Hist., 17:511 [Type-species by original designation, Hylodes augusti Dugés, 1879].

Diagnostic definition.-- (7) omosternum large; (9) maxillary arch toothed; (10) alary processes of premaxillae directed posterodorsally, moderately wide at base; (11) palatal shelf of premaxilla broad, deeply dissected; (12) facial lobe of maxilla relatively deep, not exostosed; (13) palatal shelf of maxilla of moderate width, pterygoid process large; (15) nasals very large, in broad median contact; (16) nasals in contact with maxillae, not with pterygoids; (19) frontoparietals not ornamented; (20) frontoparietals not fused to proötics; (22) epiotic

eminences large; (23) cristae paroticae long, narrow; (24) zygomatic ramus of squamosal of moderate length, not reaching maxilla; (25) otic ramus of squamosal long, as long as zygomatic ramus, expanded medially into small otic plate; (26) squamosal-maxillary angle about  $55^{\circ}$ ; (27) columella present; (28) prevomers large, entire, narrowly separated medially; (29) palatines large, broad, separated medially; (30) sphenethmoid entire, large, extending anteriorly beneath posterior edge of nasals; (31) anterior ramus of parasphenoid broad, not keeled; (32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped by median rami of pterygoids; (33) pterygoids moderate-sized, anterior rami long, reaching palatines; (34) occipital condyles moderate-sized, not stalked, widely separated medially; (36) terminal phalanges knobbed; (37) alary processes of hyoid plate on narrow stalks; (40) m. depressor mandibulae in two slips; (42) males with median subgular vocal sac; (43) body free of glands; (44) tongue large, oval, posterior edge free; (45) toes free of webbing or lateral fringes, digital tips narrow, first finger longer than second; (49) males 37 - 77, females 40 - 95 mm. SVL; (50) tympanum visible externally.

Composition.-- Two species are currently recognized (augusti and tarahumaraensis). The former is composed of four subspecies. The group was revised by Zweifel (1956b).

Distribution.-- Mexican Plateau from Arizona, New Mexico, and Texas to central México (Cordillera Volcánica and western Sierra Madre del Sur). An isolated population is known from the mountains in the Isthmus of Tehuantepec.

Remarks.-- Hylactophryne is very distinctive when compared with the Central American and Mexican leptodactylids but is less distinctive when compared with some of the South American eleutherodactylines. When I named Hylactophryne (Lynch, 1968a), I suggested that the genus was allied to Eupsophus. At that time I was under the mistaken impression that Oreobates quixensis was an Eupsophus. Subsequently, I have examined all of the species of frogs referred to the genus Eupsophus by various authors and concluded that the genus Eupsophus in the broad sense (that of Noble, 1931, and Gorham, 1966) includes representatives of five genera. One of these genera is Ischnocnema (see following account), which contains two species in South America. Hylactophryne and Ischnocnema are very similar. The skulls of the two genera differ in proportions but are otherwise the same (Figs. 102-03). These genera are tentatively separated on the basis of the presence (Hylactophryne) or absence (Ischnocnema) of a discoidal fold. The two genera may prove to be independent derivatives of Eleutherodactylus rather than primitive as I previously suggested (Lynch, 1968a). The Eleutherodactylus guentheri group of frogs bear

Figure 102. Dorsal views of skulls of Hylactophryne  
augusti (KU 56187, x 4, left) and Ischnocnema quixensis  
(KU 104388, x 8, right).



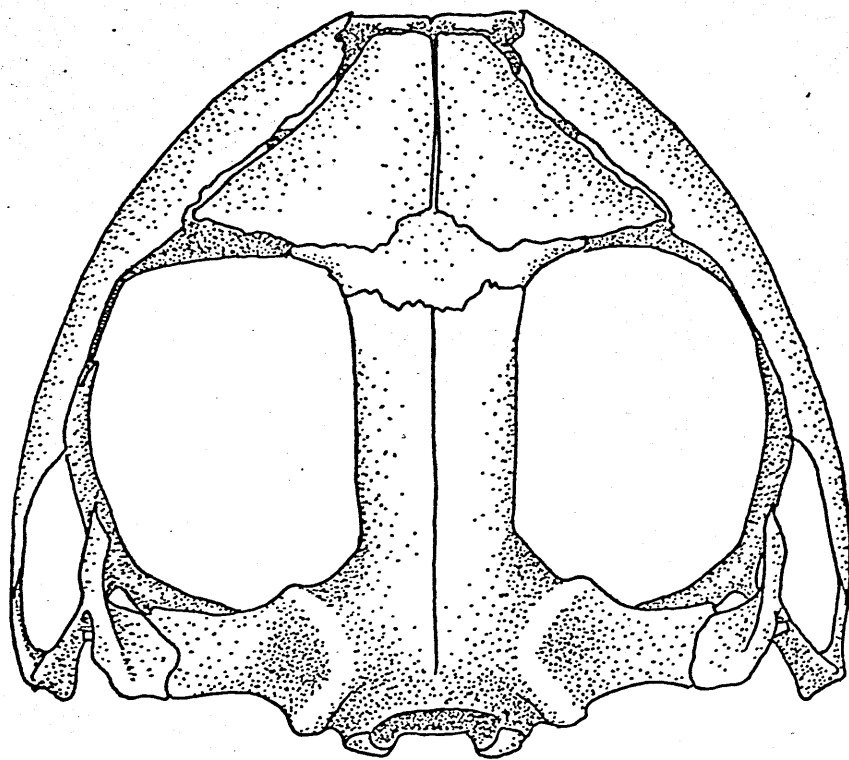
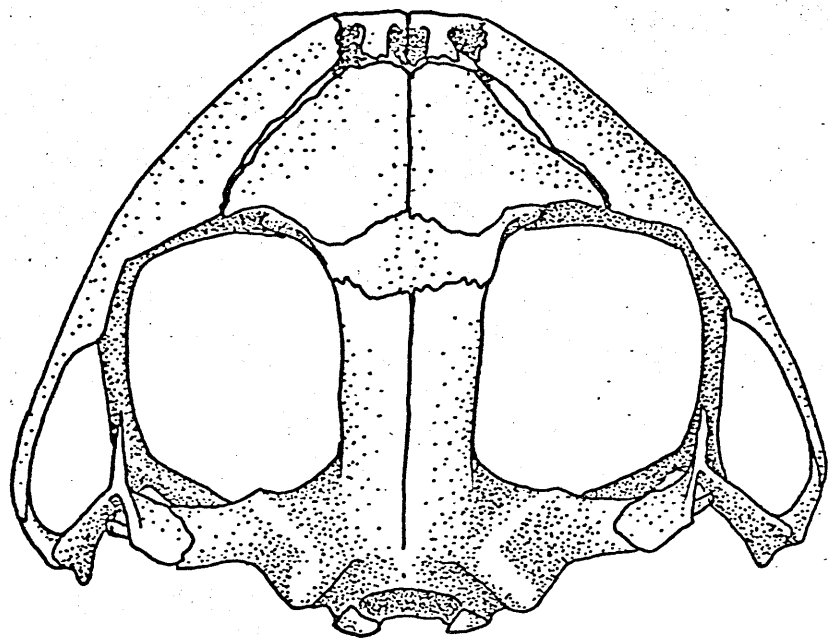
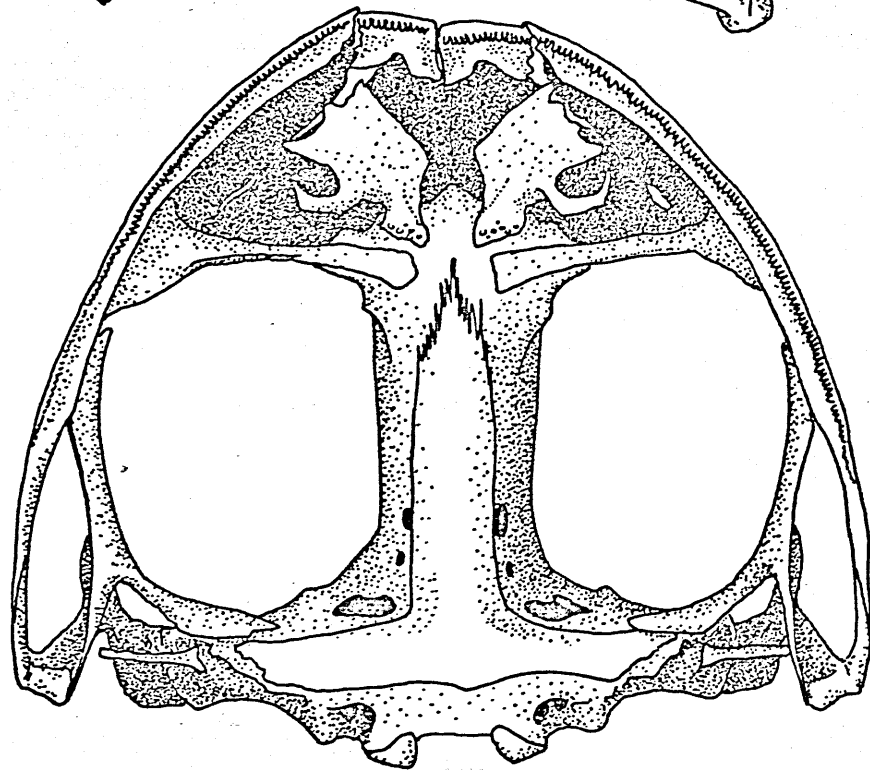
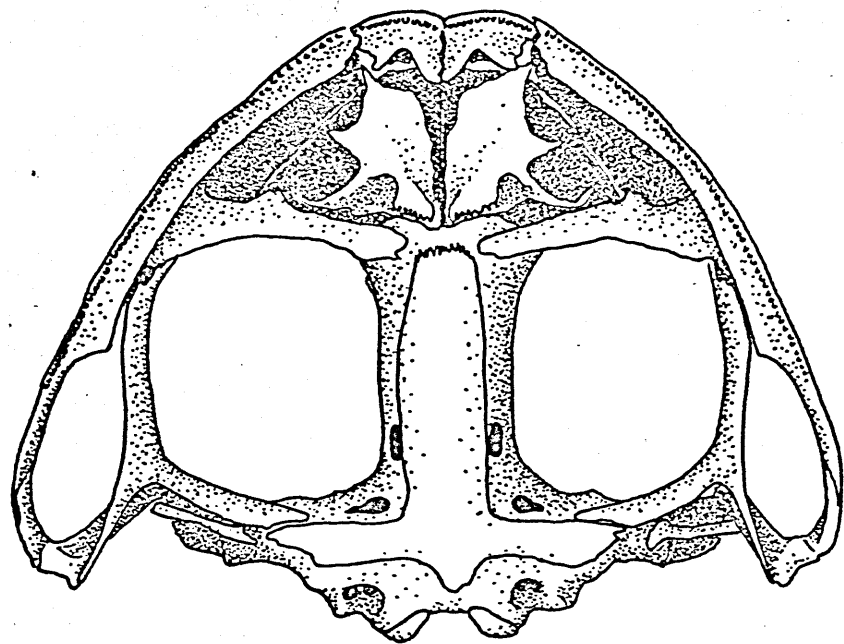
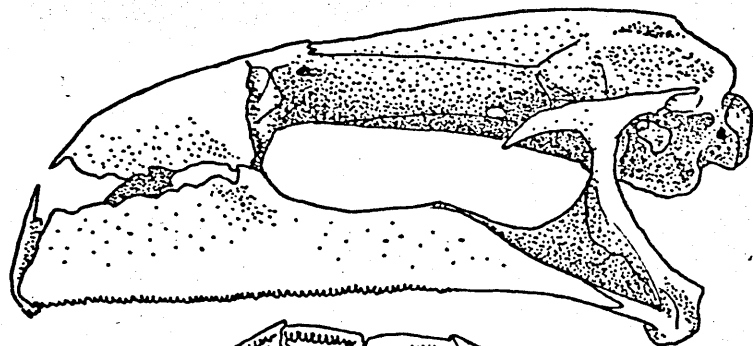
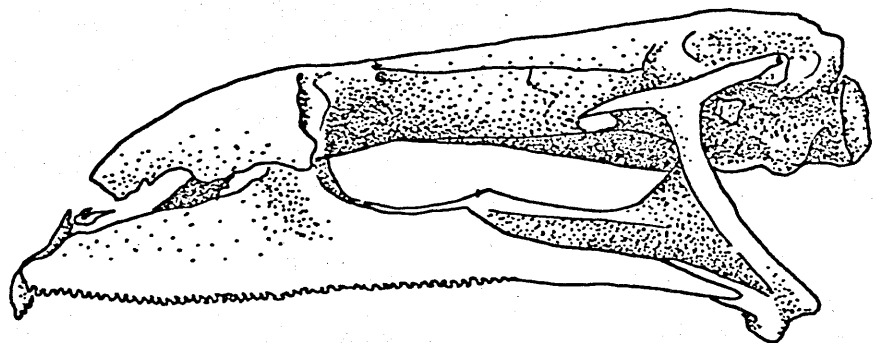


Figure 103. Lateral and ventral views of skulls of Hylactophryne augusti (KU 56187, x 5, left) and Ischnocnema quixensis (KU 104388, x 5 and x 8, right).



considerable resemblance to Ischnocnema quixensis and I. verrucosus. Eleutherodactylus carrioni of the southern Ecuadorian Andes is very similar to Hylactophryne augusti. In both cases, the species of Eleutherodactylus differ from the two genera in having T-shaped terminal phalanges (rather than knobbed phalanges) and in having the terminal transverse groove on the digital pad (rather than no groove or pad). For the present, I do not advocate combining Hylactophryne and Ischnocnema with one another or with Eleutherodactylus.

Ischnocnema Reinhardt and Lütken, 1862.

(Figs. 102-03)

Ischnocnema Reinhardt and Lütken, 1862, Vid. Meddel.

Naturh., Foren., 1861:239 [Type-species by monotypy,

Leiuperus verrucosus Reinhardt and Lütken, 1862].

Oreobates Jiménez de la Espada, 1872, An. Soc. Española

Hist. Nat., 1:87 [Type-species by monotypy, Oreobates

quixensis Jiménez de la Espada, 1872].

Diagnostic definition.-- (7) omosternum moderate-sized; (9) maxillary arch toothed; (10) alary processes of premaxillae directed dorsally, moderately wide at base; (11) palatal shelf of premaxilla relatively deep, notched; (12) facial lobe of maxilla deep, not exostosed; (13) palatal shelf of maxilla relatively narrow, pterygoid process large; (15) nasals very large, in broad median contact;

(16) nasals separated from maxillae and pterygoids; (19) frontoparietals only slightly ornamented; (20) frontoparietals not fused to proötics; (22) epiotic eminences poorly defined; (23) cristae paroticae relatively long and narrow; (24) zygomatic ramus of squamosal relatively long, widely separated from maxilla; (25) otic ramus of squamosal slightly shorter than zygomatic ramus, expanded medially into small otic plate; (26) squamosal-maxillary angle about  $50^{\circ}$ ; (27) columella present; (28) prevomers large, entire, toothed, narrowly separated medially; (29) palatines large, broad, separated medially, bearing odontoid ridge in quixensis; (30) sphenethmoid entire, extending anteriorly beneath posterior edge of nasals; (31) anterior ramus of parasphenoid relatively narrow, not keeled medially; (32) parasphenoid alae oriented at right angles to anterior ramus, slightly overlapped laterally by median rami of pterygoids; (33) pterygoids moderate-sized, anterior rami long, reaching palatines; (34) occipital condyles small, on small stalks, widely separated medially; (36) terminal phalanges knobbed; (37) alary processes of hyoid plate on narrow stalks; (40) m. depressor mandibulae in two slips; (42) males with median subgular vocal sac; (43) body lacking glands; (44) tongue large, oval, posterior edge free; (45) toes lacking webbing, digital tips narrow, first finger longer than second; (46 - 48) (49) adults to 55

mm. SVL; (50) tympanum visible externally.

Composition.-- Two species are presently known (quixensis and verrucosus).

Distribution.-- Western edge of the Amazon basin in Ecuador, northeastern Peru, and adjacent Brasil (quixensis), and in the coastal Serras of southeastern Brasil (verrucosus). Both species are found in forested habitats.

Remarks.-- As mentioned before (Hylactophryne account), Ischnocnema is very similar to Hylactophryne; the two genera are here separated on the basis of trivial external characters, geography, and a lack of knowledge concerning breeding behavior and biology. The similarities in morphology between these two geographically isolated groups of eleutherodactyline frogs is suggestive of an independent origin of each from an Eleutherodactylus stock through a departure from the arboreal adaptive zone. Typical Eleutherodactylus have toe pads (and are frequently mistaken for hylids by the uninitiated herpetologist) and are usually semi-arboreal or arboreal in habits. Both Hylactophryne and Ischnocnema are terrestrial frogs; the former lives in arid, non-forested regions and the latter lives in moist, forested environments.

Hylactophryne and Ischnocnema may represent relicts of a formerly wide-spread eleutherodactyline stock from which more successful genera (Eleutherodactylus) evolved.

At present, too little is known of the osteology of Eleutherodactylus to determine the evolutionary directions.

Niceforonia Goin and Cochran, 1963

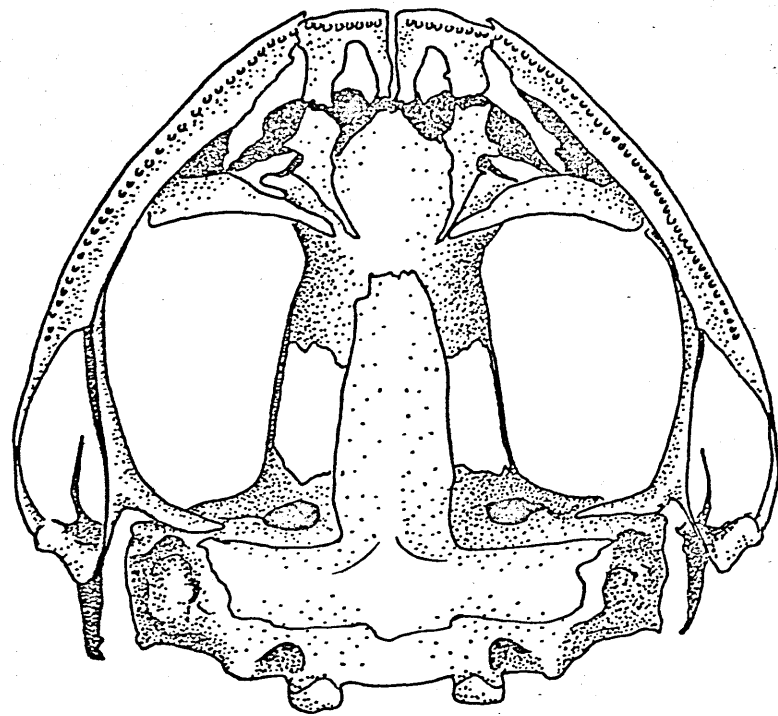
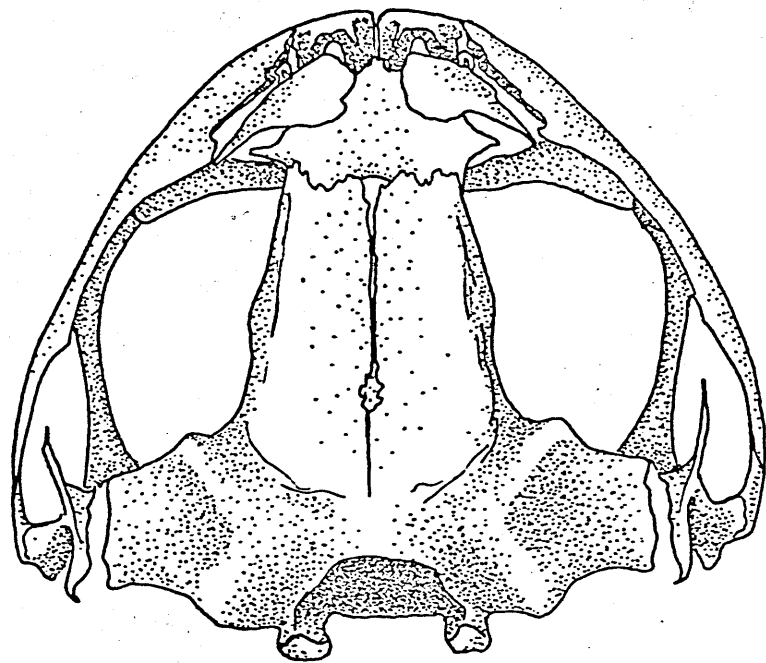
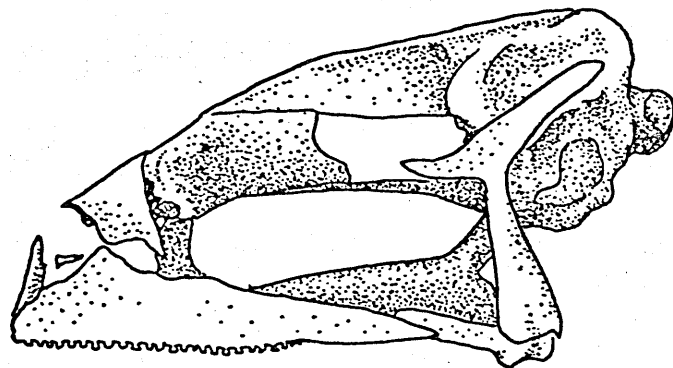
(Fig. 104)

Niceforonia Goin and Cochran, 1963, Proc. California Acad. Sci., 17:499 [Type-species by original designation, Niceforonia nana Goin and Cochran, 1963].

Diagnostic definition.-- (7) omosternum moderate-sized; (9) maxillary arch toothed; (10) alary processes of premaxillae directed dorsally, relatively broad at base; (11) palatal shelf of premaxilla broad, deeply notched; (12) facial lobe of maxilla deep anteriorly, tapering posteriorly; (13) palatal shelf of maxilla broad, pterygoid process moderate-sized; (15) nasals small, narrowly separated medially; (16) nasals in contact with maxillae, not with pterygoids; (19) frontoparietals not ornamented; (20) frontoparietals not fused with proötics; (22) epiotic eminences obsolete; (23) cristae paroticae broad, stocky; (24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; (25) otic ramus of squamosal long, expanded medially into small otic plate; (26) squamosal-maxillary angle about  $55^{\circ}$ ; (27) columella present in most species, absent in montia, probably absent in simonsii; (28) prevomers toothed or not, entire, relatively large, separated medially; (29) palatines

Figure 104. Lateral, dorsal, and ventral views  
of skull of Niceforonia montia (MCZ 24352, x 8).





slender, separated medially; (30) sphenethmoid entire, extending anteriorly beyond anterior edge of nasals; (31) anterior ramus of parasphenoid broad, long, not keeled medially; (32) parasphenoid alae oriented at right angles to anterior ramus, short, not overlapped laterally by median rami of pterygoids; (33) pterygoids small, median rami short, anterior rami relatively long, not reaching palatines; (34) occipital condyles relatively small, stalked, widely separated medially; (36) terminal phalanges knobbed; (37) alary processes on hyoid plate on narrow stalks; (40) m. depressor mandibulae in two slips; (42) males with large median subgular vocal sac; (43) body lacking glands; (44) tongue large, round, free at posterior edge; (45) toes lacking webbing and lateral fringes, digital tips narrow; (46 - 48) (49) adults small, less than 30 mm. SVL; (50) tympanum visible externally, concealed, absent (montia), or possibly absent (simonsii).

Composition.-- Lynch (1968d) included N. nana, N. festae, and N. montia as definite members of the genus and referred N. columbiana and N. simonsii to the genus. Based on examination of paratypes of Eupsophus wettsteini by stereo-radiographs, I now include that species in Niceforonia. Cei's (1968b) Syrrhophus laplacai is probably a member of Niceforonia as well.

Distribution.-- High elevations in the Andes of Colombia, Ecuador, Peru, and Bolivia.

Remarks.-- Goin and Cochran (1963) considered Niceforonia to be most closely allied to Eupsophus. In external characters, Eupsophus and Niceforonia cannot be separated. The cervical cotylar arrangement and the median separation of the occipital condyles suggests that Niceforonia is more closely related to the Eleutherodactylini than to the Alsodini. The breeding biology of Niceforonia is unknown, but the large eggs are suggestive of direct development. The very distinctive sphenethmoid of Niceforonia is duplicated by at least one species of Eleutherodactylus (bogotensis). Niceforonia is separated from Eleutherodactylus because the digital tips are narrow, there is no terminal transverse groove on the digital tips, and the terminal phalanges are knobbed. The slight median separation of the nasal bones in Niceforonia occurs in several groups of Eleutherodactylus, although the trait is uncommon in Eleutherodactylus. The other eleutherodactylines with knobbed terminal phalanges (Amblyphrynus, Holoaden, Hylactophryne, and Ischnocnema) are distinctive when compared with Niceforonia, although Holoaden resembles Niceforonia in the arrangement of the cranial bones. This osteological similarity possibly reflects convergence in view of the dissimilar morphology of the hyoid plates of these two genera.

Sminthillus Barbour and Noble, 1920

(Fig. 105)

Sminthillus Barbour and Noble, 1920, Bull. Mus. Comp.

Zool., 63:402 [Type-species by original designation,

Phyllobates limbatus Cope, 1862].

Diagnostic definition.-- (7) omosternum small, elongate; (9) maxillary arch edentate; (10) alary processes of premaxillae directed dorsolaterally, short, broad at base; (11) palatal shelf broad, deeply dissected; (12) facial lobe of maxilla shallow; (13) palatal shelf of maxilla of moderate width, no pterygoid process; (15) nasals small, narrowly separated medially; (16) nasals in tenuous contact with maxillae, separated from pterygoids; (19) frontoparietals not ornamented; (20) frontoparietals fused to proötics; (22) epiotic eminences present, small; (23) cristae paroticae very broad, stocky; (24) zygomatic ramus of squamosal very short, knobbed; (25) otic ramus of squamosal very long, no otic plate; (26) squamosal-maxillary angle about  $60^{\circ}$ ; (27) columella present; (28) prevomers minute, greatly reduced in size, entire, widely separated medially; (29) palatines slender, widely separated medially, lateral to prevomers; (30) spehenthmoid entire, extending anteriorly to middle of nasals; (31) anterior ramus of parasphenoid narrow, not keeled medially; (32) parasphenoid alae slightly deflected posteriorly, very short, not overlapped laterally by

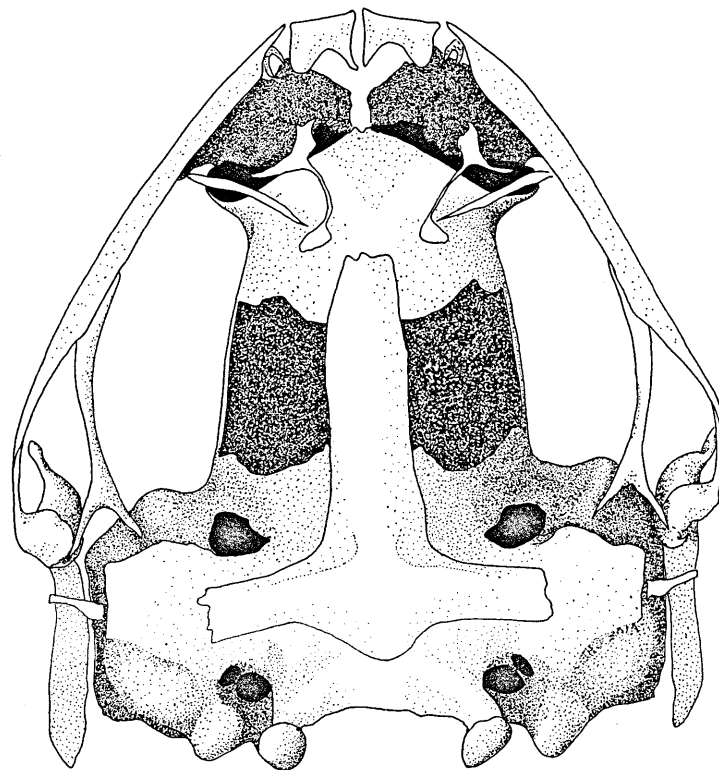
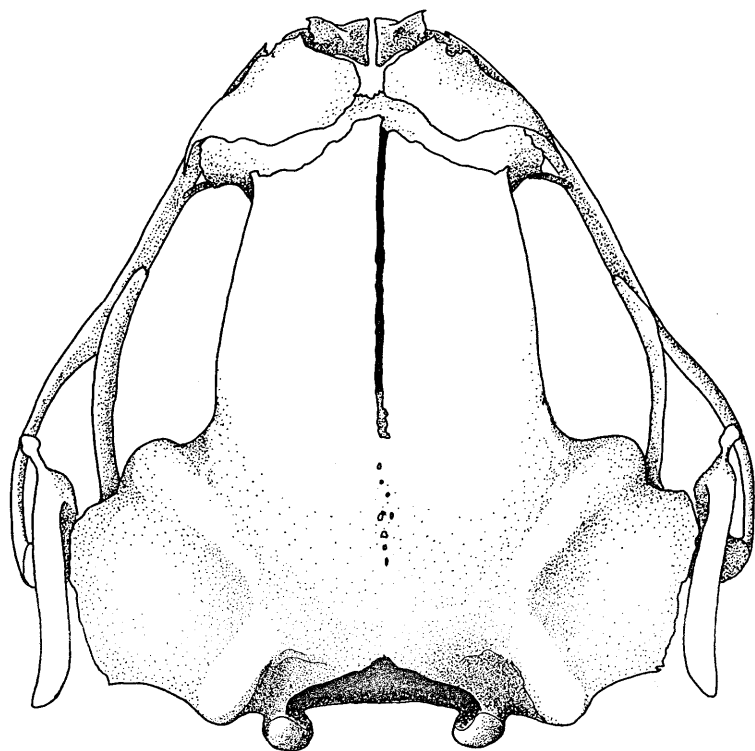
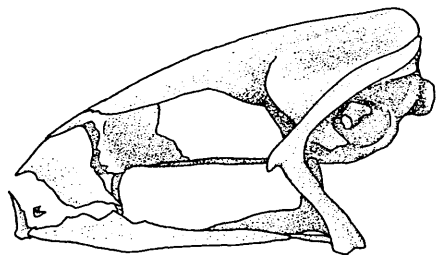
median rami of pterygoids; (33) pterygoids very small, median and posterior rami short, anterior rami relatively long, extending to middle of orbit; (34) occipital condyles small, stalked, widely separated medially; (36) terminal phalanges T-shaped; (37) hyoid plate lacking alary processes; (40) m. depressor mandibulae in two slips; (42) males with median subgular vocal sac; (43) body lacking glands; (44) tongue narrow, posterior one-third free; (45) toes lacking webbing and lateral fringes, digital tips bear pads; (49) adults small, less than 15 mm. SVL; (50) tympanum visible externally.

Composition.-- Monotypic (S. limbatus) with two subspecies.

Distribution.-- Cuba.

Remarks.-- Sminthillus is closely related to the West Indian species of Eleutherodactylus and is most similar to the E. auriculatus group or to the E. dimidiatus group (as defined by Shreve and Williams, 1963). Sminthillus differs from the Alpha division of Eleutherodactylus in two characters--the loss of teeth and the loss of the alary processes of the hyoid plate. Barbour and Noble (1920) considered Sminthillus a dendrobatid or ranoid derivative, but Griffiths (1959) demonstrated that the genus was closely related to Eleutherodactylus, an opinion often voiced by Noble (e.g., 1931).

Figure 105. Lateral (x 14.5), dorsal (x 35),  
and ventral (x 35) views of skull of Sminthillus limbatus  
(KU 68684).



Sminthillus was named by Barbour and Noble (1920) on the basis of a partial epicoracoidal fusion. However, the fusion is not as great as maintained by Noble (1926a, 1931) and occurs in many more frogs than he believed. I consider the presence of the fusion to reflect more accurately the care of a dissection than morphological divergence. The other two species named in Sminthillus are now placed in other genera--the Peruvian species (peruvianus) is placed in the Beta division of Eleutherodactylus (see pp. 507 - 509) and the Brazilian species (brasiliensis) is the only species of the genus Euparkerella.

Syrrhophus Cope, 1878

(Fig. 106)

Epirhexis Cope, 1866, J. Acad. Nat. Sci. Philadelphia, 6:96 [Type-species by original designation, Batrachyla longipes Baird, 1859; suppression of the generic name requested by Lynch, 1967].

Syrrhophus Cope, 1878, Amer. Nat., 12:253 [Type-species by monotypy, Syrrhophus marnockii Cope, 1878].

Malachylodes Cope, 1879, Proc. Amer. Philos. Soc., 18:264 [Type-species by monotypy, Malachylodes guttilatus Cope, 1879].

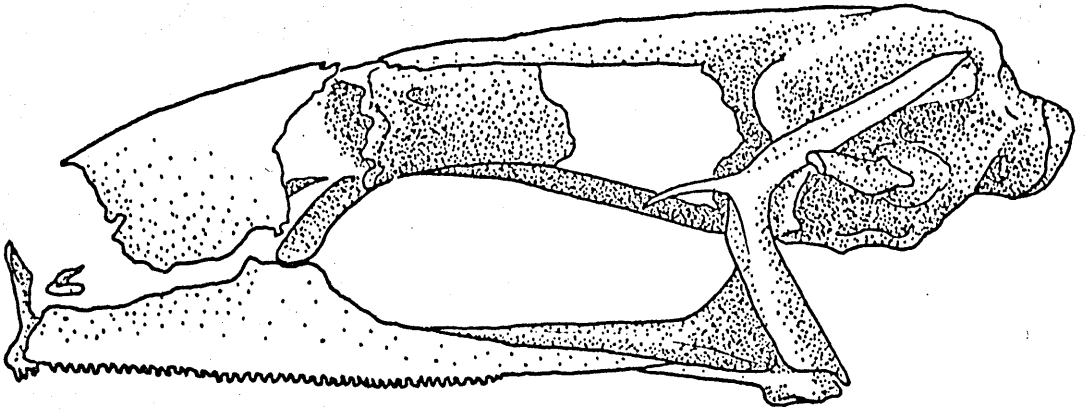
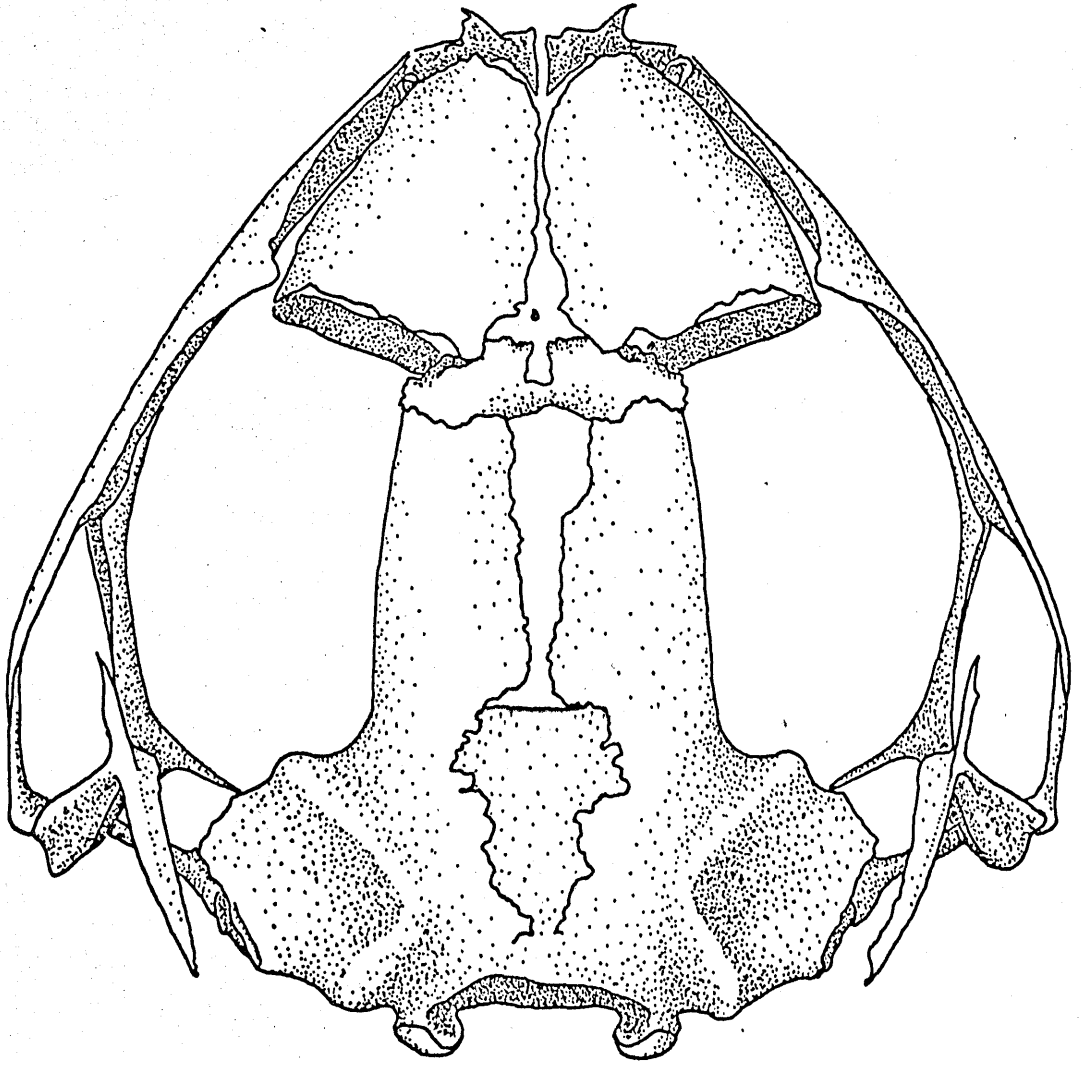
Syrrhophus Boulenger, 1888, Proc. Zool. Soc. London, p. 206 [Emendation of Syrrhophus Cope, 1878].



Syrrhaphus Günther, 1901, Biol. Cent.-Amer., Rept. and  
Batr., p. 215 [Emendation of Syrrhophus Cope, 1878;  
hence taking same type-species (marnockii) and not  
verruculatus as claimed by Gorham (1966)].

Diagnostic definition.-- (7) omosternum moderate-sized;  
(9) maxillary arch toothed; (10) alary processes of  
premaxillae directed dorsally, relatively narrow at base;  
(11) palatal shelf of premaxilla broad, deeply dissected;  
(12) facial lobe of maxilla shallow; (13) palatal shelf  
of maxilla broad anteriorly, narrowing posteriorly, no  
pterygoid process; (15) nasals large, in broad median  
contact; (16) nasals not in contact with maxillae or  
pterygoids; (19) frontoparietal not ornamented; (20)  
frontoparietal fused to proötic; (22) epiotic eminences  
obsolete; (23) cristae paroticae short, broad; (24)  
zygomatic ramus of squamosal very slender, relatively  
short; (25) otic ramus of squamosal elongated, not forming  
otic plate; (26) squamosal-maxillary angle about  $65^{\circ}$ ;  
(27) columella present; (28) prevomers reduced in size,  
dentigerous ramus lost, widely separated medially, or  
dentigerous rami present, bearing a few teeth; (29)  
palatines narrow, separated medially, in contact with  
maxillae; (30) sphenethmoid entire, extending anteriorly  
beneath posterior edge of nasals; (31) anterior ramus of  
parasphenoid broad, not keeled medially; (32) parasphenoid  
alae deflected posteriorly, short, widely separated from

Figure 106. Lateral and dorsal views of skull  
of a male Syrrhophus pipilans (KU 59950, x 12).



median rami of pterygoids; (33) pterygoids slender, all rami short; (34) occipital condyles small, not stalked, widely separated medially; (36) terminal phalanges T-shaped; (37) alary processes of hyoid plate on narrow stalks; (40) m. depressor mandibulae in two slips; (42) males with or without large median subgular vocal sac; (43) axillary and/or inguinal glands present; (44) tongue narrow to relatively broad and rounded, posterior edge free; (45) toes lacking webbing, bearing lateral fringes or not, digital tips very slightly to broadly dilated into pads; (49) adults 16 - 40 mm. SVL; (50) tympanum concealed or visible externally.

Composition.-- Lynch (1969b) recognized 12 species, two of which are polytypic: cystignathoides, dennisi, guttulatus, interorbitalis, leprus, longipes, marnockii, modestus, nivocolimae, pipilans, rubrimaculatus, and verrucipes.

Distribution.-- Discontinuous in the Pacific lowlands from Sinaloa, México, to El Salvador, also in the eastern lowlands of México from the Edwards Plateau of Texas to British Honduras. Highland species occur along the Sierra Madre Oriental up to 2000 meters.

Remarks.-- Lynch (1968a, 1969b) discussed the generic separation of Eleutherodactylus, Syrrhophus, and Tomodactylus. In external characters, Syrrhophus is not separable from all Eleutherodactylus. The osteological

peculiarities of Syrrhophus are duplicated by Tomodactylus and the Alpha division of Eleutherodactylus. Syrrhophus and Tomodactylus are distinguished in some external characters (lumbar gland, arrangement of the supernumerary plantar tubercles) and by one pedomorphic skeletal character--the sphenethmoid is usually divided in Tomodactylus and is entire in Syrrhophus. The division of the sphenethmoid is a pedomorphic feature and therefore should not be given undue weight in any classification. The separation of Syrrhophus and Tomodactylus as distinct genera is a debatable point, and I retain them as generically distinct only as a matter of convenience. The character of the glands used by Lynch (1968a) to separate the two genera tends to be less diagnostic when the species of the two genera from northwestern México are compared (S. interorbitalis, S. modestus, T. saxatilis).

Until a comprehensive revision of the genus Eleutherodactylus is completed and the skeletons of the majority of species studied, it will not be possible to argue definitively whether the genera Syrrhophus and Tomodactylus are derivatives of the Alpha or the Beta divisions of Eleutherodactylus. In an attempt to clarify this point, I studied representatives of all species groups of Central American Eleutherodactylus and found no group which exhibits the osteological characteristics of the Alpha division. If Syrrhophus and Tomodactylus were

derivatives of the South American groups of the Alpha division, one might expect some relict species to be distributed in parts of Lower Central America. However, all Central American species of Eleutherodactylus examined by me are Beta division Eleutherodactylus, as are those species of the genus found in the Chocó of Colombia and Ecuador. Therefore I suggest that the Mexican Syrrhophus and Tomodactylus are more closely related to the West Indian Eleutherodactylus (Alpha division) than to any other groups of the genus. Within the Alpha division, the auriculatus group most closely approaches the morphology of the endemic Mexican eleutherodactyline genera Syrrhophus and Tomodactylus.

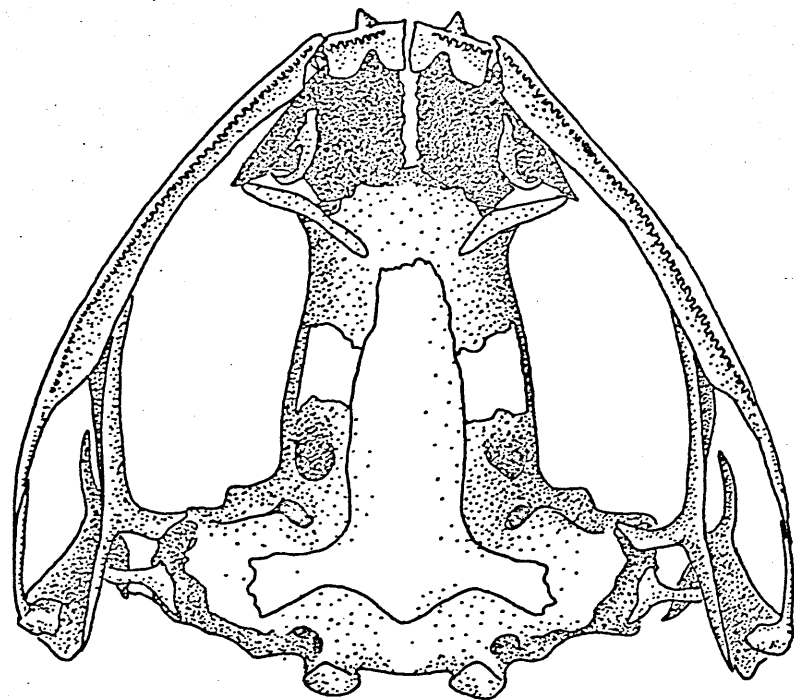
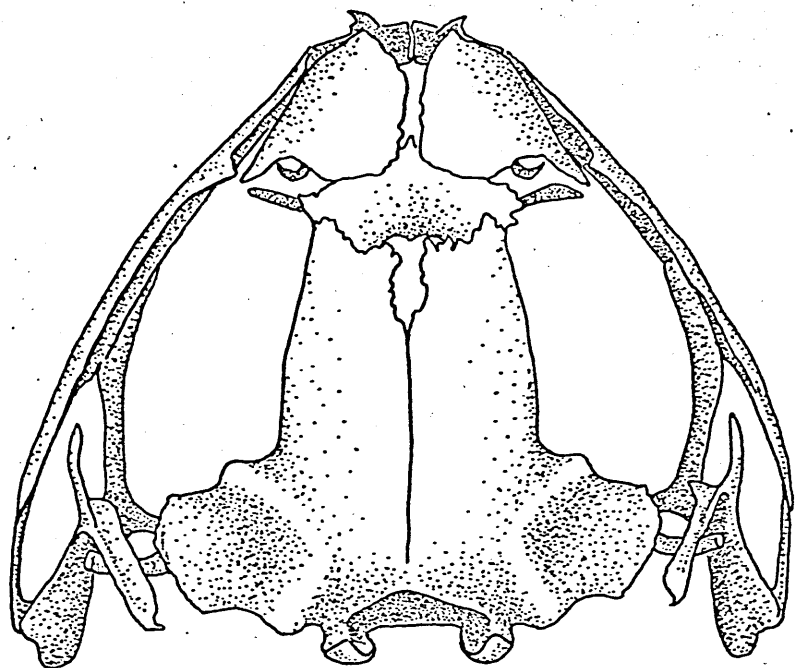
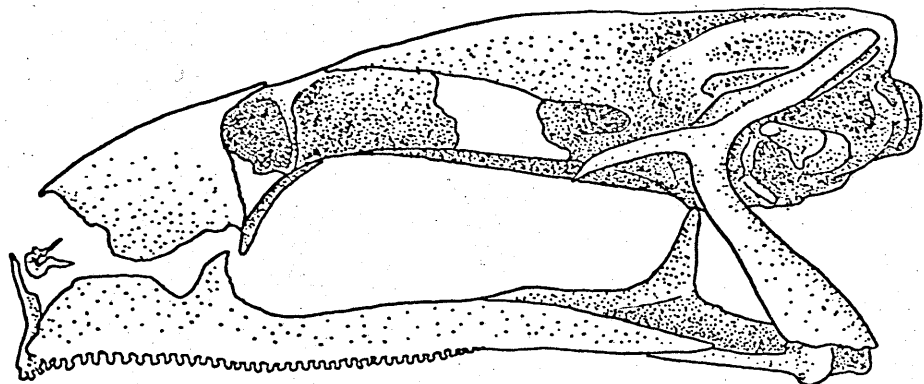
Tomodactylus Günther, 1901

(Fig. 107)

Tomodactylus Günther, 1901, Biol. Centr.-Amer., Rept. and Batr., p. 219 [Type-species by monotypy, Tomodactylus amulae Günther, 1901].

Diagnostic definition.-- (7) omosternum moderate-sized; (9) maxillary arch toothed; (10) alary processes of premaxillae directed dorsally, broad at base; (11) palatal shelf of premaxilla narrow, palatal process elongate; (12) facial lobe of maxilla shallow; (13) palatal shelf of maxilla narrow, pterygoid process moderate-sized; (15) nasals large, in broad median contact; (16) nasals not

Figure 107. Lateral, dorsal, and ventral views of skull of a female Tomodactylus nitidus (KU 102649, x 8).





in contact with maxillae or pterygoids; (18) frontoparietal fontanelle absent in adults, often present in young males; (19) frontoparietals not ornamented; (20) frontoparietal fused to prootic; (22) epiotic eminences obsolete; (23) cristae paroticae short and stocky; (24) zygomatic ramus of squamosal sliver-like, very short; (25) otic ramus of squamosal very long, no otic plate; (26) squamosal-maxillary angle  $50 - 60^{\circ}$ ; (27) columella present; (28) prevomers reduced in size, edentate, widely separated medially; (29) palatines slender, widely separated medially; (30) sphenethmoid usually divided, not extending anteriorly to nasals; (31) anterior ramus of parasphenoid relatively broad, not keeled medially; (32) parasphenoid alae deflected posteriorly, short, not overlapped by median rami of pterygoids; (33) pterygoids slender, all rami short; (34) occipital condyles small, not or but slightly stalked, widely separated medially; (36) terminal phalanges T-shaped; (37) alary processes of hyoid plate on narrow stalks; (40) m. depressor mandibulae in two slips; (42) males with large, median, subgular vocal sac; (43) lumbar gland usually well defined, axillary glands sometimes present; (44) tongue relatively small, narrow, posterior edge free; (45) toes lacking webbing, digital tips slightly to broadly dilated; (49) adults 21 - 31 mm. SVL; (50) tympanum visible externally.

Composition.-- The genus was revised by Dixon (1957) and two species were subsequently named. Nine species are presently recognized: albolabris, angustidigitorum, dilatus, fuscus, grandis, nitidus (3 subspecies), rufescens, saxatilis, and syristes. Dixon and Webb (1966) briefly commented on an unnamed species from Nevado de Colima, Jalisco, México.

Distribution.-- The Cordillera Volcánica of México from western Veracruz to Colima; the Oaxacan Plateau, the Sierra Madre del Sur of Oaxaca and Guerrero, and the Pacific lowlands from Sinaloa to Michoacán. The genus is largely allopatric to Syrrhophus.

Remarks.-- Gallardo (1965) placed Tomodactylus in the Leptodactylinae and Syrrhophus and Eleutherodactylus in the Eleutherodactylinae. This association was based on erroneous data concerning the breeding biology of Tomodactylus.

Tomodactylus is primarily a lower montane genus, whereas the closely related Syrrhophus is primarily a lowland genus (Lynch, 1969b), but the two genera are sympatric in the lowlands of western México. The differences between them are expressed to the greatest degree in eastern and southern México and expressed to a lesser degree in western México, suggesting that the generic dichotomy occurred in western México.

Tribe incertae sedisScythrophrys new genus

Type-species.-- Zachaenus sawayae Cochran, 1953.

The following characteristics of the diagnostic definition are observable: (1) sternum cartilaginous; (2) vertebral shield lacking; (6) cranial bones not dermostosed; (7) omosternum small; (8) sacral diapophyses rounded; (9) maxillary arch toothed, teeth blunt, pedicellate; (14) maxillary arch complete; (18) frontoparietal fontanelle lacking; (21) temporal arcade lacking; (24) zygomatic ramus of squamosal relatively long, widely separated from maxilla; (28) prevomers toothed, dentigerous processes large, transversely elongate, situated posterior to choanae; (36) terminal phalanges apparently knobbed; (40) m. depressor mandibulae in two slips, pars tympanicus very large, p. scapularis minute; (41) pupil horizontal; (43) body lacking glands; (44) tongue relatively large, posterior edge free; (45) toes lacking webbing but have lateral fringes, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged or spade-like, digital tips narrow on fingers, those of toes slightly dilated, thumb very short; (49) single adult female known is 16.9 mm. SVL; (50) tympanum concealed.

Etymology.-- Greek, scythros + phryne, meaning "sullen toad".

Remarks.-- A single specimen of this southeastern Brazilian frog is known; it was named as a member of Zachaenus by Cochran (1953). In external appearance, the frog resembles Physalaemus (maculiventris group) or Paratelmatobius and, in some respects, Zachaenus. Cochran (1953) considered the small tubercles on the upper eyelid as indicative of some relationship with Zachaenus but noted the many points of disagreement between parvulus and sawayae. The most striking difference between the two species is seen in the length and shape of the fingers (Fig. 94). The very short thumb of Scythrophrys is suggestive of a reduced phalangeal formula for the hand. The tympanum is recessed and smaller than indicated by Cochran (1953).

Scythrophrys is placed with confidence in the Telmatobiinae but is not assigned to any tribe, because many characters are not known. Based on the available information, I consider the genus to belong either to the Grypiscini or Eleutherodactylini, but until the osteology and breeding biology of Scythrophrys are known, definite assignment to a tribe would be presumptuous.

Cochran's (1953) description of the holotype (USNM 125530) is relatively accurate. My measurements of the holotype differ somewhat from hers, reflecting either differences in techniques or possibly shrinkage. I recorded the following measurements (in millimeters): snout-vent length 16.9, shank length 8.4, head width 6.3,

head length 5.6, eye length 1.9, eyelid width 1.7, and interorbital distance 2.6. A few cranial characters are visible through a small tear in the skin of the head. The frontoparietals are broad and a fontanelle is lacking. The nasals appear to be relatively large and in median contact. Two characters of the foot were not mentioned by Cochran. There is a small calcar on the heel and a narrow outer tarsal fold extending for the length of the tarsus onto the fifth toe.

ELOSIINAE Miranda-Ribeiro, 1926

Elosiidae Miranda-Ribeiro, 1926:27.

Elosiinae: Noble, 1931:504. Gallardo, 1965:84.

Miranda-Ribeiro (1926) proposed the Elosiidae for three genera; the concept and content of the group has remained unchanged since its proposal. Three genera are presently included in the subfamily: Crossodactylus, Hylodes (= Elosia auctorum), and Megaelosia. Cochran (1938) named Crossodactylodes, which she considered possibly related to the elosines. She thought that the digital morphology of Crossodactylodes indicated that the genus exhibited primitive elosine characters. The apparent dorsal dermal glands on the digital pads of Crossodactylodes are artifacts reflecting the Y-shaped terminal phalanges. Goin and Cochran (1963) suggested that Trachyphrynus was related to Crossodactylus. I previously discussed this

point and placed Trachyphrynus in the synonymy of Eleutherodactylus (Lynch, 1968d).

Noble (1922, 1931) considered the Elosiinae to be a bufonid group. The subfamily was associated with the Leptodactylidae by Davis (1936), who pointed out that the Bufonidae and Leptodactylidae could be familiarly distinguished. The type-genus of the subfamily, Elosia Tschudi, 1838, is a synonym of Hylodes Fitzinger, 1826 (which is not to be confused with Hylodes Fitzinger, 1843, which is a synonym of Eleutherodactylus Duméril and Bibron, 1841). The family-group name need not be changed simply because the type-genus is a synonym (see Article 40, International Code of Zoological Nomenclature, 1961). At any rate, the family-group name could not be changed so as to be based on Hylodes Fitzinger, 1826, because Günther (1859a) proposed a Hylodidae based on Hylodes Fitzinger, 1843.

Until recently, the subfamily was known only from southeastern Brasil and Misiones Province, Argentina, but it is now known to occur also in Venezuela (Cerro Duida, Guiana Massif). The subfamily is homogeneous morphologically and is readily distinguished from all other leptodactylid groups. The following diagnostic characters are common to the three genera of the Elosiinae: (1) sternum cartilaginous, tending to calcify in old adults; (2) vertebral shield lacking; (3) transverse processes of

anterior presacral vertebrae short, those of posterior presacral vertebrae also shortened; (4) cervical cotylar arrangement type I; (5) cervical and second vertebrae not fused; (6) cranial bones not involved in dermostosis; (7) omosternum present, moderate-sized; (8) sacral diapophyses rounded; (9) maxillary arch toothed, teeth pointed, pedicellate; (12) facial lobe of maxilla shallow; (13) palatal shelf of maxilla narrow, no pterygoid process; (15) nasals small, widely separated medially; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle lacking; (19) frontoparietals not ornamented; (21) temporal arcade lacking; (23) carotid artery passes dorsal to skull bones; (27) columella present; (30) sphenethmoid very large, entire, extending anteriorly to anterior edge of nasals; (36) terminal phalanges T-shaped; (37) alary processes of hyoid plate on narrow stalks; (38) cricoid cartilage not divided ventrally; (39) m. petrohyoideus anterior and m. sternohyoideus insert on lateral edge of hyoid plate; (40) m. depressor mandibulae in two slips; (41) pupil horizontal; (43) body lacking glands; (44) tongue large, not notched, posterior edge free; (45) toes bearing large lateral fringes, large flap-like tarsal fold present, outer metatarsal tubercle present, inner metatarsal tubercle not spade-like, digital tips broad; (46) larvae with 2/3 tooth rows, labial papillae broadly interrupted anteriorly; (47) amplexus axillary in

known species; (48) eggs small, numerous, laid in moist terrestrial situations or in ponds or streams; (50) tympanum visible externally; (51) each digital pad has a pair of dermal, scute-like glandular pads on dorsal surface. The vertebral arches of all elosiines are very non-imbricate and the vertebrae and coccyx are poorly ossified.

The Elosiinae are of particular interest in that the poison-arrow frogs (Dendrobatidae) are apparently derived from this leptodactylid subfamily. The two groups agree in cranial morphology, vertebral columns, the T-shaped terminal phalanges, the dermal glandular pads on top of the digital pads, and in the presence, in at least some species of each group, of toxic skin secretions (the secretions of the elosiines have not been chemically analyzed). The two groups differ in breeding biology and in the architecture of the pectoral girdle.

Crossodactylus best fits my concept of the primitive elosine but has diverged in at least one character--the loss of the quadratojugal. The genus is distinctive in its ranoid pattern of the attachment of the distal tendons of the thigh musculature. The ranoid pattern of the thigh musculature of Crossodactylus is exactly like that seen in the dendrobatids and mitigates the importance of one of the criteria used by Griffiths (1963) to associate the dendrobatids as a Neotropical subfamily of the Ranidae. Crossodactylus has a median subgular vocal sac and nuptial asperities



(cluster of spines) in the males. This condition is like that seen in most Telmatobiinae (excepting the Eleutherodactylini which lack nuptial asperities); I regard the presence of vocal sac and nuptial asperities as primitive. The tadpoles of Crossodactylus have median vents in contrast to the dextral vents of the tadpoles of Hylodes and Megaelosia. Hylodes and Megaelosia have the bufonid pattern of the arrangement of the distal tendons of the thigh musculature, derived conditions of the vocal apparatus, and quadratojugal bones. I envision the dendrobatids as having diverged from the Crossodactylus stock prior to the loss of the quadratojugal, but after Hylodes and Megaelosia had evolved.

Crossodactylus Duméril and Bibron, 1841

(Fig. 108)

Crossodactylus Duméril and Bibron, 1841, *Érpetologie générale*, 8:635 [Type-species by monotypy, Crossodactylus gaudichaudii Duméril and Bibron, 1841].

Limnocharis Bell, *in* Darwin, 1843, *Zool. Voyage Beagle*, Reptiles, 5:33 [Type-species by monotypy, Limnocharis fuscus Bell, 1843].

Tarsopterus Reinhardt and Lütken, 1862, *Vid. Meddel.*

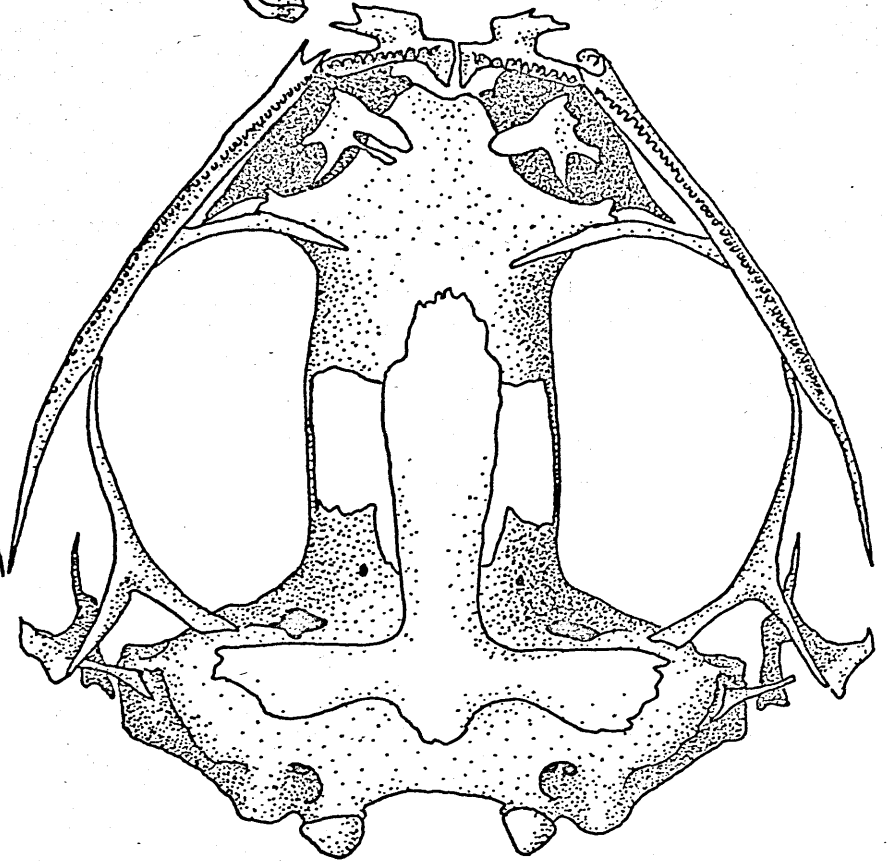
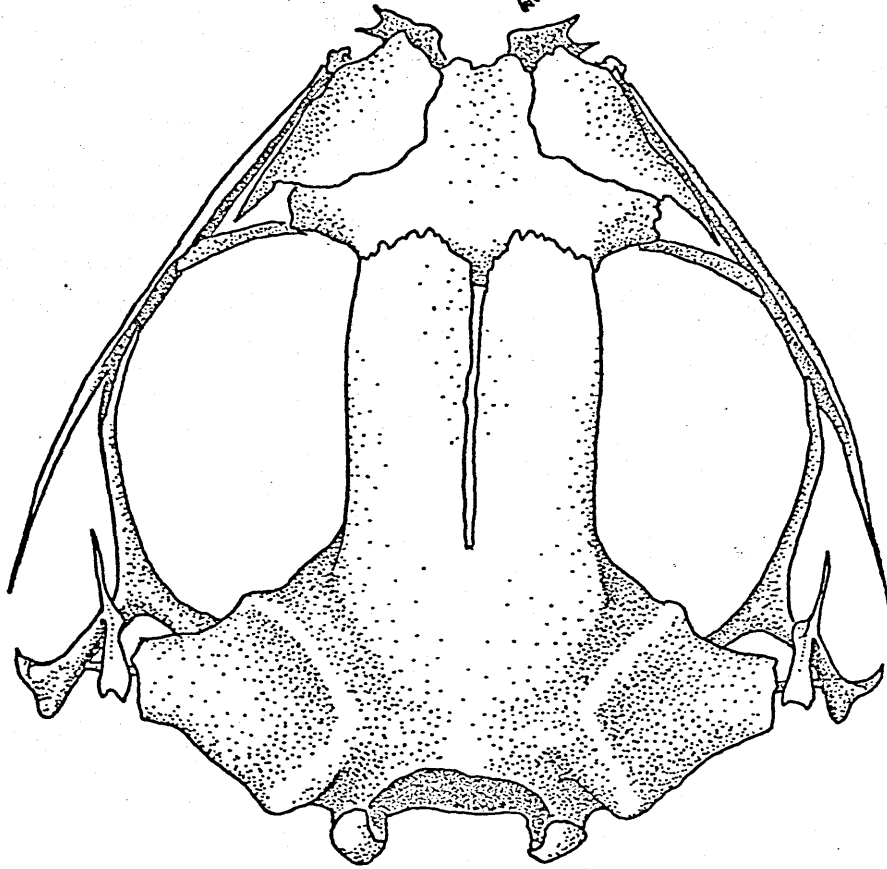
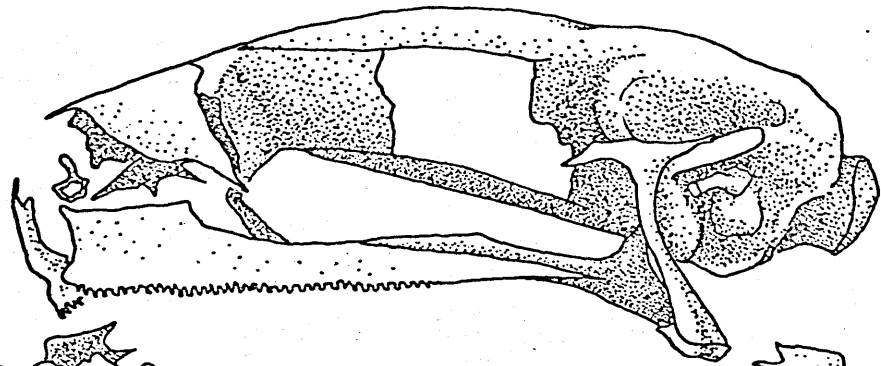
*Naturh., Foren.*, 1861:177 [Type-species by monotypy, Tarsopterus trachystomus Reinhardt and Lütken, 1862].

Calamobates DeWitte, 1930, Miss. Biol. Belge Bresil, 2:219

[Type-species by monotypy, Calamobates bouleengeri  
DeWitte, 1930].

Diagnostic definition.-- (10) alary processes of premaxillae directed anterodorsally and laterally, broad at base; (11) palatal shelf of premaxilla narrow, palatal process elongate; (14) maxillary arch incomplete, maxilla tapering posteriorly, quadratojugal absent; (16) nasals separated from both maxillae and pterygoids; (20) frontoparietal fused to proötic; (22) epiotic eminences moderately distinct; (23) cristae paroticae short, stocky; (24) zygomatic ramus of squamosal of moderate length, pointed, widely separated from maxilla; (25) otic ramus of squamosal slightly shorter than zygomatic ramus, no otic plate; (26) squamosal-maxillary angle about 50°; (28) prevomers moderately small, separated medially, dentigerous ramus lost or not, rarely toothed; (29) palatines small, narrow, widely separated medially; (31) anterior ramus of parasphenoid short, broad, not keeled medially; (32) parasphenoid alae oriented at right angles to anterior ramus, short, widely separated from median rami of pterygoids; (33) pterygoids with slender rami, anterior rami not reaching palatines; (34) occipital condyles small, stalked, widely separated medially; (35) mandible lacking odontoids; (42) males with median, subgular vocal sac, nuptial spines in a cluster in all species; (46) larvae with median vent; (49) adults

Figure 108. Lateral, dorsal, and ventral views  
of skull of Crossodactylus gaudichaudii (KU 92759, x 8).



relatively small, less than 40 mm. SVL.

Composition.-- Six species are presently recognized (aeneus, dispar, gaudichaudii, grandis, schmidti, and trachystoma), although some authors favor regarding dispar and grandis as conspecific. The most recent revision of the genus (Cochran, 1955) did not treat C. grandis B. Lutz, 1951, or C. schmidti Gallardo, 1961.

Distribution.-- Southeastern Brasil in the lowlands from southern Minas Gerais to Misiones Province, Argentina.

Remarks.-- The generic synonymy of Crossodactylus has been stable for many years. Cochran (1955) and Gallardo (1961) presented studies of intrageneric variation and relationships. Crossodactylus is primitive to the other elosines in tadpole morphology (median vent) and in the secondary sex characteristics (median subgular vocal sac and nuptial asperities), but is specialized in the loss of the quadratojugal. Hylodes is similar to Crossodactylus in having a poorly ossified quadratojugal, but differs from Crossodactylus in the other characteristics mentioned.

The ranoid pattern of the attachment of the distal tendons of the thigh musculature of Crossodactylus distinguishes the genus from the other elosines, as well as from all other Neotropical leptodactylids. The thigh musculature of Crossodactylus adds yet another character to the impressive list of characters shared by the

dendrobatids and Crossodactylus. Noble (1931) argued that the Dendrobatinae were derived from the bufonid genus Crossodactylus, because he found the digital pad structure of the two groups to be identical and to exist in no other Neotropical bufonoid frogs. Noble argued that the condition of the epicoracoidal cartilages of Crossodactylus is precursorial to the condition seen in developing Phyllobates (= Colostethus) subpunctatus. Noble considered his data adequate to demonstrate that the firmisternal dendrobatids passed through an arciferal condition in ontogeny.

Griffiths (1959, 1963) sought to ally the dendrobatids with ranids and argued that the dendrobatids do not pass through an arciferal stage in development. The developmental pattern of the pectoral girdle exhibited by Colostethus subpunctatus is clearly ranoid. My own study of this subject completely supports that of Griffiths.

Griffiths (1963) rejected Noble's argument that the thigh musculature was of primary importance in anuran classification, but cited the thigh musculature as additional evidence supporting his contention that dendrobatids are a ranid subfamily. Griffiths cited the similar development of the digital pads of the Petropedetinae (Ranidae) as supportive evidence for the close relationship between the dendrobatids and ranids. His argument requires that we ignore the many similarities between elosines and dendrobatids and regard several

character complexes as evolving in a parallel fashion in leptodactylids and ranids. Associating the dendrobatids with the bufonoids requires that we regard the firmisternal pectoral girdles of dendrobatids and ranids to have been independently evolved. This position is made less objectionable by the occurrence of a nearly complete transition from arcifery to firmisterny within the Neotropical Bufonidae. Noble's (1922) position that the firmisternal pectoral girdle has appeared more than once is regarded as correct.

Griffiths (1963) cited several other characters as exclusively ranoid. The bursa angularis oris is not restricted to dendrobatids and ranids as Griffiths stated but occurs in most, if not all, groups of advanced frogs (Baldauf and Tanzer, 1965, Trueb, 1966, 1968, 1969, and Starrett, 1968).

The dendrobatids are amply distinct from the elosline leptodactylids. I do not intend to present an argument that the two families ought to be combined, because I think that there is value in recognizing the small, brightly colored, poisonous Neotropical dendrobatid frogs as familially distinct. The dendrobatids have lost the palatines, which are retained, although they are small, in elosline leptodactylids. The firmisternal architecture of the pectoral girdle of dendrobatids is markedly different from the arciferal architecture exhibited by all

leptodactylids. The breeding behavior and biology of the dendrobatids is not unique among frogs but is very different from that of the elosiine leptodactylids. Dendrobatid tadpoles usually have 2/3 tooth rows, although several species have reduced numbers (Starrett, 1960). The tadpoles of all dendrobatids have a broad anterior interruption of the labial papillae as do most leptodactylids. Dendrobates has either a median or dextral vent, whereas all known tadpoles of Colostethus and Phyllobates have dextral vents.

Hylodes Fitzinger, 1826

(Fig. 109)

Hylodes Fitzinger, 1826, Neue Class. Rept., p. 38

[Type-species by monotypy, Hylodes ranoides (= Hyla ranoides Spix, 1824)].

Enydrobius Wagler, 1830, Nat. Syst. Amph., p. 202

[Substitute name for Hylodes Fitzinger, 1826; hence taking same type-species].

Elosia Tschudi, 1838, Classif. Batr., p. 77 [Type-species

by monotypy, Elosia nasuta Tschudi, 1838].

Scinacodes Fitzinger, 1843, Syst. Rept., p. 32 [Type-species

by original designation, Hyla nasus Lichtenstein, 1823].

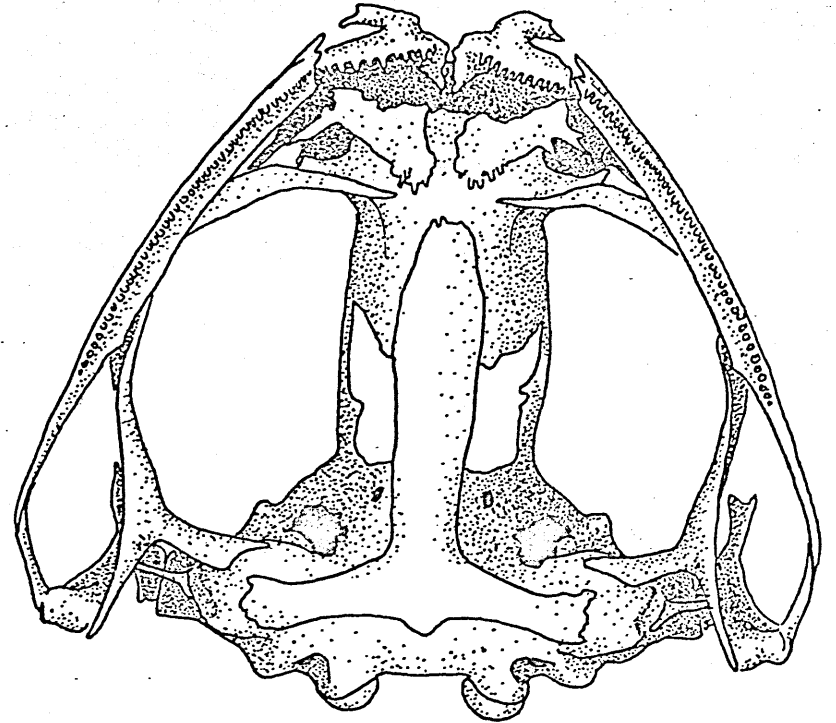
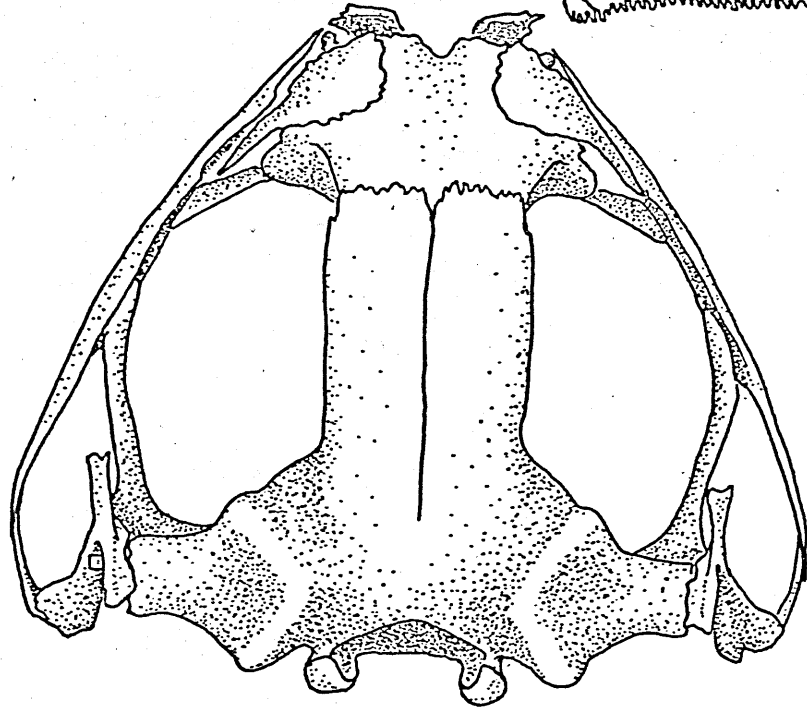
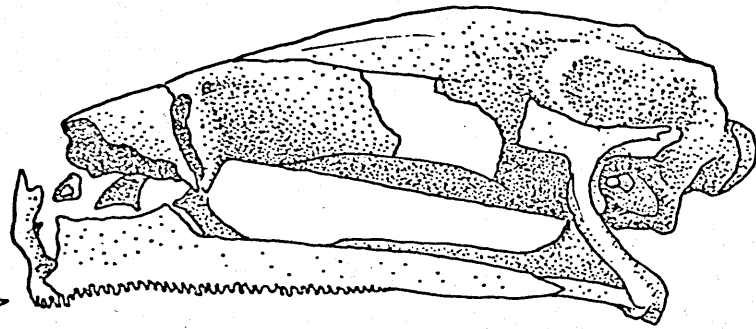
Diagnostic definition.-- (10) alary processes of premaxillae directed anterodorsally and laterally, broad



at base; (11) palatal shelf of premaxilla relatively narrow, palatal process relatively small; (14) maxillary arch complete, quadratojugal poorly ossified; (16) nasals not in contact with maxillae or pterygoids; (20) frontoparietals fused to proötics; (22) epiotic eminences moderately distinct; (23) cristae paroticae short, stocky; (24) zygomatic ramus of squamosal short, truncate, widely separated from maxilla; (25) otic ramus of squamosal about as long as zygomatic ramus, not expanded into otic plate; (26) squamosal-maxillary angle about  $40^{\circ}$ ; (28) prevomers entire, toothed, separated medially; (29) palatines long, narrow, widely separated medially; (31) anterior ramus of parasphenoid short, broad, keeled medially in at least some species; (32) parasphenoid alae oriented at right angles to anterior ramus, narrowly overlapped laterally by median rami of pterygoids; (33) pterygoids relatively small, rami slender, anterior rami elongate, reaching palatines; (34) occipital condyles small, not stalked, widely separated medially; (35) mandible lacking odontoids; (42) males with paired, lateral, membranous vocal sacs, absent in one species, and with nuptial asperities in a pad on thumb; (46) larvae with dextral vent; (49) adults 30 - 45 mm. SVL.

Composition.-- Bokermann (1966) listed nine species (aspera, glabrus, lateristrigatus, magalhaesi, mertensi, meridionalis, nasus, perplicatus, and pulcher) in the

Figure 109. . Lateral, dorsal, and ventral views  
of skull of Hylodes asper (KU 92870, x 6).



genus, then known only from southeastern Brasil. Gorham (1966) listed glabrus as a synonym of lateristrigatus and meridionalis as a subspecies of nasus. Bokermann (1967) named an additional species from Rio de Janeiro (ornata), and Rivero (1968) named duidensis from Venezuela. All of these authors used the generic name Elosia, as did Cochran (1955) in her study of the species of southeastern Brasil.

Distribution.-- Coastal southern and southeastern Brasil from Rio Grande do Sul north to Minas Gerais. One species occurs on Cerro Duida in amazonian Venezuela.

Remarks.-- Frogs of this genus exhibit relatively little intrageneric variation and have been recognized as a distinctive generic unit for many decades. The nomenclatorial problems of the genus are by no means minor. Myers (1962) pointed out that the proper generic name for these frogs is Hylodes Fitzinger, 1826, and not Elosia Tschudi, 1838, the name which had been applied more or less universally for 60 years. The usage of one generic name in preference to another in a significant work must be taken into account when dealing with any question of priority and/or nomenclatorial stability. It is therefore significant that Cochran (1955) used Elosia in her important study of the frogs of southeastern Brasil. However, the argument against usage of Hylodes as the

proper generic name is based on the fact that Fitzinger proposed Hylodes twice, each time with a different type-species. Fitzinger (1826) proposed Hylodes for Hylaranoides Spix, 1824, a member of the group later named Elosia by Tschudi (1838), and in 1843 proposed Hylodes for Hylodes martinicensis Tschudi, 1838, the type-species of Eleutherodactylus Duméril and Bibron, 1841. I am in complete agreement with Myers (1962), because there is no longer any confusion of what Hylodes is--the last author to use it in the sense of Fitzinger (1843) was Melin (1941). We have used Eleutherodactylus as the proper generic name since the early part of this century when Stejneger (1904) pointed out the synonymies of Fitzinger's names. The genus Hylodes (or Elosia) is a small one; even the least conservative author would not recognize a dozen species. The genus is restricted in distribution, and the species of the genus are relatively rare and therefore have not been frequently mentioned in the literature. A nomenclatorial change at the generic level creates relatively little instability even when the generic name used is one that has a junior homonym that is far better known. I do not regard the use of Elosia defensible while there are two older generic names (Hylodes and Enydrobius) for the group.

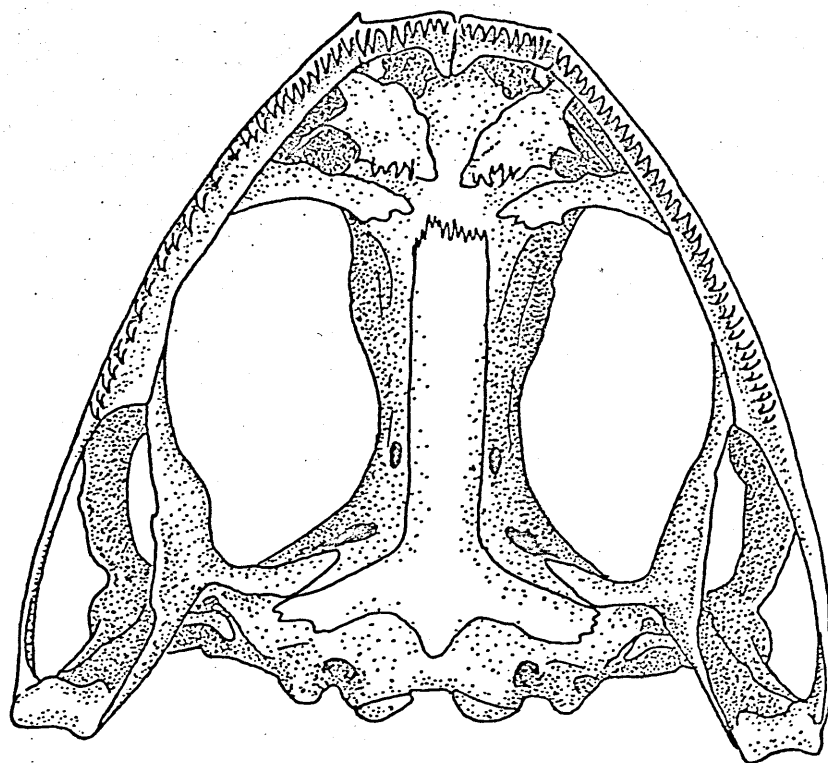
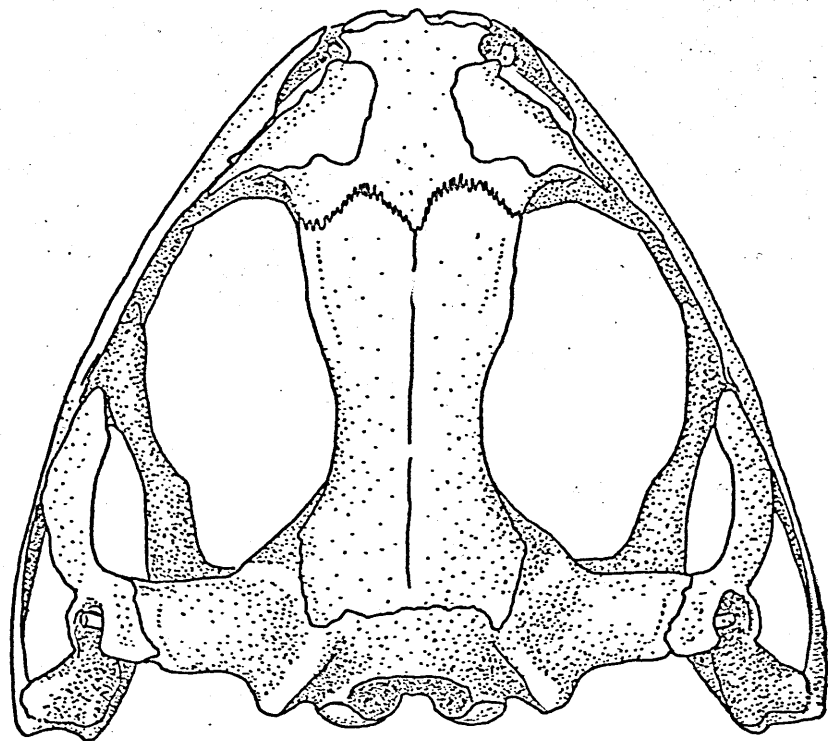
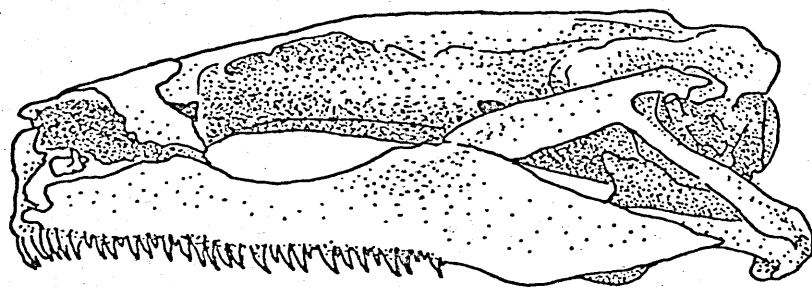
Megaelosia Miranda-Ribeiro, 1923

(Fig. 110)

Megaelosia Miranda-Ribeiro, 1923, Rev. Mus. Paulista, 13:819 [Type-species by monotypy, Megaelosia bufonia Miranda-Ribeiro, 1923].

Diagnostic definition.-- (9) maxillary teeth very long; (10) alary processes of premaxillae directed sharply posterodorsally; (11) palatal shelf of premaxilla of moderate depth, palatal process elongate; (14) maxillary arch complete, posterior end of maxilla expanded, quadratojugal present, deep; (16) nasals in contact with maxillae, separated from pterygoids; (20) frontoparietals not fused to prootics; (22) epiotic eminences obsolete; (23) cristae paroticae broad, stocky; (24) zygomatic ramus of squamosal long, expanded, in broad contact with maxilla; (25) otic ramus of squamosal relatively long, expanded medially into small otic plate; (26) squamosal-maxillary angle about  $15^{\circ}$ ; (28) prevomers moderate-sized, entire, toothed; (29) palatines elongate, relatively broad, widely separated medially; (31) anterior ramus of parasphenoid elongate, narrow, not keeled medially; (32) parasphenoid alae deflected posteriorly, broadly overlapped laterally by median rami of pterygoids; (33) pterygoids large, anterior rami not reaching middle of orbits; (34) occipital condyles moderately large, not stalked, narrowly separated medially; (35) mandible bearing a serrated

Figure 110. Lateral, dorsal, and ventral views  
of skull of Megaelosia goeldi (KU 106271, x 4).





odontoid ridge; (42) males lacking vocal sac and nuptial asperities; (46) larvae with dextral vent; (49) males reach 70 mm., females reach 120 mm. SVL.

Composition.-- Monotypic (goeldi); the type-species of the genus is a junior synonym.

Distribution.-- The Coastal Ranges of southeastern Brasil (Estados Rio de Janeiro and adjacent Minas Gerais and São Paulo).

Remarks.-- Ever since its separation from Hylodes (Elosia auctorum), Megaelosia has been a poorly defined genus. Noble (1931) and Cochran (1955) remarked that Megaelosia was merely a giant Elosia with somewhat enlarged maxillary teeth. Cochran (1955) recognized the genus because of its greater adult size.

Megaelosia has diverged markedly from the other elosines. The external morphology of M. goeldi compels me to retain it in the Elosiinae. The skull of this monotypic genus is strikingly different from those of the other genera of the subfamily (see Figs. 108 - 10). In contrast to the rather delicate maxillary arch in the other genera of the subfamily, Megaelosia has a large, massive maxilla and quadratojugal. The teeth of Megaelosia are fang-like and much larger than those of the other genera of the subfamily. The squamosal architecture of Megaelosia is very different from that seen in the other elosines; the zygomatic ramus is enlarged and in broad

contact with the maxilla, and the otic ramus of Megaelosia is more like that seen in the Grypiscini (Telmatobiinae) than that in Hylodes or Crossodactylus. The very large (compared to those of the other eloslines) occipital condyles of Megaelosia are suggestive that the genus is primitive. In external morphology, Megaelosia goeldi is very similar to Hylodes. The tadpoles of the two genera are very difficult to separate. These data suggest that the two genera are indeed related although the skull morphology suggests that the external similarities are convergent or parallel.

LEPTODACTYLINAE Berg, 1896 (1838)

Cystignathi Tschudi, 1838:78.

Cystignathidae: Günther, 1859a:26.

Pleurodema Cope, 1866:95.

Paludicolina Mivart, 1869:290.

Plectromantidae Mivart, 1869:291.

Cystignathina: Mivart, 1869:293-94.

Leptodactylidae Berg, 1896:161 [A replacement name for the Cystignathidae, whose type-genus is a synonym of Leptodactylus].

Cystignathinae: Gadow, 1901:211.

Paludicolidae: Miranda-Ribeiro, 1926:153

Leptodactylinae: Noble, 1931:504.

Pseudopaludicolinae Gallardo, 1965:84.

The unifying characteristic of this subfamily is the bony style or osseous plate in the sternum as compared with the cartilaginous sterna of the other leptodactylids. The group is strictly Neotropical and ranges south to southern Chile and north to the southern United States. For the most part, the group is a lowland component. The widespread genus Leptodactylus rarely reaches elevations above 1000 meters. The genus Pleurodema occurs in the Andean system in Chile, Bolivia and southern Peru, and therefore reaches elevations exceeding 4000 meters. Even at these elevations, the group breeds in ponds. The pond-breeding habits of the Leptodactylinae have restricted the dispersal of the group to lower elevations. Many of the species of the subfamily are the wide-spread, common, lowland frogs encountered in most tropical situations in the Americas.

The following characteristics of the diagnostic definitions are common to all ten of the included genera:

- (1) sternum containing an osseous element;
- (2) vertebral shield lacking;
- (3) transverse processes of anterior presacral vertebrae not expanded or shortened;
- (5) cervical and second vertebrae not fused;
- (6) cranial bones not involved in dermostosis;
- (7) omosternum present, manubrium expanded in all genera except Paratelmatobius and Physalaemus;
- (9) maxillary arch usually toothed, if present, teeth blunt, pedicellate;
- (11) palatal process of premaxilla

long; (20) frontoparietal not fused to proötic; (21) temporal arcade lacking; (23) carotid artery passes dorsal to skull bones; (24) zygomatic ramus of squamosal widely separated from maxilla; (30) sphenethmoid entire; (35) mandible lacking odontoids; (38) cricoid cartilage not divided ventrally; (40) m. depressor mandibulae in two slips; (44) posterior edge of tongue free; (45) outer metatarsal tubercle present; (47) amplexus axillary in all observed species.

Most herpetologists familiar with the Neotropical fauna have recognized two informal groups of aquatic breeding leptodactyline frogs--those associated with Leptodactylus (Hydrolaetare, Leptodactylus, Limnomedusa, and Lithodytes) and those long called "Paludicola" (Engystomops, Eupemphix, Paratelmatoobius, Physalaemus, Pleurodema, and Pseudopaludicola). The rare genus Edalorhina is usually associated with the latter group but bears considerable resemblance to Lithodytes.

Boulenger (1882) was familiar with most of the generic groups here included in the Leptodactylinae. Hydrolaetare and Paratelmatoobius were described subsequent to his studies. Boulenger included Engystomops and Eupemphix in the Bufonidae and incorrectly associated Hylorina with the Leptodactylinae, because he believed that H. sylvatica had a bony sternum. One of the genera recognized by Boulenger was Paludicola, which he considered

to be wide-spread and generalized. Méhely (1904) and Parker (1927) pointed out the heterogeneity of Boulenger's Paludicola and each proposed a partitioning based on osteological characters. Méhely divided Paludicola into two genera--Paludicola and Pleurodema. Parker (1927) divided it into three genera--Physalaemus, Pleurodema, and Pseudopaludicola. Méhely separated Boulenger's Paludicola into one group with prevomerine teeth and a simple (non-bifurcate) sternal style (Pleurodema) and into another group without prevomerine teeth and with a bifurcate sternal style (Paludicola). Nieden (1923) uncritically followed Méhely's system and included Edalorhina in Pleurodema. Parker (1927) criticized Méhely's arrangement because relatively few species had been studied; he proposed another classification of the paludicoline frogs based on loss of the prevomerine teeth, loss of the quadratojugal, shape of the sternal style, and the presence of an antebrachial tubercle. Parker (1927) characterized Pseudopaludicola as having an elongate, cartilaginous, or calcified sternum. Virtually all subsequent authors have repeated Parker's characterization of the sternum of Pseudopaludicola (Barrio, 1954, Cochran, 1955, Rivero, 1961, and Gallardo, 1965). Principally on the basis of the cartilaginous sternum and breeding habits, Gallardo (1965) proposed a new subfamily for Pseudopaludicola. In the present study, at least one specimen of each of

five currently recognized species of Pseudopaludicola was cleared and stained. The sternal style is narrow and elongate and is much more dense than the epicoracoidal cartilages, but is not more dense than the coracoid bones. I consider the sternal style of Pseudopaludicola to be osseous. Parker (1927) reported simple and T-shaped terminal phalanges in frogs of the genus Pseudopaludicola. All specimens which I examined have knobbed terminal phalanges.

The foam-nesting habits of leptodactylines have been known for some time and have been used in the classification of the group (Noble, 1927, Breder, 1946, Bokermann, 1962). Barrio (1954) first reported the ethological differences between Physalaemus and Pseudopaludicola. Pseudopaludicola lays its eggs singly or in small clumps in water without the benefit of a foam-nest. The species of Physalaemus (including Engystomops and Eupemphix) lay their eggs in a foam-nest floating on water (Plate 1). Frogs of the genus Leptodactylus also make foam-nests but there is considerable variation within the genus. The species of the melanonotus and ocellatus groups lay their eggs in a foam-nest floating on water, as do Physalaemus and Pleurodema. The species of the pentadactylus group differ only slightly in that the foam-nest is deposited in pot holes filled with water along the edges of streams or ponds. The species in the fuscus or sibilatrix group

deposit their eggs in a foam-nest in a burrow, and the tadpoles emerge after the nest is inundated. This recalls the situation seen in Heleioporus. The frogs of the marmoratus group deposit their few, large eggs in a terrestrial underground incubating chamber in a foam-nest. There are no aquatic larvae. Edalorhina has aquatic larvae (R. Etheridge, in litt.). Reproductive data are unavailable for Barycholos, Hydrolaetare, Limnomedusa, Lithodytes, and Paratelmatobius.

The subfamily Leptodactylinae was defined by Noble (1931) on the basis of the presence of an osseous style in the sternum. Other authors suggested that the foam-nesting habits are characteristic of the subfamily, but these authors mistakenly believed that Pseudopaludicola is not related to the Leptodactylinae. In view of the appearance and variability of sternal styles and osseous plates elsewhere among the Salientia, it can be argued that the subfamily Leptodactylinae is poorly defined and possibly polyphyletic (see generic account for Paratelmatobius, pp. 628 - 31). Progressively graduated vicinal similarities of several characters within this group of genera were used to infer relationship through the whole set of genera.

The sternum is an osseous plate in Paratelmatobius with a large cartilaginous xiphisternum. In the other nine genera of the subfamily, the sternum is a style. In Pleurodema the style is relatively broad, and in

Limnomedusa, Barycholos, Edalorhina, and Physalaemus, the style is only slightly narrower than that of Pleurodema. The sternal style is elongate and narrow in Hydrolaetare, Leptodactylus, Lithodytes, and Pseudopaludicola. I consider the presence of a discrete style in the sternum as sound evidence of close relationship. The relationships of Paratelmatoobius are obscure--it does not have a bony style in the sternum. The transverse processes of the posterior presacral vertebrae are somewhat shortened in Lithodytes, Paratelmatoobius, Physalaemus, Pleurodema, and Pseudopaludicola, but are not shortened in Barycholos, Edalorhina, Hydrolaetare, Leptodactylus, or Limnomedusa. The occipital condyles are relatively large and narrowly separated in Limnomedusa and Pleurodema. Limnomedusa has a type II cervical cotylar arrangement whereas, all other genera of the subfamily have a type I cervical cotylar arrangement.

I consider Pleurodema most like the primitive leptodactyline stock because it has a generalized body form, pectoral architecture, skeleton, and tadpole. Pleurodema is specialized in one interesting character--the loss of the quadratojugal. Pleurodema is externally similar to Eupsophus, and the external similarity reflects the similarity in the osteology of these two genera. The two genera are readily distinguished by the loss of the quadratojugal in Pleurodema and the presence of



a bony style in the sternum of Pleurodema. The tadpole of Pleurodema has a median vent, 2/3 tooth rows, and a broad anterior interruption of the labial papillae, as do the tadpoles of Eupsophus and Leptodactylus. The tadpoles of Physalaemus and Pseudopaludicola have a dextral vent, 2/3 tooth rows, and a broad anterior interruption of the labial papillae. Noble (1931) suggested that Physalaemus was the stem genus of the Leptodactylinae, but my study suggests that Pleurodema more accurately fills this role. Physalaemus has departed from other leptodactylines in several morphological features, the most striking of which is the hyolaryngeal apparatus.

Pleurodema Tschudi, 1838

(Fig. 111)

Pleurodema Tschudi, 1838, Class. Batr., p. 47 [Type-species by monotypy, Pleurodema bibroni Tschudi, 1838].

Leiuperus Duméril and Bibron, 1841, Érpétologie générale, 8:420 [Type-species by monotypy, Leiuperus marmoratus Duméril and Bibron, 1841].

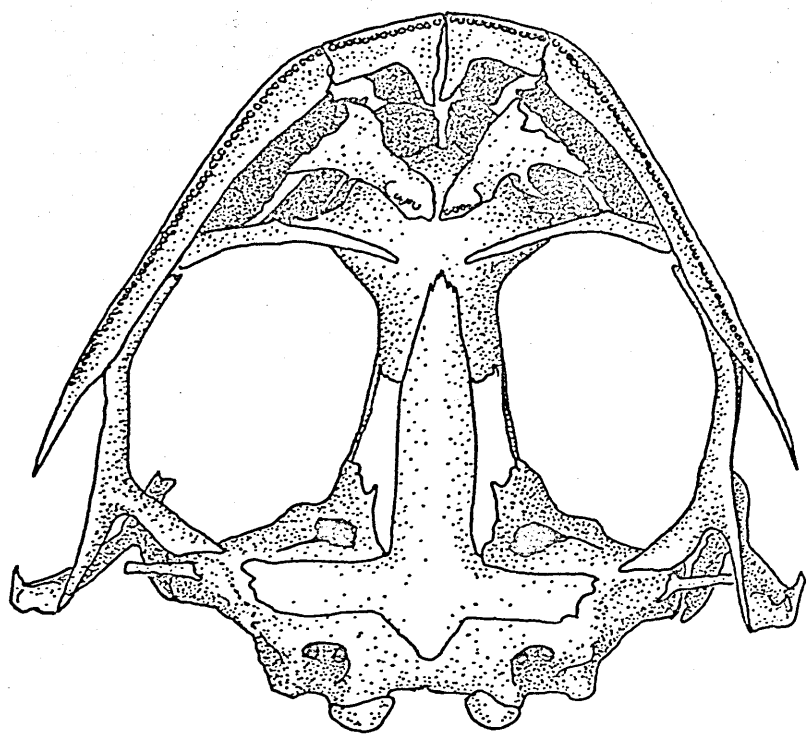
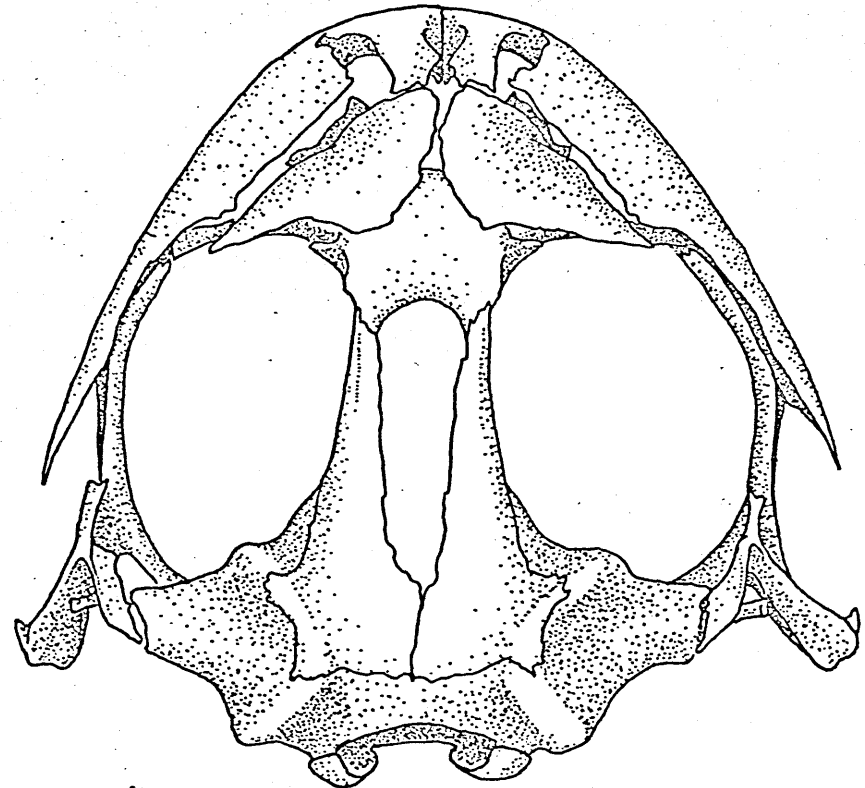
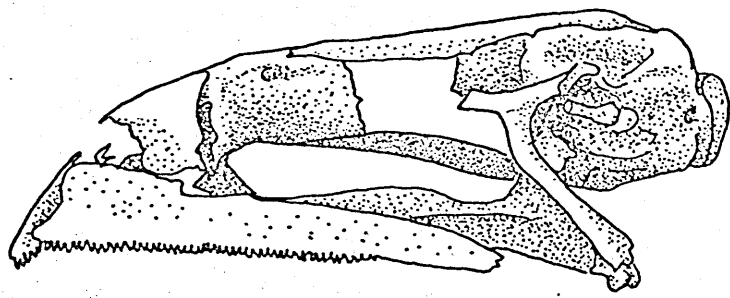
Physalaemus Fitzinger (non Physalaemus Fitzinger, 1826), 1843, Syst. Rept., p. 31 [Type-species by original designation, Cystignathus bibroni of Duméril and Bibron, 1841 (= Pleurodema bibroni Tschudi, 1838)].

Lystris Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, 20:312 [Type-species by monotypy, Lystris brachyops

Cope, 1868].

Diagnostic definition.-- (1) sternum bearing a broad, osseous style which tends to bifurcate in large adult females; (3) transverse processes of posterior presacral vertebrae somewhat shortened; (4) cervical cotylar arrangement type I; (7) omosternum cartilaginous, usually not elongated, manubrium large; (8) sacral diapophyses slightly dilated; (9) maxillary arch toothed; (10) alary processes of premaxillae directed posterodorsally, broad at base; (11) palatal shelf of premaxilla broad; (12) facial lobe of maxilla deep; (13) palatal shelf of maxilla narrow, pterygoid process lacking; (14) maxillary arch incomplete, quadratojugal lacking; (15) nasals in median contact, relatively small; (16) nasals not in contact with maxillae or pterygoids; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle large; (19) frontoparietals not ornamented; (22) epiotic eminences small; (23) cristae paroticae relatively short, narrow; (24) zygomatic ramus of squamosal relatively short; (25) otic ramus of squamosal slightly longer than zygomatic ramus, no otic plate; (26) squamosal-maxillary angle  $40 - 45^{\circ}$ ; (27) columellae present; (28) prevomers relatively large, toothed, narrowly separated medially; (29) palatines relatively narrow, arched, narrowly separated medially; (30) sphenethmoid large, extending anteriorly to posterior edge of nasals;

Figure 111. Lateral, dorsal, and ventral views of skull of Pleurodema cinerea (KU 80836, x 6.5).



(31) anterior ramus of parasphenoid long, narrow, not keeled medially; (32) parasphenoid alae oriented at right angles to anterior ramus, broadly separated from median rami of pterygoids; (33) pterygoids relatively slender, anterior rami long, reaching palatines; (34) occipital condyles large, not stalked, widely separated medially; (36) terminal phalanges knobbed; (37) alary processes of hyoid plate on narrow stalks; (39) m. petrohyoideus anterior and m. sternohyoideus insert on lateral edge of hyoid plate; (41) pupil horizontal; (42) males with median subgular vocal sac, nuptial asperities on thumb; (43) lumbar glands present or not; (44) tongue large, round; (45) toes lacking webbing, with lateral fringes or not, metatarsal tubercles spade-like or not, digital tips narrow; (46) larvae with median vent, 2/3 tooth rows, labial papillae broadly interrupted anteriorly; (48) eggs laid in foam-nest in water, small and numerous; (49) adults 35 - 65 mm. SVL; (50) tympanum visible externally or concealed.

Composition.-- Ten species are presently recognized: bibroni, brachyops, bufonina, cinerea, darwinii, diplolistris, guayapae, marmorata, nebulosa, and tucumana. The widespread P. bibroni is probably a composite superspecies.

Distribution.-- Central Andean Peru south to southern Chile and Argentina and northeastward to Uruguay, along the coastal lowlands of extreme eastern Brasil in

non-forested habitats; the arid and semiarid coastal belt from the Guayanas through Venezuela to the Maricaibo Basin, the islands north of Venezuela, and in the savanas of central Panamá.

Remarks.--- With the exception of P. brachyops and P. diplolistris, frogs of the genus Pleurodema are restricted to southern South America and temperate climates; P. diplolistris occurs in the subtropical areas of eastern Brasil, and P. marmorata ranges northward in the high Andes to central Peru. Leiuperus verrucosus Reinhardt and Lütken was placed in Pleurodema by Parker (1927), who was uncritically followed by all subsequent authors. The species is a member of the genus Ischnocnema (Telmatobiinae, Eleutherodactylini).

Parker (1927) included 18 nominal species in Pleurodema. Since his revision of the genus one new species (guayapae) has been named; Pleurodema illota is now placed in Eupsophus, and P. mexicanus is an Eleutherodactylus. Parker recognized P. pseudophryne Philippi and P. montevidense Philippi, which are now considered synonyms of P. bibroni and P. darwini, respectively. Parker included Pleurodema coquimbensis in Physalaemus, but Cei (1962a) pointed out that it is a synonym of Pleurodema bibroni.

At present, the most pressing systematic problem in the genus Pleurodema is the status of the species presently

called P. bibroni and P. cinerea. Schmidt (1954b) recognized P. plebeya Philippi for the southern populations now called P. bibroni. Cei (1962a) combined the two nominal species but realized that the complex is seriously in need of further study. Pleurodema cinerea is closely related to P. bibroni; the two species are distinguished only by the external expression of the tympanum (concealed in bibroni, evident in cinerea). The bibroni-cinerea complex is much in need of a detailed review.

Of the ten species of Pleurodema recognized here, five (bibroni, brachyops, bufonina, cinerea, and darwinii) have lumbar or lumbo-inguinal glands. These glands are well-defined, often brightly patterned, and present in both sexes. At least some of these species use the glands in a defense posture. The frog arches its back and tucks its head down thus presenting the large, patterned glands to a predator or aggressor. In this position, the glands appear to be large eyes (Cei, 1962a). The lumbar glands are moderate-sized in bibroni, brachyops, cinerea, and darwinii, and very large in bufonina.

Parker (1927) suggested that the species of Pleurodema with prevomerine teeth were more primitive than those lacking prevomerine teeth. Like so many other herpetologists of the 19th and early 20th centuries, Parker (1927) regarded the presence or absence of prevomerine teeth as a major character in leptodactylid classification.

His primary "key character" in subdividing the genus was the presence or absence of prevomerine (vomerine) teeth. As has been repeatedly pointed out in recent years, the prevomerine teeth are readily lost in many groups of frogs. The teeth may be present but concealed beneath the tissue of the palate (as in Eleutherodactylus myersi) or they may be lost entirely. In most of the cases where the presence of prevomerine teeth has been reported to be variable within a species, I have found that the teeth are present but concealed beneath the tissue of the palate. Main (1957) criticized the use of the presence of prevomerine teeth as the primary character in the division of the species of Crinia into two groups.

In four species of Pleurodema (bibroni, bufonina, cinerea, and marmorata), the metatarsal tubercles are not enlarged. In these species, the outer metatarsal tubercle is small and conical and the inner metatarsal tubercle is an elongate oval. In the other six species of the genus, the inner metatarsal tubercle is enlarged, laterally compressed, and spade-like. In these six species, the outer metatarsal tubercle is enlarged and either compressed (brachyops, diplolistris, guayapae, and nebulosa) or not (darwinii and tucumana).

Pleurodema bibroni and cinerea have a short inner tarsal fold, and bufonina has a long inner tarsal fold; all other species of the genus lack tarsal folds.



Pleurodema diplolistris has a prominent tarsal tubercle, much like that seen in many species of Physalaemus.

Pleurodema nebulosa has a fimbriated anal flap, whereas no other species of the genus has more than a low transverse ridge above the anal opening. The significance of these characters is not apparent at this time, although the presence of a tarsal fold in bibroni, cinerea, and bufonina is suggestive that they are closely related. These three species also agree in having lumbar glands and in having small, non-compressed metatarsal tubercles.

Of the eleven species listed in the genus Pleurodema by Gorham (1966), two are not included in this genus by me: sagittifer O. Schmidt, 1857, is here treated as a species inquierenda, and verrucosus Reinhardt and Lütken, 1862, is placed in the genus Ischnocnema (Telmatobiinae, Eleutherodactylini).

Limnomedusa Fitzinger, 1843

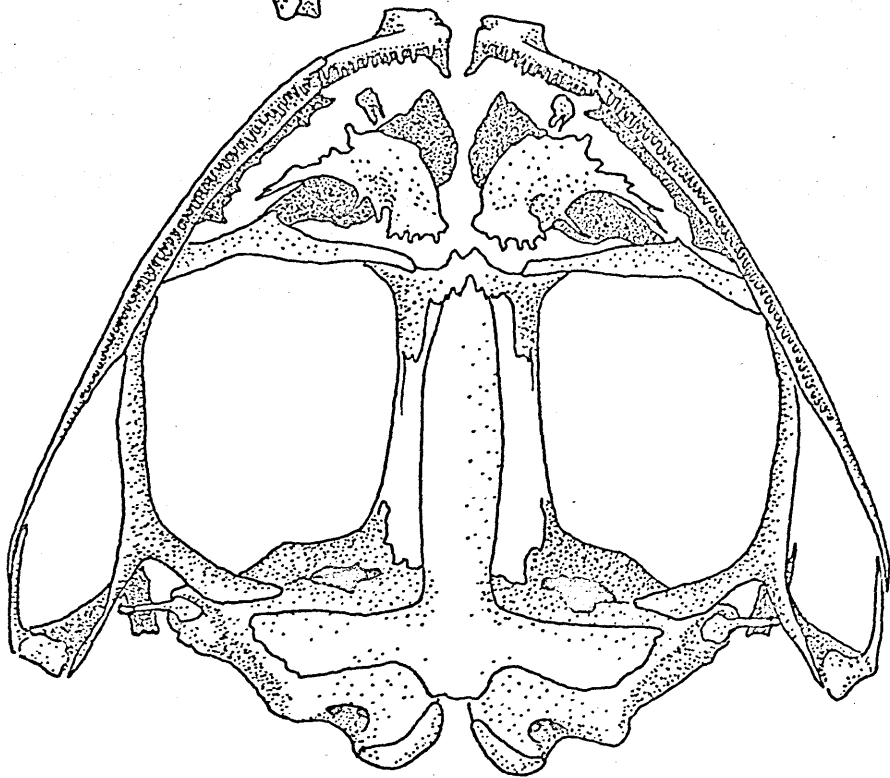
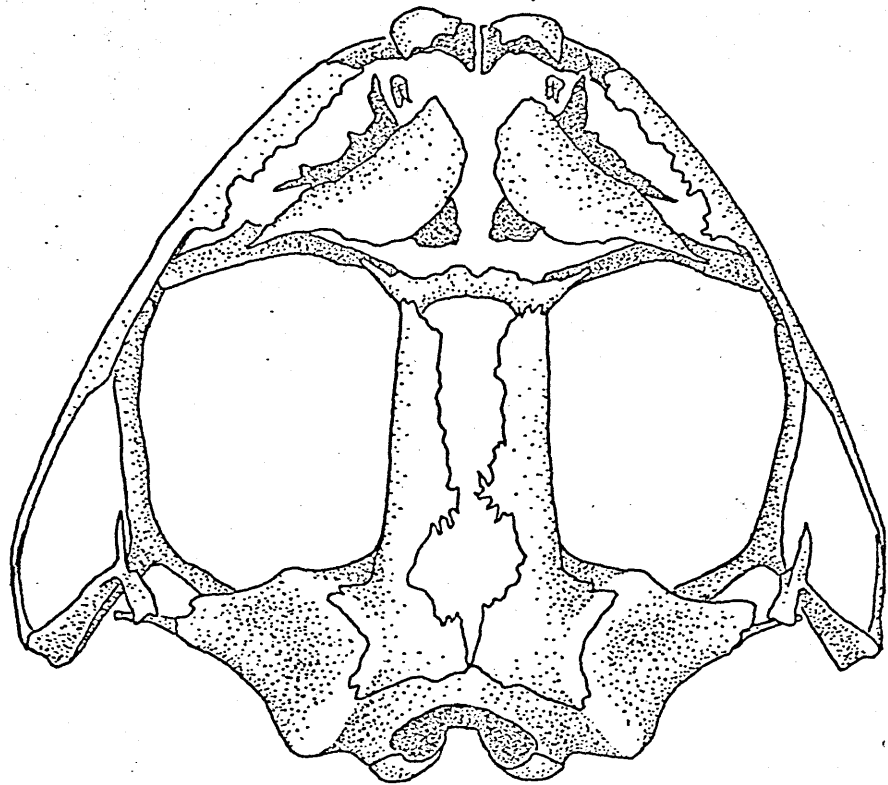
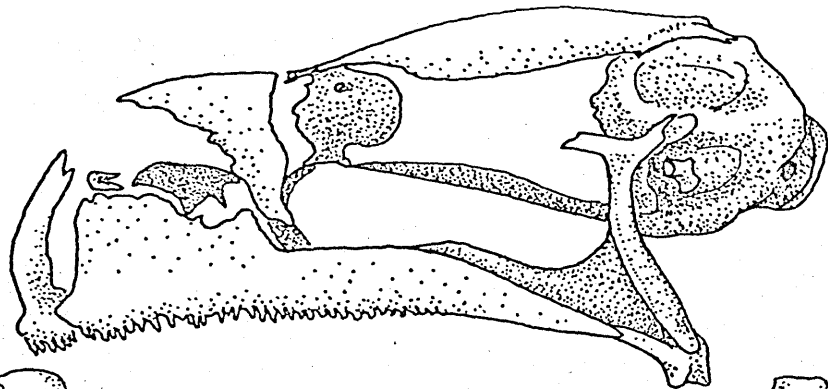
(Fig. 112)

Limnomedusa Fitzinger, 1843, Syst. Rept., p. 31 [Type-species by original designation, Cystignathus macroglossus Duméril and Bibron, 1841].

Litopleura Jiménez de la Espada, 1875, Vert. Viaje Pacif., Batr., p. 82 [Type-species by monotypy, Litopleura maritimum Jiménez de la Espada, 1875].

Diagnostic definition.-- (1) sternum bearing a broad osseous style; (3) transverse processes of posterior presacral vertebrae not shortened; (4) cervical cotylar arrangement type II; (7) omosternum cartilaginous, somewhat elongated, manubrium large; (8) sacral diapophyses round; (9) maxillary arch toothed; (10) alary processes of premaxillae directed dorsally, broad at base; (11) palatal shelf of premaxilla relatively narrow; (12) facial lobe of maxilla moderately deep; (13) palatal shelf of maxilla narrow, pterygoid process small; (14) maxillary arch complete; (15) nasals relatively small, narrowly separated medially; (16) nasals not in contact with maxillae or pterygoids; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle large; (19) frontoparietals not ornamented; (22) epiotic eminences moderately large; (23) cristae paroticae short, stocky; (24) zygomatic ramus of squamosal short; (25) otic ramus of squamosal long, no otic plate; (26) squamosal-maxillary angle about  $40^{\circ}$ ; (27) columellae present; (28) prevomers small, entire, toothed, widely separated medially; (29) palatines slender, widely separated medially; (30) sphenethmoid not reaching nasals; (31) anterior ramus of parasphenoid narrow, not keeled; (32) parasphenoid alae oriented at right angles to anterior ramus, narrowly overlapped laterally by median rami of pterygoids; (33) pterygoids small, all rami slender, anterior rami long,

Figure 112. Skull of Limnomedusa macroglossa.  
Dorsal, ventral, and lateral views. (KU 92960, x 6).



reaching palatines; (34) occipital condyles large, not stalked, narrowly separated medially; (36) terminal phalanges knobbed; (37) hyoid plate lacking alary processes; (39) m. petrohyoideus anterior and m. sternohyoideus insert on lateral edge of hyoid plate; (41) pupil vertical; (42) males with median subgular vocal sac, nuptial asperities on thumb; (43) body free of glands; (44) tongue large, round; (45) toes fringed, basally webbed, metatarsal tubercles not enlarged, digital tips narrow; (46 - 48) (49) adults less than 60 mm. SVL; (50) tympanum visible externally.

Composition.-- Two species are recognized: macroglossa and misiones.

Distribution.-- Coastal lowlands of southern Brazil, Uruguay, and adjacent Misiones Province, Argentina. In Brazil, the genus is found in Paraná, Santa Catarina, and Rio Grande do Sul.

Remarks.-- Frogs of this genus bear considerable external resemblance to Leptodactylus but differ from it in having vertical pupils, a nuptial pad on the thumb of the male, and a broad sternal style. Limnomedusa differs from all other leptodactylines in having a type II cervical cotylar arrangement.

Nothing is known of the breeding biology of the frogs of this genus. The presence of a nuptial pad on the thumb suggests that clasping takes place in water.

Hydrolaetare Gallardo, 1963

(Figs. 113-14)

Hydrolaetare Gallardo, 1963, Neotropica, 9:42 [Type-species by original designation, Limnomedusa schmidti Cochran and Goin, 1959].

Diagnostic definition.-- (1) sternum bearing an elongate osseous style; (3) transverse processes of posterior presacral vertebrae not shortened; (4) cervical cotylar arrangement type I; (7) omosternum large, elongate, cartilaginous; (8) sacral diapophyses rounded; (9) maxillary arch toothed; (10) alary processes of premaxillae directed posterodorsally, broad at base; (11) palatal shelf of premaxilla broad; (12) facial lobe of maxilla deep; (13) palatal shelf of maxilla moderately wide, no pterygoid process; (14) maxillary arch complete; (15) nasals relatively large, in broad median contact; (16) nasals in broad contact with maxillae, separated from pterygoids; (17) nasals in broad contact with frontoparietals; (18) frontoparietal fontanelle lacking; (19) frontoparietal bearing sagittal crest, slight exostosis; (22) epiotic eminences large posteriorly; (23) cristae paroticae narrow, relatively short; (24) zygomatic ramus of squamosal elongate; (25) otic ramus of squamosal relatively short, expanded medially into small otic plate; (26) squamosal-maxillary angle about 30°; (27) columella present; (28) prevomers large, toothed, in median contact;

Figure 113. Dorsal and lateral views of skull  
of Hydrolaetare schmidtii (KU 110613, x 3).

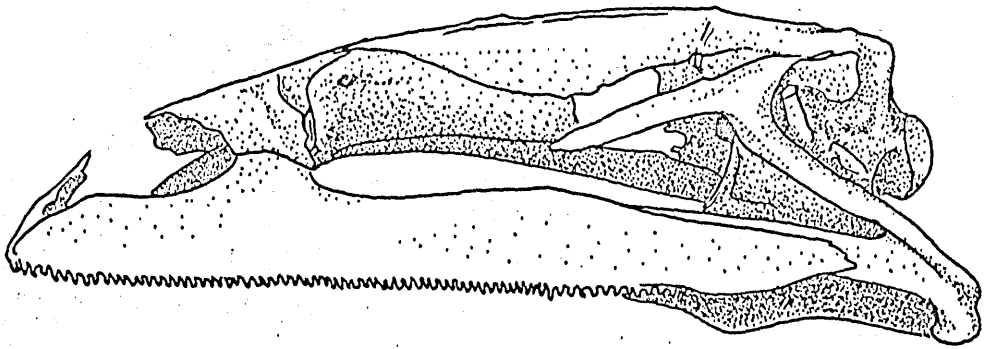
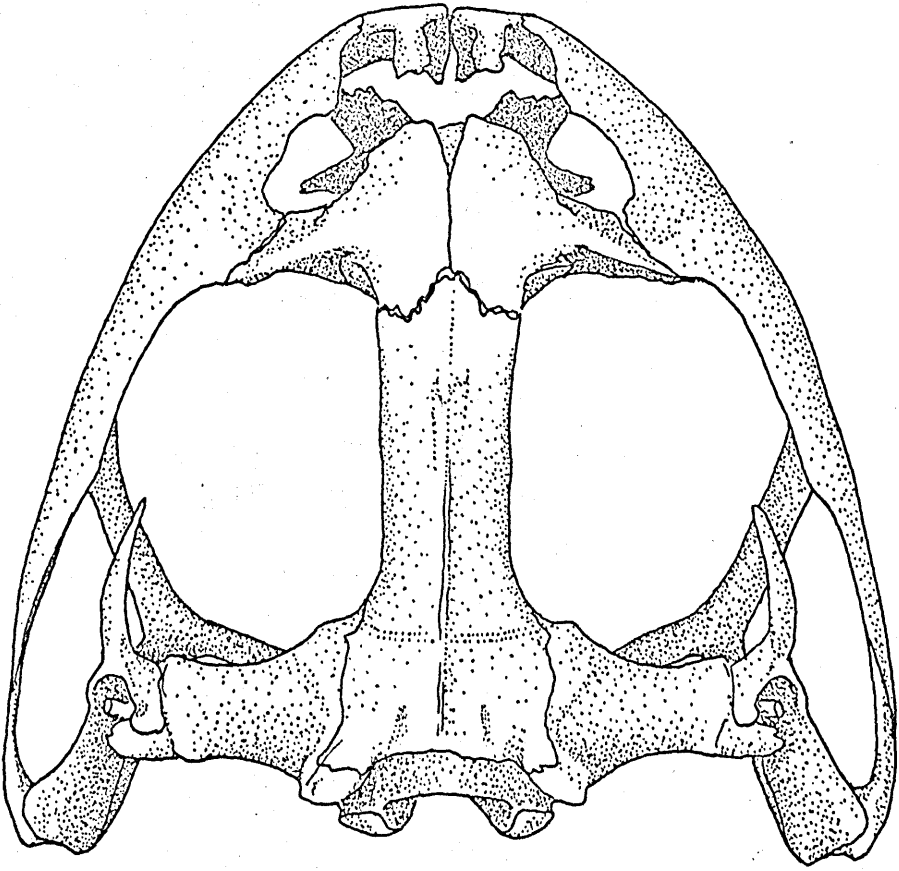
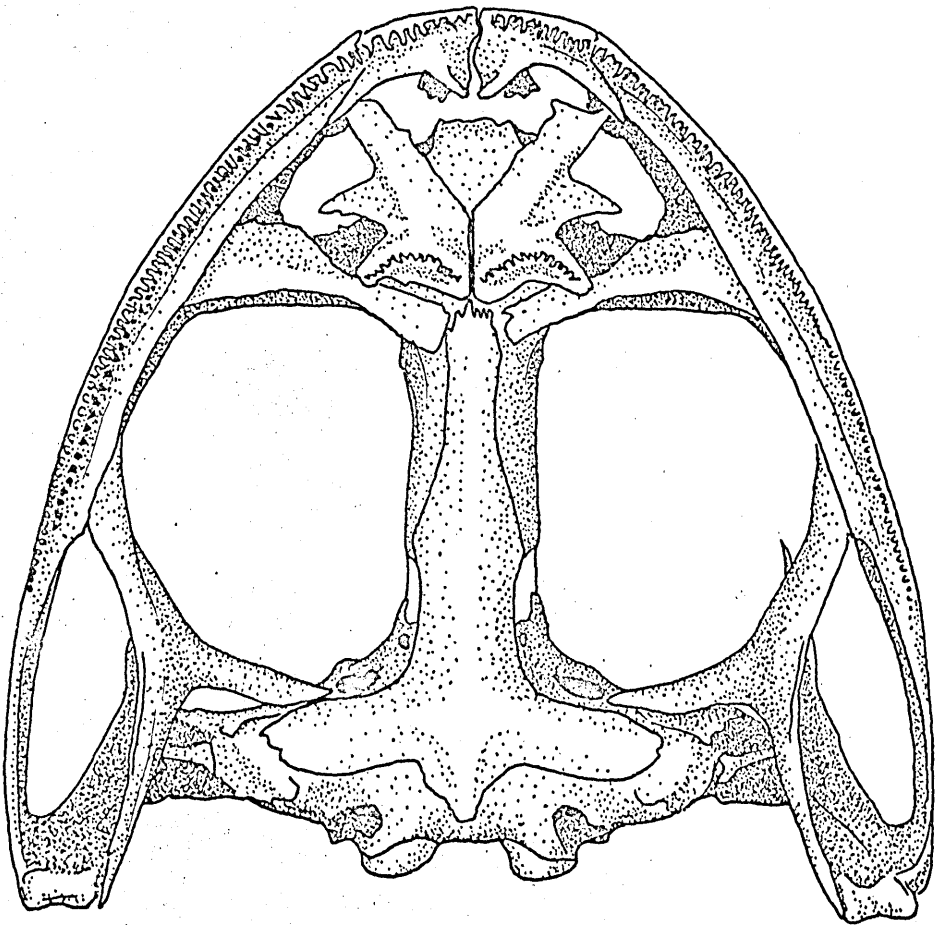




Figure 114. Ventral view of skull of Hydrolaetare  
schmidti (KU 110613, x 3).



(29) palatines broad, separated medially by anterior ramus of parasphenoid, bearing odontoid ridge; (30) sphenethmoid extending anteriorly to middle of nasals; (31) anterior ramus of parasphenoid narrow anteriorly, extending to between palatines, not keeled medially; (32) parasphenoid alae deflected posteriorly, broadly overlapped by median rami of pterygoids; (33) pterygoids large, anterior rami extending to middle of orbit, prominent ventral flange present; (34) occipital condyles of moderate size, not stalked, widely separated medially; (36) terminal phalanges knobbed; (37) alary processes of hyoid plate wing-like; (39) m. petrohyoideus anterior and m. sternohyoideus insert on lateral edge of hyoid plate; (41) pupil vertical; (42) males with median subgular vocal sac, no nuptial asperities; (43) body lacking glands; (44) tongue large, deeply notched posteriorly; (45) toes fully webbed, metatarsal tubercles not enlarged, digital tips narrow; (46 - 48) (49) adults large, known specimens 80 - 105 mm. SVL; (50) tympanum visible externally.

Composition.-- Monotypic.

Distribution.-- Amazonian South America.

Remarks.-- Cochran and Goin (1959) named Limnomedusa schmidti on the basis of a single specimen collected near Leticia, Colombia. They pointed out that the new species was strikingly different from the other two species of Limnomedusa. Gallardo (1963) reported additional specimens

of the species and named a new genus for it (Hydrolaetare). Hydrolaetare and Limnomedusa share only two significant characters--vertical pupils and an osseous element in the sternum.

Several osteological characters of Hydrolaetare suggest that the genus is allied to the Grypiscini (Telmatobiinae). As in Cycloramphus and Zachaenus, Hydrolaetare has a relatively deep maxilla and quadratojugal, the nasals are relatively large, in broad median contact, and in broad contact with the maxillae, the nasals are in broad contact with the frontoparietals, the skull lacks a fontanelle and has a sagittal crest, the zygomatic ramus of the squamosal is elongate, and the pterygoid bears a ventral flange. Unfortunately, reproductive data are lacking for Hydrolaetare, but the species lacks nuptial pads on the thumb, suggesting that amplexus occurs in terrestrial situations (as in the Grypiscini). The three genera now included in the Grypiscini have large, cartilaginous sterna, in contrast to the leptodactyline sternum of Hydrolaetare. On the basis of the skull alone, I would place Hydrolaetare in the Grypiscini, but the sternal apparatus and striking similarity between Hydrolaetare and Leptodactylus (ocellatus and pentadactylus groups) suggest that the genus is a leptodactyline. Hydrolaetare lacks one important character of the Grypiscini; the otic ramus of the squamosal of Hydrolaetare

is not medially curved to form a broad otic plate. The otic plate of Hydrolaetare is small and like that seen in the melanonotus, ocellatus, and pentadactylus groups of Leptodactylus.

Edalorhina Jiménez de la Espada, 1870

(Fig. 115)

Edalorhina Jiménez de la Espada, 1870, J. Sci. Math. Phys.

Nat., Lisboa, 3:58 [Type-species by monotypy,

Edalorhina perezii Jiménez de la Espada, 1870].

Bubonias Cope, 1874, Proc. Acad. Nat. Sci. Philadelphia,

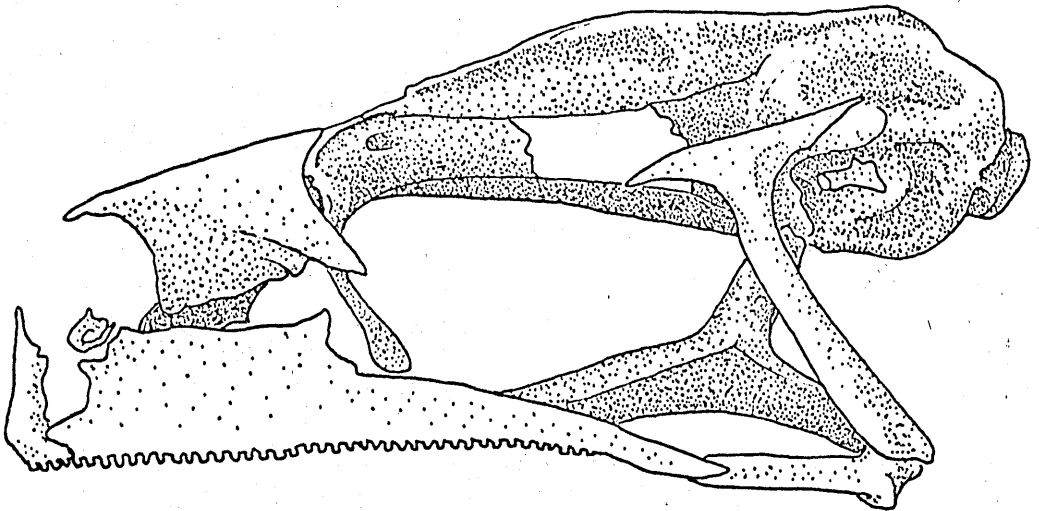
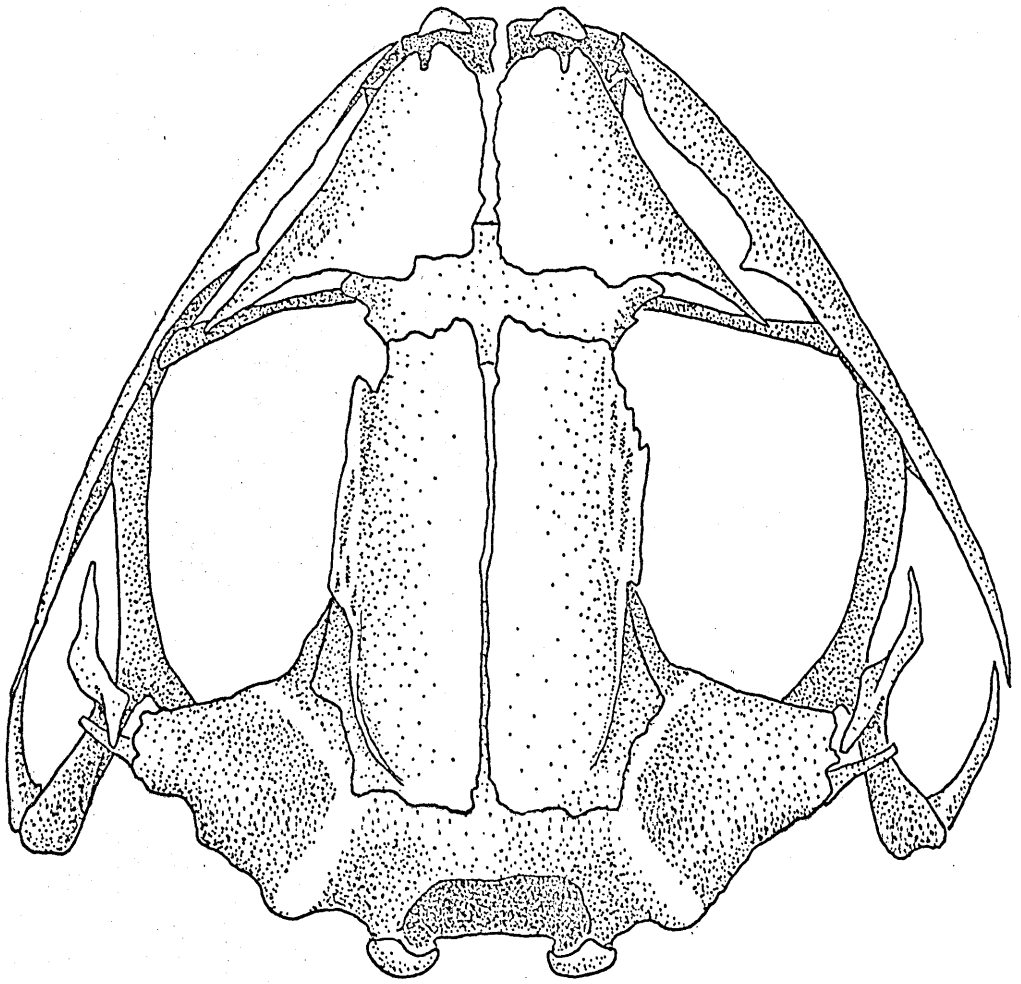
26:124 [Type-species by monotypy, Bubonias plicifrons

Cope, 1874].

Diagnostic definition.-- (1) sternum bearing broad osseous style; (3) transverse processes of posterior presacral vertebrae not shortened; (4) cervical cotylar arrangement type I; (7) omosternum elongate, cartilaginous, manubrium large; (8) sacral diapophyses rounded; (9) maxillary arch toothed; (10) alary processes of premaxillae directed dorsally, moderately wide at base; (11) palatal shelf of premaxilla of moderate width; (12) facial lobe of maxilla deep; (13) palatal shelf of maxilla relatively narrow, pterygoid process small; (14) maxillary arch complete; (15) nasals large, in broad median contact; (16) nasals not in contact with maxillae or pterygoids; (17) nasals not in contact with frontoparietals; (18)

frontoparietal fontanelle lacking; (19) frontoparietals bear large, exostosed, lateral crests; (22) epiotic eminences obsolete; (23) cristae paroticae short, stocky; (24) zygomatic ramus of squamosal of moderate length; (25) otic ramus of squamosal as long as zygomatic ramus, no otic plate; (26) squamosal-maxillary angle about  $50^{\circ}$ ; (27) columella present; (28) prevomers relatively small, entire, toothed, separated medially, dentigerous processes lie posterior to choanae; (29) palatines slender, separated medially; (30) sphenethmoid short, extending anteriorly to posterior edge of nasals; (31) anterior ramus of parasphenoid broad, relatively short, not keeled medially; (32) parasphenoid alae oriented at right angles to anterior ramus, narrowly overlapped laterally by median rami of pterygoids; (33) pterygoids slender, anterior rami long, nearly reaching palatines; (34) occipital condyles small, not stalked, widely separated medially; (36) terminal phalanges knobbed; (37) alary processes of hyoid plate on narrow stalks; (39) m. petrohyoideus anterior and m. sternohyoideus insert on lateral edge of hyoid plate; (41) pupil horizontal; (42) males with median subgular vocal sac, nuptial asperities on thumb; (43) inguinal glands present; (44) tongue large; (45) toes lacking webbing, metatarsal tubercles not enlarged, digital tips narrow; (46 - 48) larvae aquatic; (49) adults small, less than 45 mm. SVL; (50)

Figure 115. Dorsal and lateral views of skull of Edalorhina perezii (KU 124225, x 8).





tympaanum visible externally.

Composition.-- Two species are currently recognized: nasuta and perezi.

Distribution.-- Amazonian lowlands of Ecuador and northern and central Peru, and in extreme western Brasil.

Remarks.-- The genus was reviewed by Dunn (1949), who combined the nominal species buckleyi, perezi, and plicifrons, but noted that the Peruvian population of perezi usually lacks a snout projection, whereas the Ecuadorian population has one. Dunn also pointed out that Shreve's (1941) Edalorhina pustulata (Pacific lowlands of Ecuador) was not an Edalorhina but is closely related to the Middle American Engystomops pustulosus. I concur with Dunn but include Engystomops in Physalaemus.

Parker (1927) and Noble (1931) considered Edalorhina to be merely a Physalaemus with cranial crests and elongate papillae on the eyelids. Dunn (1949) disagreed and suggested that Edalorhina was more closely related to Pleurodema. I consider the genus to be intermediate between Lithodytes and Physalaemus. The breeding biology of Edalorhina is unknown and could provide useful clues to the relationships of the genus to the paludicoline leptodactylids.

Lithodytes Fitzinger, 1843

(Figs. 116-17)

Lithodytes Fitzinger, 1843, Syst. Rept., p. 31 [Type-species by original designation, Rana lineata Schneider, 1799].

Diagnostic definition.-- (1) sternum bearing an elongate osseous style; (3) transverse processes of posterior presacral vertebrae somewhat shortened; (4) cervical cotylar arrangement type I; (7) omosternum bearing an elongate osseous style and large cartilaginous manubrium; (8) sacral diapophyses rounded; (9) maxillary arch toothed; (10) alary processes of premaxillae directed dorsally, broad at base; (11) palatal shelf of premaxilla relatively broad; (12) facial lobe of maxilla relatively deep, not exostosed; (13) palatal shelf of maxilla relatively broad, no pterygoid process; (14) maxillary arch complete; (15) nasals large, in tenuous median contact; (16) nasals not in contact with maxillae or pterygoids; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle lacking; (19) frontoparietals not ornamented; (22) epiotic eminences small; (23) cristae paroticae broad, stocky; (24) zygomatic ramus of squamosal relatively long; (25) otic ramus of squamosal short, expanded medially into small otic plate; (26) squamosal-maxillary angle about  $50^{\circ}$ ; (27) columella present; (28) prevomers large, entire, toothed, narrowly separated medially; (29) palatines relatively narrow, widely separated medially; (30) sphenethmoid extending anteriorly to middle of nasals; (31) anterior ramus of parasphenoid broad,

Figure 116. Dorsal and lateral views of skull of  
Lithodytes lineatus (KU 104340, x 8).

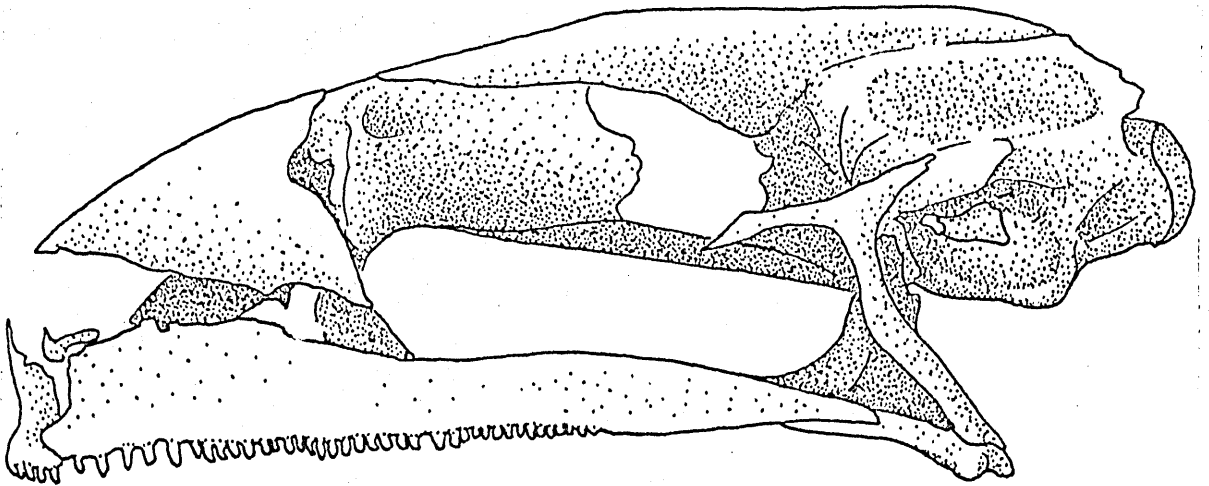
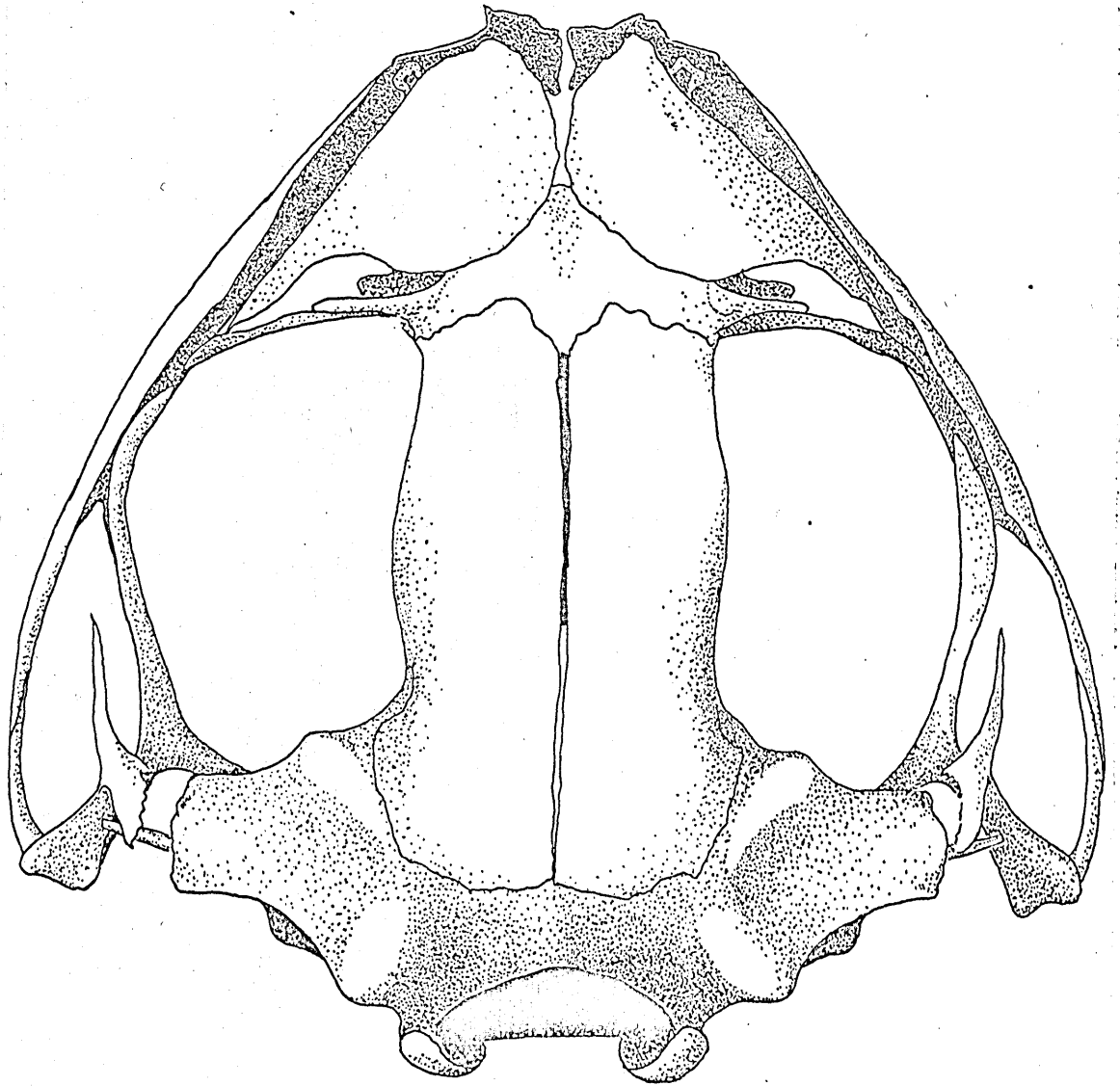
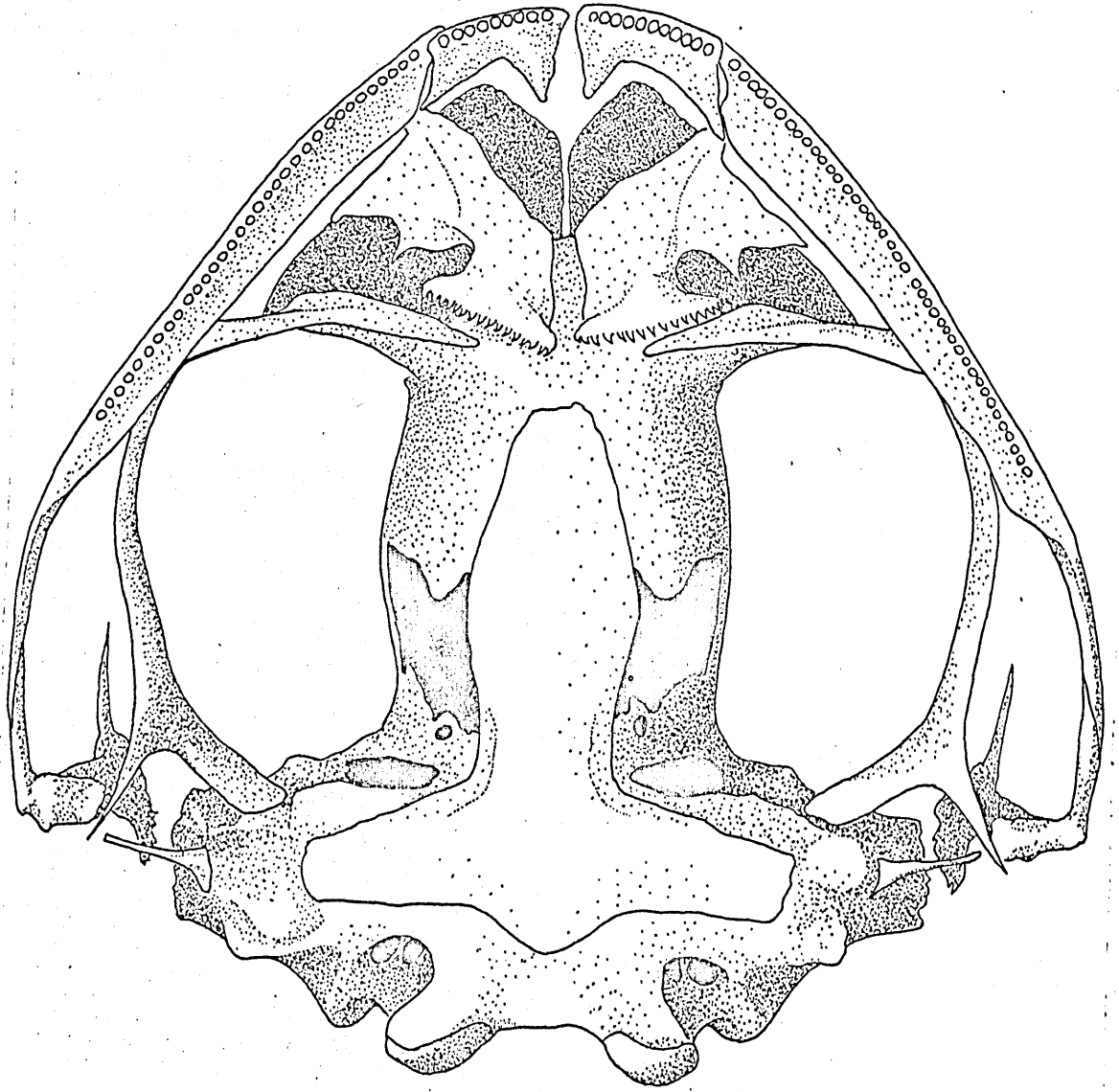


Figure 117. Ventral view of skull of Lithodytes  
lineatus (KU 104340, x 8).



relatively short, not keeled medially; (32) parasphenoid alae deflected posteriorly, short, not overlapped laterally by median rami of pterygoids; (33) pterygoids slender, anterior rami long, not reaching palatines; (34) occipital condyles small, not stalked, widely separated medially; (36) terminal phalanges T-shaped; (37) alary processes of hyoid plate on narrow stalks; (39) m. petrohyoideus anterior and m. sternohyoideus insert on lateral edge of hyoid plate; (41) pupil horizontal; (42) male with median subgular vocal sac, no nuptial asperities; (43) body lacking glands; (44) tongue large, rounded; (45) toes lacking webbing, metatarsal tubercles not enlarged, digital tips dilated, each pad bearing terminal transverse groove; (46 - 48) (49) adults medium-sized, to 50 mm. SVL; (50) tympanum visible externally.

Composition.-- Monotypic.

Distribution.-- Edge of the Amazon Basin from Guayana to Bolivia.

Remarks.-- Several authors have placed Lithodytes lineatus in Eleutherodactylus. Some did so following Noble (1917), who ignored the presence of osseous styles in the omosternum and sternum and placed extra weight on the presence of T-shaped terminal phalanges. Ruthven (1919) effectively rejected Noble's arguments.

Rana lineata Schneider has been frequently confused with Hylodes lineatus Brocchi. The latter is a Guatemalan species of Eleutherodactylus and bears no resemblance to the Amazonian Lithodytes lineatus. Lithodytes lineatus bears considerable superficial resemblance to some species of the Eleutherodactylus fitzingeri group. Dunn (1931) named Lithodytes gaigeae (erroneously spelled gaigei), a species found in Costa Rica and Panamá, and Piatt (1934) correctly pointed out that gaigeae was a species of Eleutherodactylus. The two species are strikingly similar in color pattern.

The skull of Lithodytes bears considerable resemblance to those of the paludicoline genera, but the sternal style is elongate, like that of Leptodactylus. The hyolaryngeal apparatus of Lithodytes is like that seen in Edalorhina, Leptodactylus, and Pleurodema. Nothing is known of the breeding biology of Lithodytes, but the lack of nuptial asperities suggests that the genus clasps on land and may exhibit direct development like the species of the Leptodactylus marmoratus group.

Physalaemus Fitzinger, 1826

(Figs. 118-19)

Physalaemus Fitzinger, 1826, Neue Class. Rept., p. 39

[Type-species by monotypy, Physalaemus cuvieri

Fitzinger, 1826 (a nomen nudum)].

Paludicola Wagler, 1830, Syst. Amph., p. 206 [Type-species



by monotypy, Bufo albifrons Spiz, 1824].

Gomphobates Reinhardt and Lütken, 1862, Vid. Meddel.

Naturh. Foren., 1861:172 [Type-species by monotypy,

Gomphobates notatus Reinhardt and Lütken, 1862].

Eupemphix Steindachner, 1863, Sber. Akad. Wiss. Wien, 48:188

[Type-species by monotypy, Eupemphix nattereri

Steindachner, 1863].

Nattereria Steindachner, 1864, Verh. Zool.-Bot. Ges.

Wien, 1864:279 [Type-species by monotypy, Nattereria

lateristrigata Steindachner, 1864].

Iliobates Fitzinger in Steindachner, 1867, Reise Novara,

p. 12 [Listed as a generic synonym (manuscript name)

of Gomphobates fuscomaculatus Steindachner; this generic name is invalid and not available].

Engystomops Jiménez de la Espada, 1872, An. Soc. Española

Hist. Nat., 1:86 [Type-species by monotypy, Engystomops

petersi Jiménez de la Espada, 1872].

Microphryne W. Peters, 1873, Mtber. k. Preuss. Akad.

Wiss. Berlin, 1873:616 [Type-species by monotypy,

Paludicola (Microphryne) pustulosa Cope, 1864].

Peralaimos Jiménez de la Espada, 1875, Vert. Viaje

Pacif. Batr., p. 163 [Type-species by monotypy, Bufo

stentor Jiménez de la Espada, 1872].

Hyperoodon Philippi, 1902, Supl. Bat. Chilenas, p. 1

[Type-species by monotypy, Hyperoodon asper Philippi, 1902;

preoccupied by Hyperoodon Lacépède, 1804 (Mammalia: Cetacea)].

Diagnostic definition.-- (1) sternum bearing relatively broad osseous sternal style; (3) transverse processes of posterior presacral vertebrae somewhat shortened; (4) cervical cotylar arrangement type I; (7) omosternum elongate, cartilaginous, manubrium small to large; (8) sacral diapophyses slightly dilated; (9) maxillary arch toothed or not; (10) alary processes of premaxillae directed dorsally or slightly anterodorsally, relatively narrow at base; (11) palatal shelf of premaxilla relatively broad; (12) facial lobe of maxilla short, of moderate depth; (13) palatal shelf of maxilla narrow, no pterygoid process; (14) maxillary arch complete; (15) nasals relatively large, in broad median contact; (16) nasals not in contact with maxillae or pterygoids; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle lacking; (19) frontoparietals not ornamented; (22) epiotic eminences small; (23) cristae paroticae short, stocky; (24) zygomatic ramus of squamosal short; (25) otic ramus of squamosal short, no otic plate; (26) squamosal-maxillary angle about  $60^{\circ}$ ; (27) columella present; (28) prevomers entire, small, usually toothless, widely separated medially; (29) palatines long, slender, widely separated medially; (30) sphenethmoid extending anteriorly beneath posterior part

Figure 118. Lateral, dorsal, and ventral views  
of skull of Physalaemus pustulosus (KU 68271, x 8).

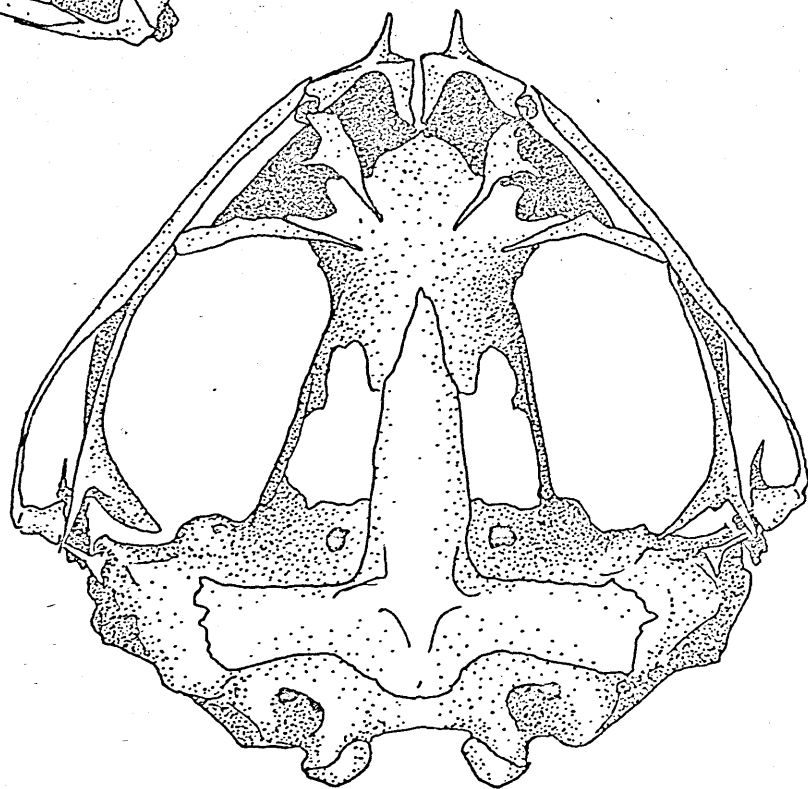
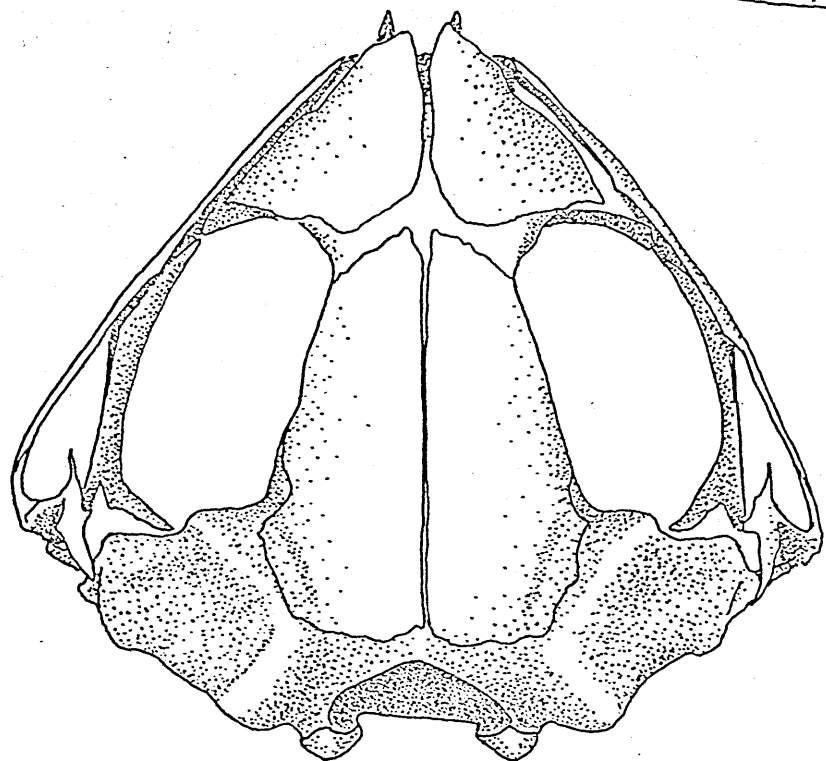
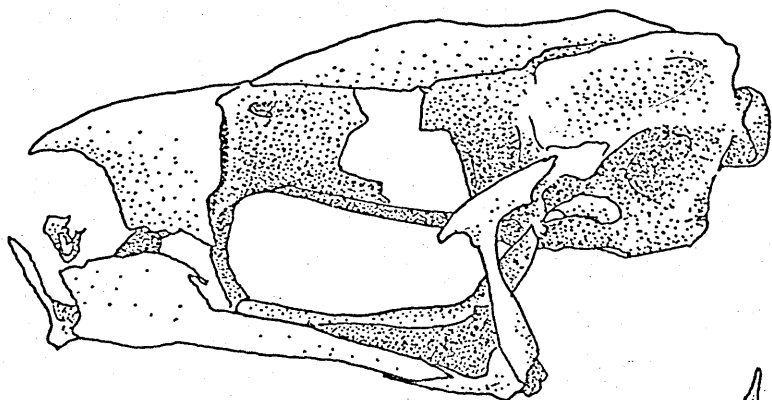
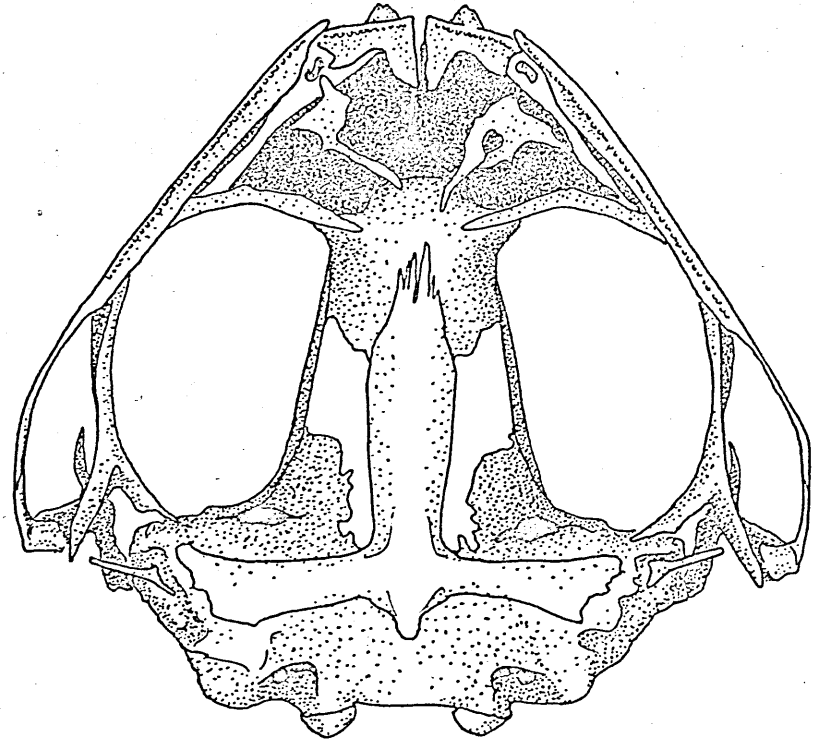
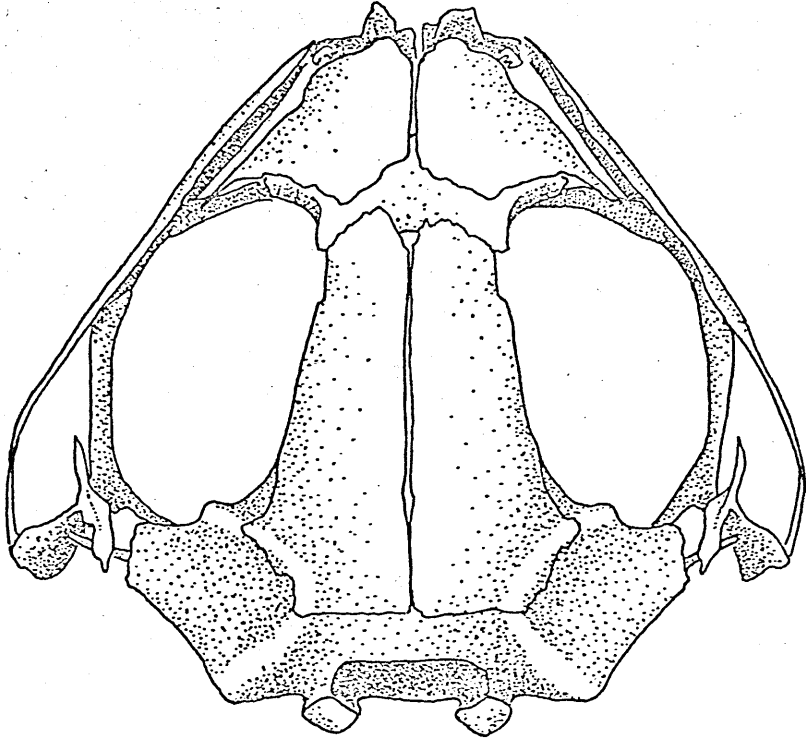
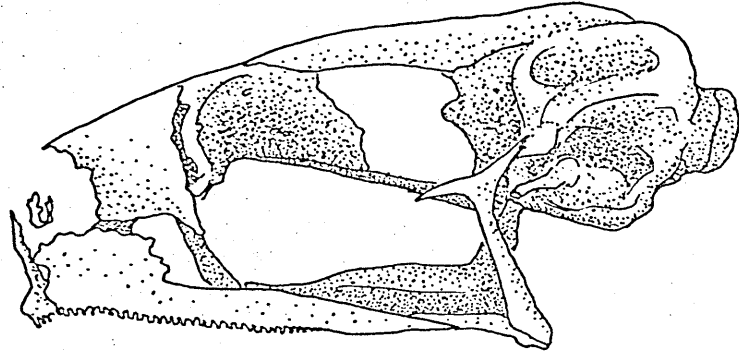


Figure 119. Lateral, dorsal, and ventral views of skull of Physalaemus ephippifer, (KU 93005, x 8).



of nasals; (31) anterior ramus of parasphenoid narrow, not keeled medially; (32) parasphenoid alae oriented at right angles to anterior ramus, narrowly separated from or narrowly overlapped laterally by median rami of pterygoids; (33) pterygoids slender, rami long, anterior rami reaching palatines; (34) occipital condyles small, on short stalks, widely separated medially; (36) terminal phalanges knobbed; (37) alary processes of hyoid plate broad and wing-like; (39) m. petrohyoideus anterior and m. sternohyoideus insert on hyoid plate near midline; (41) pupil horizontal; (42) males with large external subgular vocal sacs, tending to bilobe, males with nuptial pads on thumb; (43) parotoid glands present or absent, inguinal glands present or absent, flank glands present or absent; (44) tongue relatively narrow; (45) toes free of webbing and lateral fringes, tarsus bearing tubercle on inner edge or not, metatarsal tubercles enlarged and spade-like or not, digital tips narrow; (46) larvae with dextral vent, 2/3 tooth rows, labial papillae broadly interrupted anteriorly; (48) eggs small, numerous, laid in foam nest floating on water; (49) adults range in size from 17 - 60 mm. SVL; (50) tympanum usually concealed, visible externally in pustulatus.

Composition.-- With the combination of the nominal genera Engystomons, Eupemphix, and Physalaemus into a

single genus, Physalaemus is one of the larger genera of leptodactylids. I recognize 34 nominal species (aguirrei, albifrons, albonotatus, barrioi, biligonigerus, centralis, cicada, cuvieri, enesefae, ephippifer, evangelistai, fernandezae, fuscomaculatus, gracilis, henseli, kroeyeri, jordanensis, maculiventris, moreirae, nanus, nattereri, obtectus, olfersi, paraensis, petersi, pustulatus, pustulosus, riograndensis, santafecinus, schereri, signiferus, soaresi, stentor, and ternetzi).

Distribution.-- Southern México to Argentina in lowland non-forested regions (and through second growth and occasionally primary forest) except for the very arid Pacific lowlands south of Ecuador and over most of central and southern Argentina and Chile.

Remarks.-- In a separate paper, I (Lynch, 1969c) justified the combination of Engystomops, Eupemphix, and Physalaemus. In that paper I suggested the recognition of at least four species groups--the petersi group, the maculiventris group, the curvieri group, and the fuscomaculatus group.

Physalaemus has the crinine pattern of insertion of the hyoid musculature on the hyoid plate. The only other Neotropical leptodactylids with this pattern are the species of the Leptodactylus marmoratus group and the genus Pseudopaludicola, although the hyoid plate of Hydrolaetare is like that seen in Physalaemus and



Pseudopaludicola. For the present I consider Physalaemus and Pseudopaludicola to be relatively closely related but realize that the two genera differ in many respects. In some characteristics Physalaemus is closest to Leptodactylus and Pleurodema, but in others it is closer to Edalorhina, Lithodytes, and Paratelmatoobius.

Paratelmatoobius B. Lutz and Carvalho, 1958

(Fig. 120)

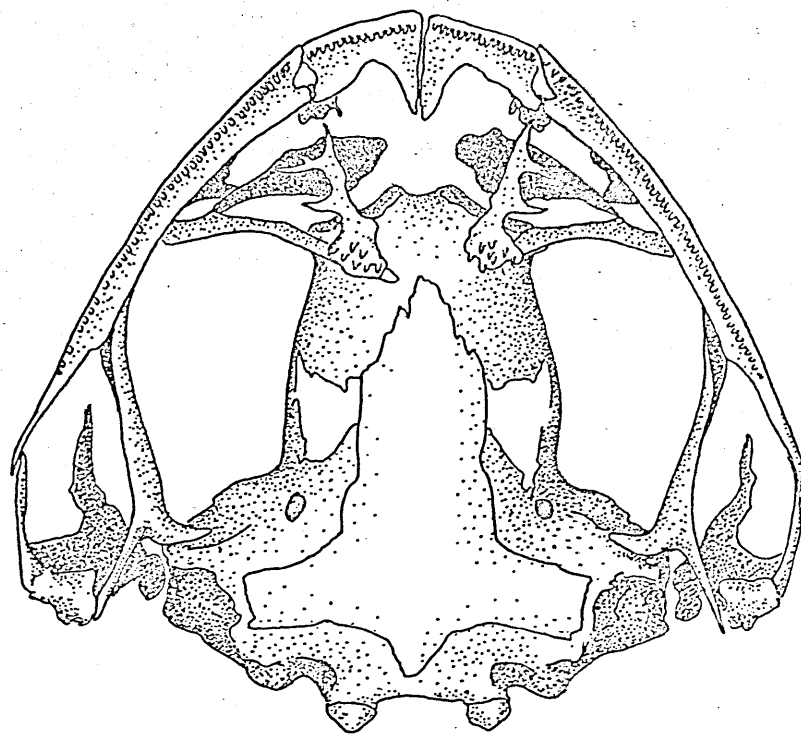
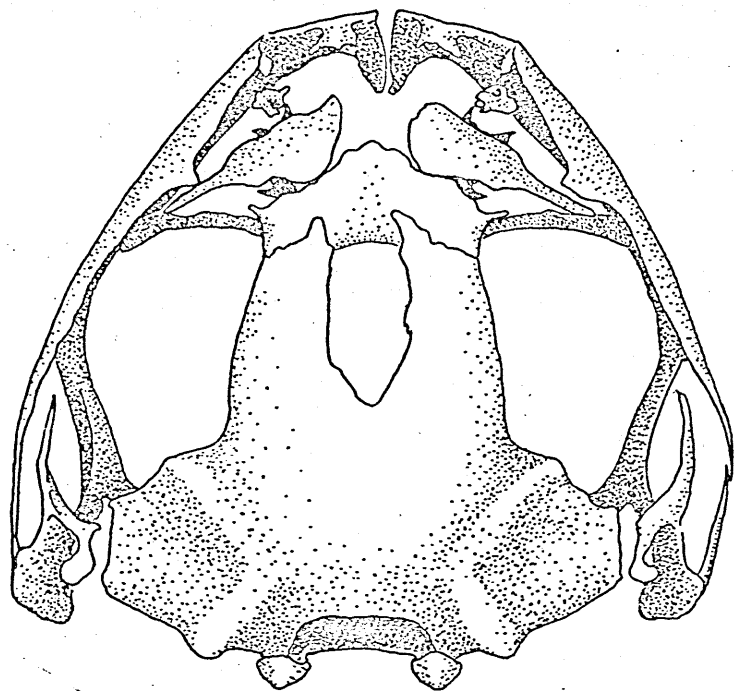
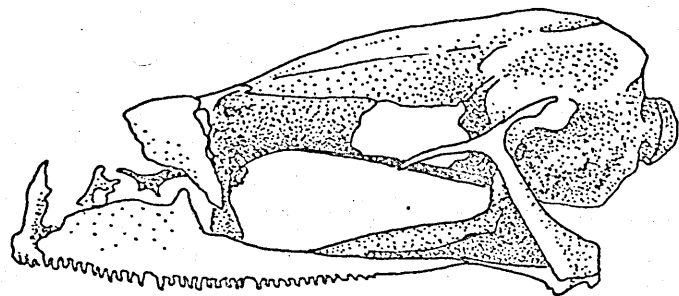
Paratelmatoobius B. Lutz and Carvalho, 1958, Mem. Inst.

Oswaldo Cruz, 56:241 [Type-species by original designation, Paratelmatoobius lutzi B. Lutz and Carvalho, 1958].

Diagnostic definition.-- (1) sternum bearing a broad osseous plate; (2) transverse processes of posterior presacral vertebrae shortened; (3) cervical cotylar arrangement type I; (4) omosternum present, small, cartilaginous, manubrium minute; (5) sacral diapophyses dilated; (6) maxillary arch toothed; (7) alary processes of premaxillae directed dorsally, narrow at base; (8) palatal shelf of premaxilla broad; (9) facial lobe of maxilla shallow, expanded in snout region; (10) palatal shelf of maxilla broad, pterygoid process moderate-sized; (11) maxillary arch complete; (12) nasals small, narrow, separated medially; (13) nasals not contacting maxillae or pterygoids, nasal with elongate maxillary process which nearly reaches maxilla; (14) nasals not in contact with

frontoparietals; (18) frontoparietal fontanelle moderate-sized; (19) frontoparietals not ornamented; (22) epiotic eminences well defined; (23) cristae paroticae short, stocky; (24) zygomatic ramus of squamosal relatively long, slender; (25) otic ramus of squamosal short, curved medially to form small otic plate; (26) squamosal-maxillary angle about  $55^{\circ}$ ; (27) columella absent; (28) prevomers small, entire, toothed, widely separated medially; (29) palatines twin, elongate, broadly separated medially; (30) sphenethmoid extending anteriorly to middle of nasals; (31) anterior ramus of parasphenoid broad, short, lacking median keel; (32) parasphenoid alae short, narrow, deflected posteriorly, not overlapped laterally by median rami of pterygoids; (33) pterygoids small, median rami short, anterior rami not reaching palatines; (34) occipital condyles large, not stalked, widely separated medially; (36) terminal phalanges knobbed; (37) alary processes of hyoid plate on narrow stalks; (39) m. petrohyoideus anterior and m. sternohyoideus insert on lateral edge of hyoid plate; (41) pupil horizontal; (42) males lacking vocal sac, nuptial pads on first two fingers; (43) body lacking glands; (44) tongue large, round; (45) toes fully webbed, metatarsal tubercles not enlarged, digital tips narrow; (46 - 48) (49) adults small, less than 30 mm. SVL; (50) tympanum concealed.

Figure 120. Lateral and dorsal (KU 107089) and ventral (KU 92981) views of skulls of Paratelmatoobius lutzi . All x 12.



Composition.-- Two species are presently known (lutzi and gaigeae). The latter was named P. pictiventris A. Lutz in B. Lutz and Carvalho (1958) but is a nomen nudum and an obligate synonym of Leptodactylus gaigeae Cochran, 1938.

Distribution.-- The coastal ranges in Estado Rio de Janeiro, Brasil.

Remarks.-- Aldopho Lutz collected the first specimens of this genus in December 1931. He made water color sketches of the two specimens and noted that they represented a new species of Paludicola or Eupemphix. However, he never described the specimens or otherwise published on them. Cochran (1938) who received these two specimens, named and described them as Leptodactylus gaigeae. She suggested that the species was related to L. marmoratus and served as a generic link between Leptodactylus and Zachaenus. Lutz and Carvalho (1958) discovered a new species allied to the frogs collected by A. Lutz nearly 30 years before and named it as a new genus and new species, Paratelmatoobius lutzi; at the same time they published A. Lutz's figures of the other species and used his manuscript name, P. pictiventris, for them. They suggested that Paratelmatoobius was intermediate between the endemic southeastern Brazilian genus Cycloramphus and the Andean Telmatoobius.

The architecture of the otic ramus of the squamosal of Paratelmatoobius is identical to that seen in the Grypiscini, and the four genera bear considerable external resemblance to one another. The sternal plate in Paratelmatoobius is not like the sternal style seen in the leptodactylines but appears to be an ossification of the sternal plate--an advancement over the calcification of the same element seen in old individuals of a variety of leptodactylid genera and species. Nevertheless, Paratelmatoobius differs in several osteological characters from the Grypiscini--the presence of a frontoparietal fontanelle, the wide median separation of the nasals, the absence of a ventral flange on the pterygoid.

In summary, Paratelmatoobius is osteologically intermediate between the Leptodactylinae and the Grypiscini (Telmatobiinae). This might be regarded as some evidence for polyphyly of the Telmatobiinae since one group of Telmatobiinae (i.e., Alsodini) undoubtedly gave rise to the Leptodactylinae and I am here pointing out the possibility of genetic relationship between Paratelmatoobius and the Grypiscini. The squamosal architecture of Paratelmatoobius and the Grypiscini may be a parallel (or convergent) development rather than a result of relationship. The appearance of a very similar otic plate in Megaelosia (Elosiinae) is very suggestive that the appearance of this sort of otic ramus is a labile feature and should not be

used in primary inferences of relationships. In the Grypiscini, several other osteological characters combine to render this character confirmatory and therefore it is used in the diagnosis of that group (p. 460). I am tentatively assigning Paratelmatoobius to the Leptodactylinae. In several respects the genus bears some similarity to Physalaemus, although I do not regard the relationship (if any) to be close.

The presence of nuptial asperities and a frontoparietal fontanelle, although small, in Paratelmatoobius suggest that the genus is not allied with the Eleutherodactylini. The nature of the occipital condylar-cervical articulation as well as a variety of other osteological and external characters does not permit its association with the Ceratophryinae, Alsodini, Odontophrynini or Telmatobiini. The Elosiinae is a compact group, and the external and many internal features serve to illustrate the lack of correspondence between Paratelmatoobius and the Elosiinae. If a new family group is not proposed for this small genus, then the genus must belong to the Grypiscini or the Leptodactylinae. I have fewer difficulties associating it with the latter, perhaps because the latter is a more heterogeneous group. The presence of an osseous plate in the sternum, although it is rather unlike the sternal style seen in the other genera of the subfamily, is not

contrary to the diagnostic feature of the subfamily. No other leptodactylid known to me normally possesses an osseous post-zonal element. Although the presence of an osseous post-zonal sternal element is the only uniform character in the subfamily, I consider the subfamily to be monophyletic (see the generic account of Hydrolaetare for further comment).

Pseudopaludicola Miranda-Ribeiro, 1926

(Fig. 121)

Pseudopaludicola Miranda-Ribeiro, 1926, Arch. Mus. Nac.

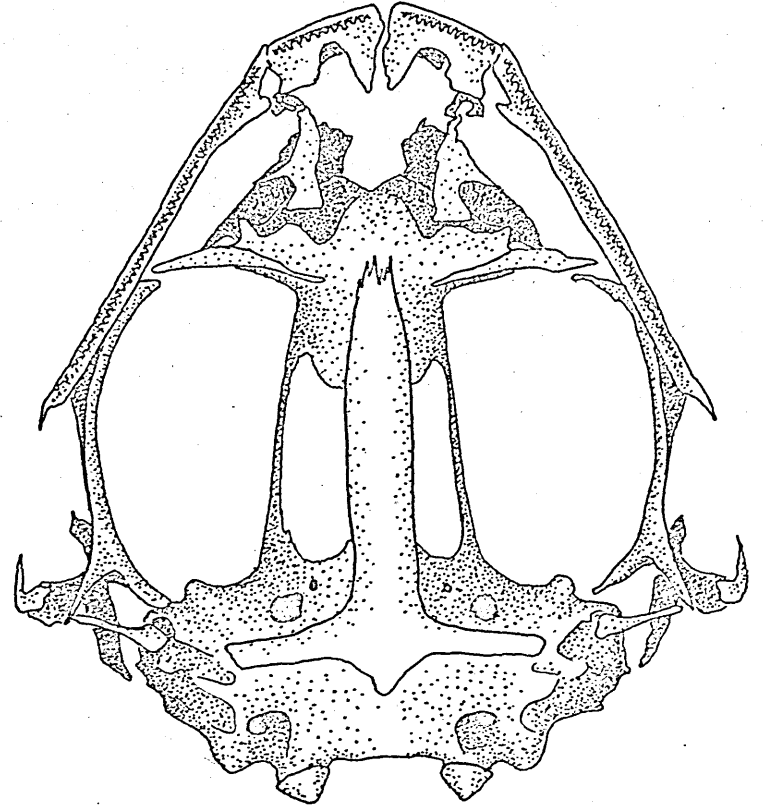
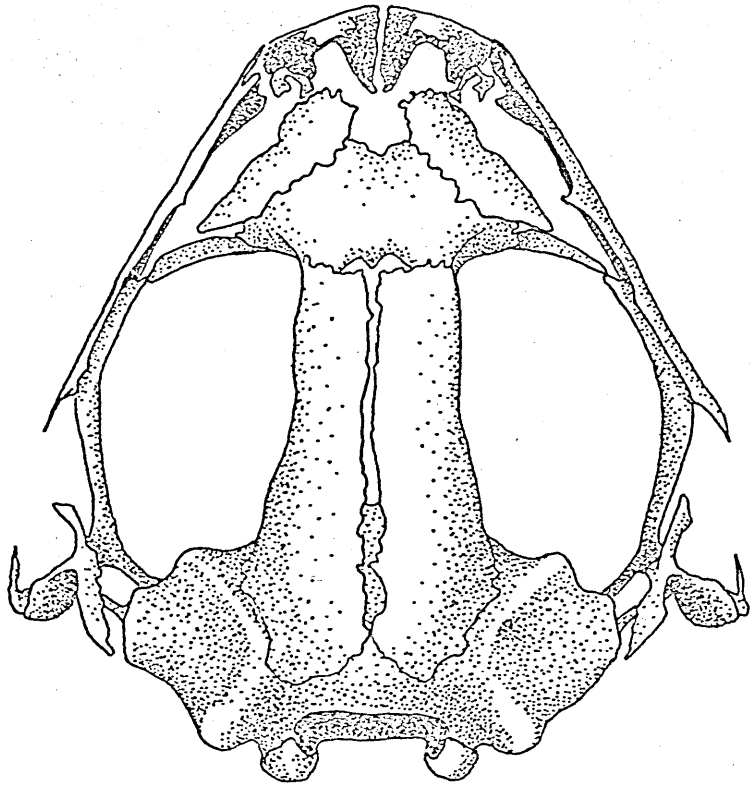
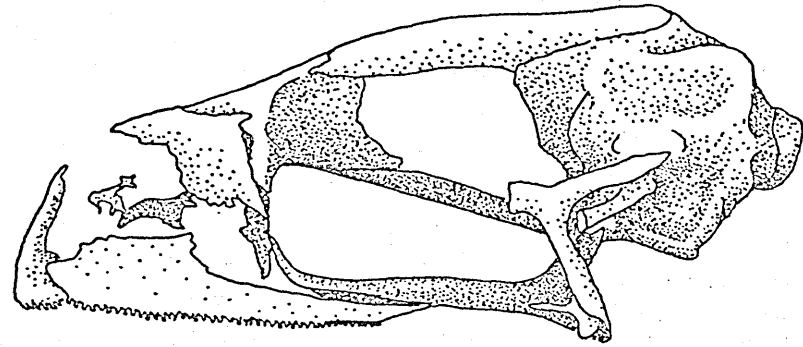
Rio de Janeiro, 27:152 [Type-species by monotypy,

Liuperus (sic) falcipes Hensel, 1867].

Diagnostic definition.-- (1) sternum bearing an elongate, osseous or calcified style; (3) transverse processes of posterior presacral vertebrae shortened; (4) cervical cotylar arrangement type I; (7) omosternum elongate, cartilaginous, manubrium small; (8) sacral diapophyses rounded; (9) maxillary arch toothed; (10) alary processes of premaxillae directed dorsally, broad at base; (11) palatal shelf of premaxilla broad; (12) facial lobe of maxilla shallow; (13) palatal shelf of maxilla narrow, no pterygoid process; (14) maxillary arch incomplete, quadratojugal absent; (15) nasals small, widely separated medially; (16) nasals not in contact with maxillae or pterygoids; (17) nasals not in contact



Figure 121. Lateral, dorsal, and ventral views  
of skull of Pseudopaludicola falcipes (KU 93068, x 12).



with frontoparietals; (18) frontoparietal fontanelle absent, frontoparietals usually narrowly separated for entire length; (19) frontoparietals not ornamented; (22) epiotic eminences obsolete; (23) cristae paroticae very short, broad; (24) zygomatic ramus of squamosal relatively short; (25) otic ramus of squamosal long, expanded medially into narrow otic plate; (26) squamosal-maxillary angle  $50 - 60^{\circ}$ ; (27) columella present; (28) prevomers small, reduced to sliver-like elements, dentigerous rami lost, widely separated medially; (29) palatines narrow, sliver-like, in contact with maxillae, widely separated medially; (30) sphenethmoid very short, extending anteriorly to posterior edge of nasals; (31) anterior ramus of parasphenoid narrow, not reaching palatines, not keeled medially; (32) parasphenoid alae long, oriented at right angles to anterior ramus of parasphenoid, narrowly separated from median rami of pterygoids; (33) pterygoids small, median and posterior rami minute, anterior rami long, reaching to palatines; (34) occipital condyles small, stalked, widely separated medially; (36) terminal phalanges knobbed; (37) alary processes of hyoid plate wing-like; (39) m. petrohyoideus anterior and m. sternohyoideus insert on hyoid plate near midline; (41) pupil horizontal; (42) males with bilobed subgular vocal sac, nuptial asperities lacking; (43) body lacking glands; (44) tongue large, oval; (45) toes lacking webbing and lateral fringes,

metatarsal tubercles not enlarged, digital tips narrow; (46) larvae with dextral vent, 2/3 tooth rows, labial papillae broadly interrupted anteriorly; (48) eggs small, numerous, laid singly or in small clumps attached to submerged vegetation; (49) males reach 16 mm., females reach 19 mm. SVL; (50) tympanum concealed; (51) the antebrachial tubercles are generically unique.

Composition.-- Parker (1927) recognized five species of the genus (ameghini, boliviana, falcipes, pusilla, and saltica). Bokermann (1966) recognized five species in the coastal lowlands of eastern and southern Brasil (ameghini, falcipes, mystacalis, saltica, and ternetzi), which Milstead (1963) had pronounced identical. I consider boliviana and pusilla to be conspecific (see "Remarks") and recognize six species (ameghini, falcipes, mystacalis, pusilla, saltica, and ternetzi).

Distribution.-- The coastal lowlands of Brasil from Bahía to northeastern Argentina; Amazonian Bolivia, Paraguay, and Venezuela, and in the coastal ranges of Venezuela and the Santa Marta mountains of Colombia.

Remarks.-- The genus Pseudopaludicola gained wide acceptance through the work of Parker (1927) and Barrio (1954). Parker included five species in the genus and considered two of these (boliviana and pusilla) to have T-shaped terminal phalanges. All species of the genus

have elongate, knobbed terminal phalanges and agree in all details of skull ossification. Parker incorrectly characterized the genus as having a cartilaginous sternum (see account of pectoral girdles, pp. 181-82) and has been followed by all subsequent authors. I include the genus in the Leptodactylinae and consider it closely related to the paludicoline genera in spite of the ethological differences pointed out by Barrio (1954). The structure of the hyolarynx of Pseudopaludicola is not greatly different from that of Physalaemus but very different from that of all other Neotropical leptodactylids except Hydrolaetare and the Leptodactylus marmoratus group.

The species of this genus are readily distinguished from all other small leptodactylid frogs by their slender habitus, lack of digital webbing, unexpanded digital tips, concealed tympanum, and the presence of an antebrachial tubercle. The skeletons of the five nominal species available to me are indistinguishable.

Parker separated boliviana and pusilla on slight differences in leg length and coloration. I tentatively consider the two nominal species identical because I am unable to separate paratypes and topotypic material of each from one another. Rivero (1961) reported "pusilla" from Amazonian Venezuela and Parker (1935) reported "boliviana" from British Guiana and Paraguay. In view of the ethological differences recently discovered between

the Brazilian species (W. C. A. Bokermann, pers. comm.), it might prove premature to combine the cis-Andean populations of Pseudopaludicola as a single species. The specimens examined by me represent a single morphological species. The Brazilian species were pronounced conspecific by Milstead (1963). Bokermann has since examined most of the types of this genus and is familiar with all of the Brazilian species in the field; he informs me that most of the previously named kinds represent valid species, and there are yet undescribed species living in the coastal lowlands of southeastern Brasil. All of the Brazilian species can be separated on the basis of call, leg length, and color pattern.

Leptodactylus Fitzinger, 1826

(Figs. 122-24)

Leptodactylus Fitzinger, 1826, Neue Class. Rept., p. 38

[Type-species by subsequent designation, (Fitzinger, 1843), Leptodactylus typhonia (= Rana typhonia Daudin, 1803, non Rana typhonia Linné, 1758). Rana typhonia Daudin is R. sibilatrix Wied, 1824, which Heyer (1968) considered identical with Rana fusca Schneider, 1799, for which he designated a neotype. However, at least some of the syntypes of Rana fusca are extant (W. C. A. Bokermann, pers. comm.), and study of these must be made before Heyer's action can be accepted].

Cystignathus Wagler, 1830, Syst. Amph., p. 202 [Type-species by present designation, Rana mystacea Spix, 1824].

Gnathophysa Fitzinger, 1843, Syst. Rept., p. 31

[Type-species by original designation, Rana labyrinthica Spix, 1824].

Sibilatrix Fitzinger, 1843, Ibid., p. 31 [Type-species by original designation, Cystignathus gracilis Duméril and Bibron, 1841].

Plectromantis W. Peters, 1862, Mber. k. Preuss. Akad.

Wiss. Berlin, 1862:232 [Type-species by monotypy,

Plectromantis wagneri W. Peters, 1862].

Adenomera Steindachner, 1867, Reise Novara, Zool. Amph.,

p. 37 [Type-species by monotypy, Adenomera marmorata

Steindachner, 1867].

Entomoglossus W. Peters, 1870, Mber. k. Preuss. Akad.

Wiss. Berlin, 1870:647 [Type-species by monotypy,

Entomoglossus pustulatus W. Peters, 1870].

Pachypus A. Lutz, 1930, Mem. Inst. Oswaldo Cruz, 23:22

[Proposed as a subgeneric name of Leptodactylus; no

type-species was designated. Preoccupied by Pachypus

Billberg, 1820 (Insecta: Coleoptera), Pachypus d'Alton,

1840 (Mammalia), and Pachypus Cambridge, 1873 (Arachnida)].

Cavicola A. Lutz, 1930, Ibid., 23:22 [Proposed as a

subgeneric name of Leptodactylus; no type-species was

designated. Preoccupied by Cavicola Ancy, 1887

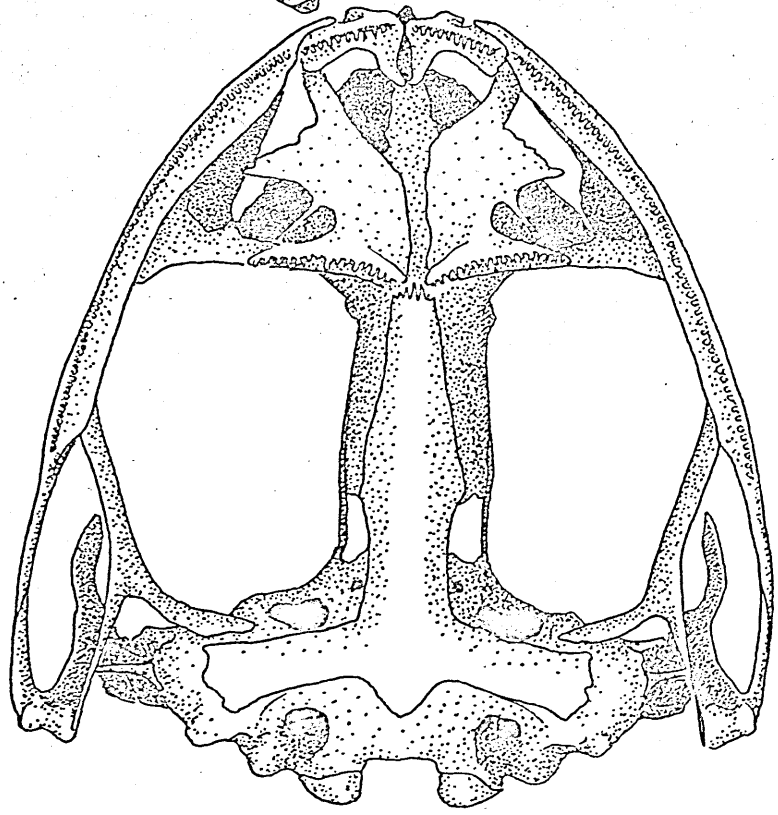
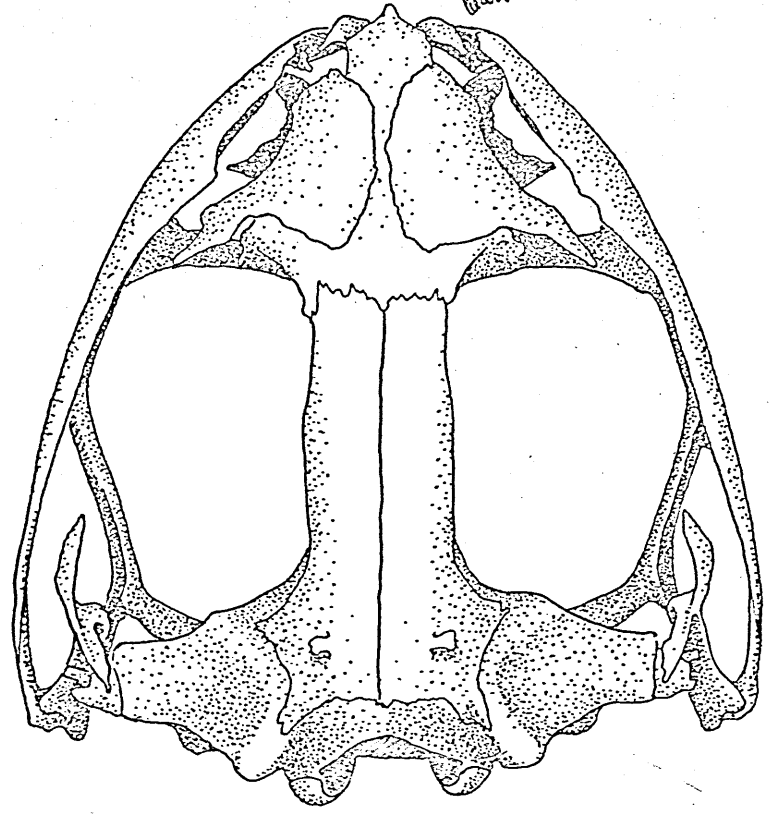
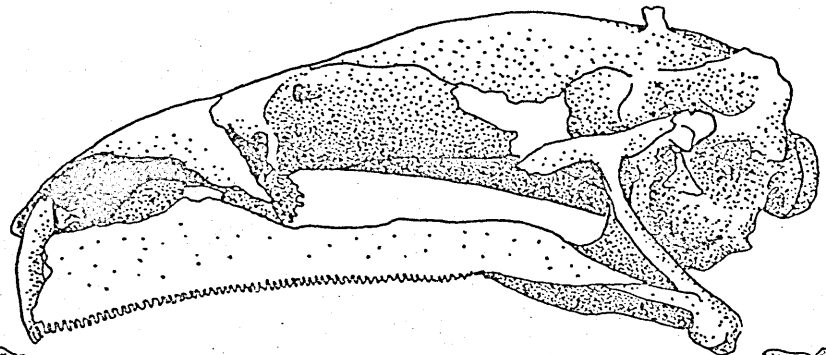
(Mollusca)].

Parvulus A. Lutz, 1930, Ibid., 23:22 [Proposed as a subgeneric name in Leptodactylus; type-species by subsequent designation (Parker, 1932:342), Leptodactylus nanus L. Müller, 1922].

Diagnostic definition.-- (1) sternum bearing an elongate osseous style; (3) transverse processes of posterior presacral vertebrae not shortened; (4) cervical cotylar arrangement type I; (7) omosternum large, elongate, cartilaginous, manubrium large; (8) sacral diapophyses rounded; (9) maxillary arch toothed, teeth frequently pointed; (10) alary processes of premaxillae directed dorsally or posterodorsally, broad at base; (11) palatal shelf of premaxilla moderately broad; (12) facial lobe of maxilla relatively shallow, entire maxilla same depth anterior to end of tooth row; (13) palatal shelf of maxilla relatively narrow, no pterygoid process; (14) maxillary arch complete; (15) nasals large, narrowly separated medially; (16) nasals usually not in contact with maxillae, never in contact with pterygoids, nasals have elongate maxillary processes in most species; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle lacking; (19) frontoparietals bearing some ornamentation posteriorly in old adults of the larger species; (22) epiotic eminences well defined posteriorly; (23) cristae paroticae moderately long, somewhat stocky; (24) zygomatic ramus of squamosal



Figure 122. Lateral, dorsal, and ventral views of skull of Leptodactylus quadrivittatus (KU 41030, x 6), a member of the fuscus group.



somewhat expanded, relatively short; (25) otic ramus of squamosal slightly longer than zygomatic ramus, expanded into narrow otic plate which usually rests tenuously on crista parotica; (26) squamosal-maxillary angle less than  $45^{\circ}$ ; (27) columella present; (28) prevomers large, entire, toothed, narrowly separated medially; (29) palatines broad, narrowly separated medially, sometimes bearing odontoid ridge; (30) sphenethmoid extending anteriorly to middle of nasals in marmoratus, melanonotus, ocellatus, and pentadactylus groups, extending anteriorly to a point anterior to nasals and usually anterior to premaxillae in fuscus group; (31) anterior ramus of parasphenoid narrow, not keeled medially, reaching to palatines; (32) parasphenoid alae deflected posteriorly, narrowly overlapped laterally by median rami of pterygoids in fuscus, melanonotus, ocellatus, and pentadactylus groups, separated in the marmoratus group; (33) pterygoids slender, anterior rami reaching to middle of orbit; (34) occipital condyles moderate-sized, not stalked, moderate to wide median separation; (36) terminal phalanges knobbed; (37) alary processes of hyoid on narrow stalks in fuscus, melanonotus, ocellatus, and pentadactylus groups, wing-like in marmoratus group; (39) m. petrohyoideus anterior and m. sternohyoideus insert on lateral edges of hyoid plate in fuscus, melanonotus, ocellatus, and pentadactylus groups, insert on hyoid plate near midline in marmoratus group;

Figure 123. Dorsal views of skull of Leptodactylus pentadactylus (KU 68159, x 3) and L. wagneri (KU 104389, x 3).

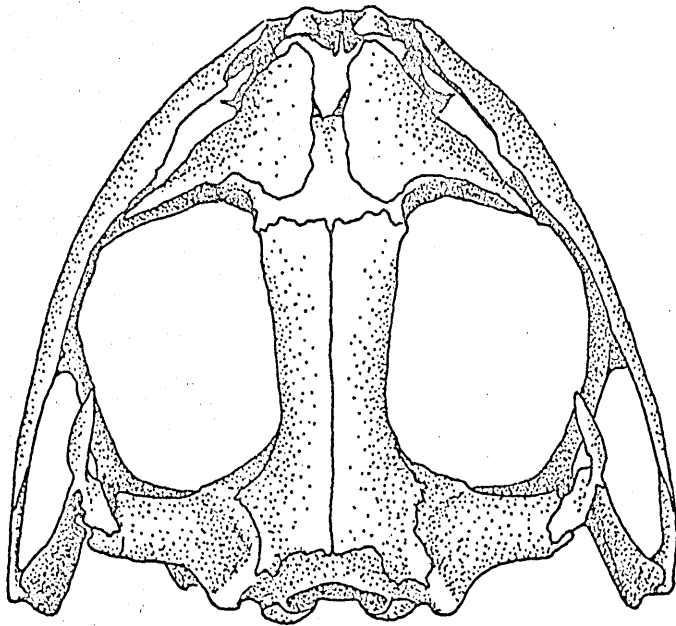
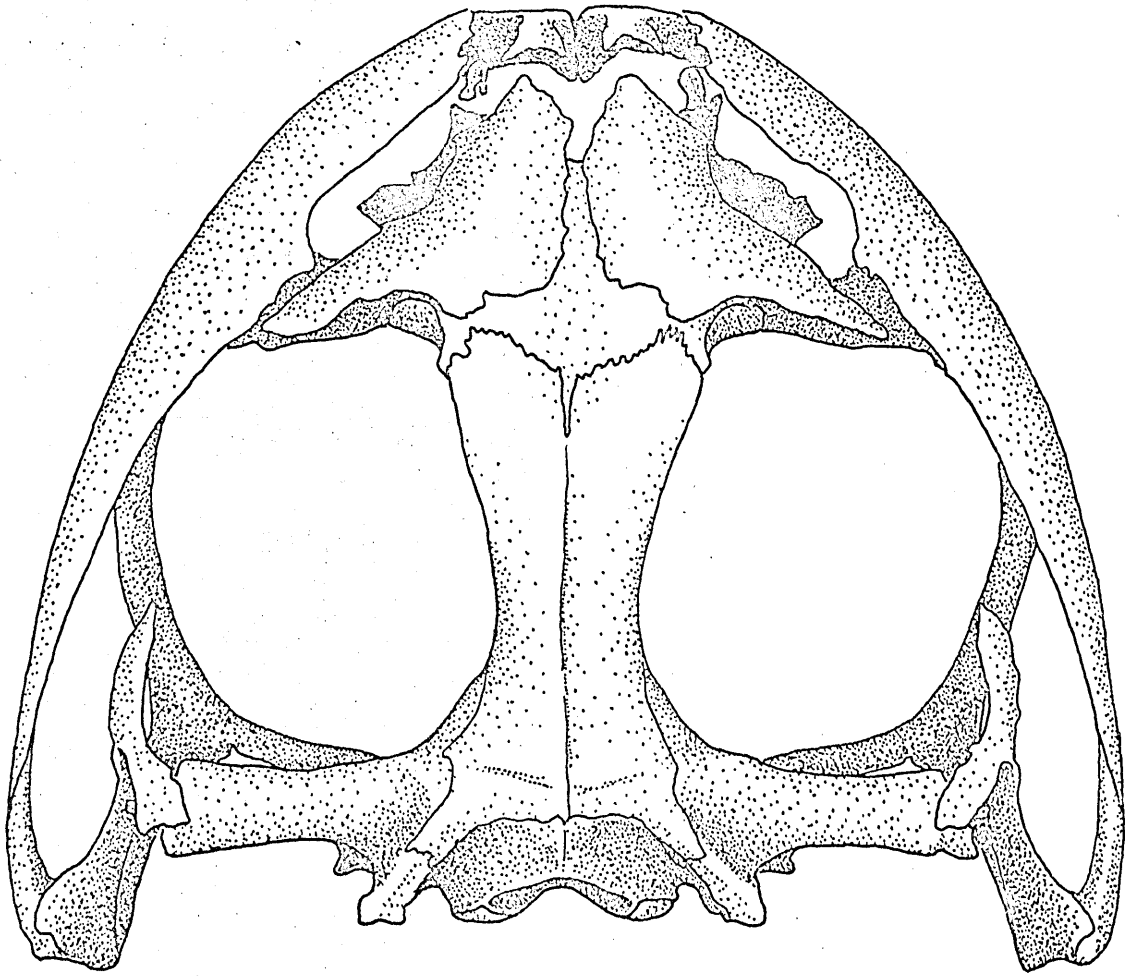
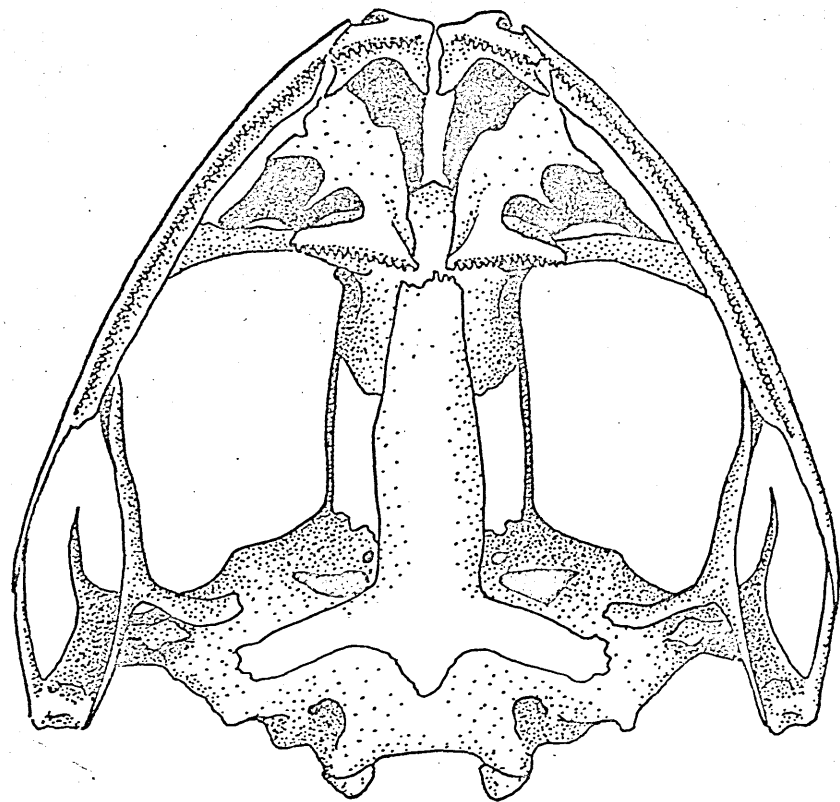
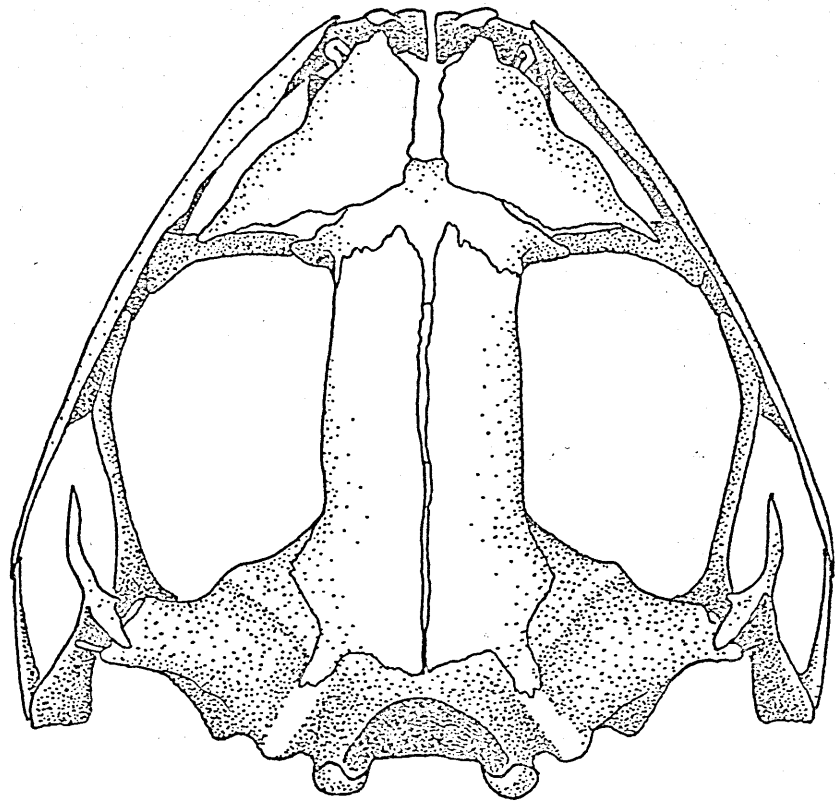
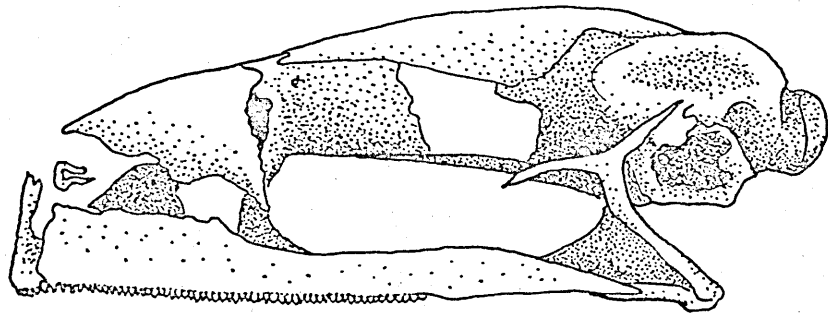


Figure 124. Lateral, dorsal, and ventral views  
of skull of Leptodactylus hylaedactylus (KU 119387, x 8).



(41) pupil horizontal; (42) males with median subgular or paired lateral vocal sacs or none, males of fuscus and marmoratus groups lack nuptial asperities, males of melanonotus, ocellatus, and pentadactylus groups have spines on the thumb, males of the pentadactylus group have spines on the chest and thumb; (43) body with diffuse ventral and flank glands or not, many species have glandular folds on the dorsum, species of the pentadactylus group have inguinal glands; (44) tongue large, with two long posterior horns; (45) toes not webbed, species of the melanonotus and ocellatus groups have lateral fringes on the toes, metatarsal tubercles not enlarged, digital tips narrow, first finger slightly longer than second in marmoratus group, much longer than second in other species groups except for a few species in the melanonotus group; (46) frogs of marmoratus group do not have tadpoles, in other groups larvae with median vent, 2/3 tooth rows, labial papillae broadly interrupted anteriorly; (48) eggs laid in foam nest floating on water in melanonotus, ocellatus, and pentadactylus groups, in these groups the eggs are small and numerous; in the fuscus group eggs are deposited in a foam nest in an underground burrow and hatch when the nest is inundated; in the marmoratus group the eggs are large, few in number, and are deposited in an underground nest in foam; development is direct in the marmoratus group but the other groups have aquatic larvae;



(49) adults range in size from 20 - 200 mm. SVL; (50) tympanum visible externally or concealed.

Composition.-- Gorham (1966) listed 60 species in the genus. Of these, three belong to other genera (L. gaigeae = Paratelmatobius gaigeae; L. pulcher = Barycholos pulcher; L. tubercluosus = Ischnocnema quixensis). Heyer (1969a) recognized only 32 species. His system is admittedly conservative, but is a considerable improvement over that presented by Gorham.

Distribution.-- Middle American lowlands from Sonora, México, and southern Texas to the Argentine Chaco and Guayas region of Ecuador in South America, and on the Lesser Antilles and Hispaniola. All localities for the species of the genus are lowland (usually below 1200 meters).

Remarks.-- No new generic synonyms are added here. The generic synonymy of Leptodactylus has been stable for many decades, because the genus is rather morphologically uniform in external characteristics. Heyer (1969a) solved many systematic problems of the genus, among which was the discovery of the identity of Plectromantis wagneri. This species is a widespread species of the Amazon Basin and has accumulated nearly a dozen synonyms.

I studied the skeletons of 18 species of the genus in formulating my concepts of the genus. This study illustrated the remarkable osteological homogeneity of the

frogs of this genus. Accordingly, I do not advocate the use of subgenera such as those proposed by A. Lutz (1930). Lutz placed the species of the genus in six subgenera; of these, two are generic homonyms, one is a valid generic name of Asiatic ranids (Platymantis), and one (Plectromantis) was based on erroneous data.

A major advancement in the systematics of this genus was provided by Heyer, who divided the genus into five species groups based on external morphology, thigh musculature, jaw musculature, developmental patterns and tadpole morphology, some osteological characters, and vocalization. Heyer utilized secondary sex characters in his classification; his classification appears to be a realistic one. I contend that his melanonotus group is a composite with part of the species (those with arched prevomerine dentigerous processes of the prevomerine bones) being members of the ocellatus group.

Heyer advocated placing the marmoratus group in a separate subgenus, Adenomera; this action is one of preference, but in keeping with the criteria followed throughout this review of the family, I choose not to recognize the subgenus. The frogs of the subgenus Adenomera differ from those of the subgenus Leptodactylus in that the former exhibit direct development whereas the latter have aquatic tadpoles. Heyer cited additional characteristics to distinguish the marmoratus group from

other Leptodactylus but these additional characters are shared by some other species groups. The musculature of the hyolarynx of the frogs of the marmoratus group is like that seen in Physalaemus and Pseudopaludicola (the crinine pattern). The frogs of the marmoratus group resemble Barycholos pulcher (see following account) in some but not all morphological characters. When the breeding biology of all of the genera of the Leptodactylinae becomes known, the generic status of Adenomera and Barycholos should become more apparent.

Barycholos Heyer, 1969

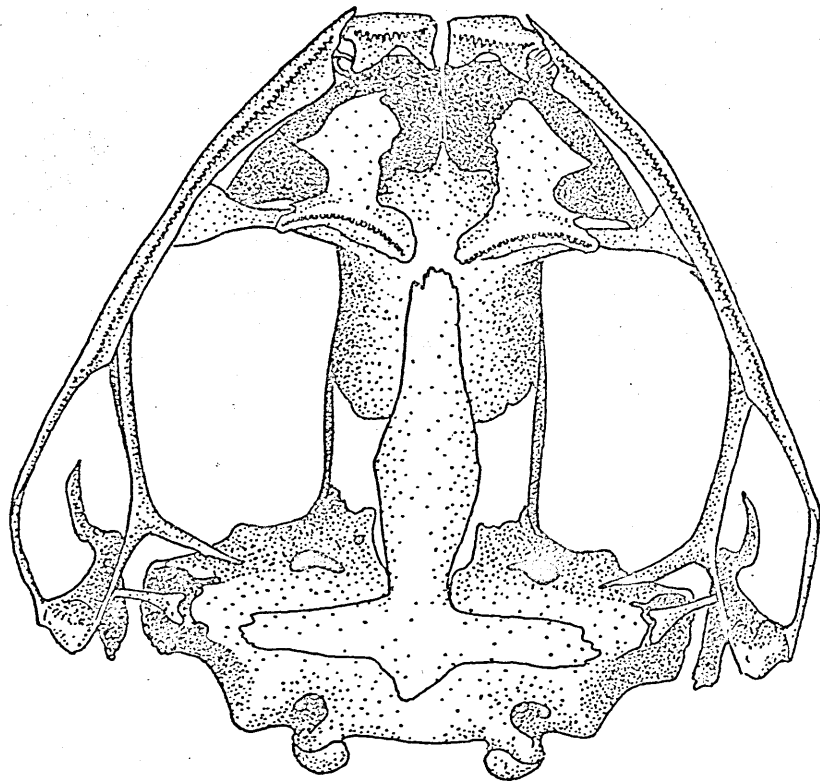
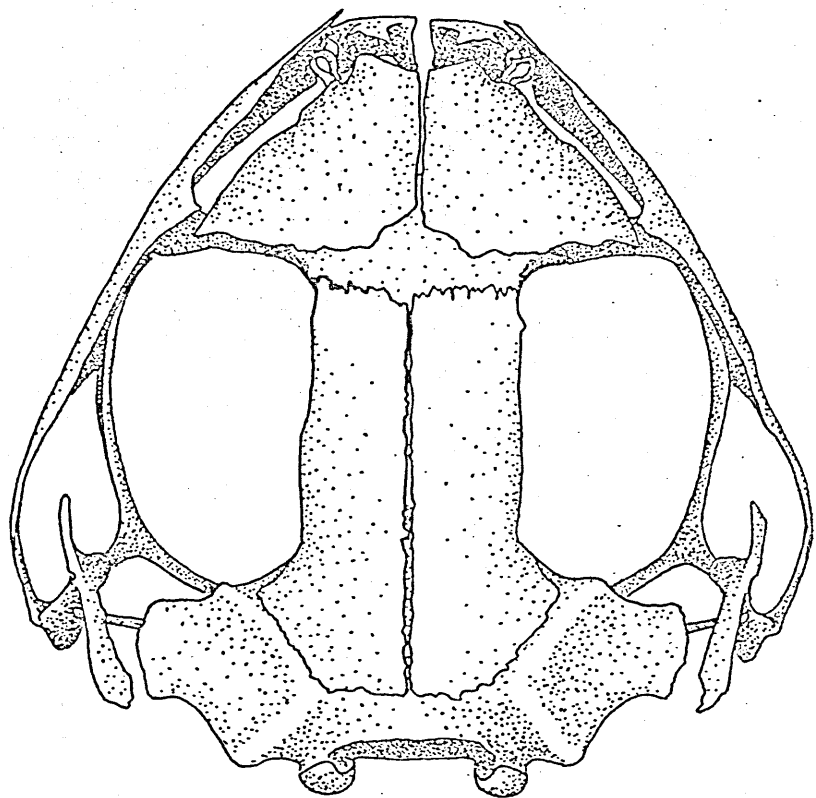
(Fig. 125)

Barycholos Heyer, 1969, Cont. Sci. Los Angeles Co. Mus., 155:6 [Type-species by original designation, Leptodactylus pulcher Boulenger, 1898].

Diagnostic definition.-- (1) sternum containing a calcified style, bifurcate posteriorly; (3) transverse processes of posterior presacral vertebrae slightly shortened; (4) cervical cotylar arrangement type I; (7) omosternum moderate-sized, manubrium elongate, partly calcified; (8) sacral diapophyses slightly dilated; (9) maxillary arch toothed; (10) alary processes of premaxillae directed dorsally, broad at base; (11) palatal shelf of premaxilla relatively deep, deeply incised; (12) facial lobe of maxillae relatively shallow;

(13) palatal shelf of maxilla broad anteriorly, narrowing posteriorly, no pterygoid process; (14) maxillary arch complete; (15) nasals large, in broad median contact; (16) nasals narrowly separated from maxillae, widely separated from pterygoids; (17) nasals in tenuous contact with frontoparietals; (18) frontoparietal fontanelle lacking; (19) frontoparietals not ornamented; (22) epiotic eminences moderately well defined; (23) cristae paroticae relatively short, stocky; (24) zygomatic ramus of squamosal relatively short, broadly separated from maxilla; (25) otic ramus of squamosal relatively long, expanded medially to form small otic plate; (26) squamosal-maxillary angle  $55^{\circ}$ ; (27) columella present; (28) prevomers small, irregular in outline, widely separated medially, bearing large, arched, transverse, toothed, dentigerous processes; (29) palatines slender, lacking odontoid ridge; (30) sphenethmoid entire, extending anteriorly beneath nasals; (31) anterior ramus of parasphenoid narrow, not keeled, reaching prevomerine dentigerous processes; (32) parasphenoid alae oriented at right angles to anterior ramus, not overlapped laterally by median rami of pterygoids; (33) pterygoids small, all rami slender, anterior rami not reaching middle of orbit; (34) occipital condyles small, not stalked, widely separated medially; (36) terminal phalanges T-shaped;

Figure 125. Dorsal and ventral views of skull  
of Barycholos pulcher (UMMZ S-2881, x 9).



(37) alary processes of hyoid plate small, on narrow stalks; (38 - 39) (41) pupil horizontal; (42) males lacking nuptial asperities, vocal sac large, external, median, subgular; (43) body lacking glands; (44) tongue round, posterior edge free; (45) toes lacking webs and lateral fringes, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged, digital tips dilated, no circumferential groove on discs, first finger much longer than second; (46 - 48) (49) adults small, about 25 mm. SVL; (50) tympanum visible externally.

Composition.-- Monotypic, B. pulcher.

Distribution.-- Pacific lowlands of Ecuador (Heyer, 1969b).

Remarks.-- In external appearance, Barycholos pulcher is simply a small Leptodactylus of the marmoratus group. Heyer (1969b) concluded that Barycholos is not closely allied to Leptodactylus or Lithodytes, but is most closely related to Eleutherodactylus. He did not consider the relationship between Barycholos and Eleutherodactylus to be close.

Barycholos pulcher exhibits the following characteristics which are more Eleutherodactylus-like than Leptodactylus-like: (11), (15), (22), (32), and (36). Barycholos more closely resembles Leptodactylus in the following characteristics: (1), (13), and (45). Heyer (1969b) suggested that the life history of Barachylos is

more like that of Eleutherodactylus than Leptodactylus. Heyer examined a single adult female of Barycholos pulcher which contained 43 ova about 2.8 mm. in diameter and concluded that the species probably exhibits direct development. I agree with Heyer on this point, but do not agree that this character, even in coincidence with T-shaped terminal phalanges, indicates a closer relationship to Eleutherodactylus than to Leptodactylus. Heyer (1969a) characterized the marmoratus group of Leptodactylus in having "4 - 25 eggs per nest; egg diameter 2.1 - 3.0 mm.". In preserved L. hylaedactylus, females usually contain about 20 eggs. The species of the marmoratus group were assigned to the subgenus Adenomera by Heyer (1969a, 1969b); the subgenus was in large part defined on the basis of direct development. As pointed out by Cochran (1955:309), species of the marmoratus group have enlarged digital pads and some indication of T-shaped terminal phalanges. The phalanges are intermediate between the knobbed phalanges of the subgenus Leptodactylus and the distinctly T-shaped phalanges of Eleutherodactylus, Heleophryne, Lithodytes, Sminthillus, Syrrhophus, Taudactylus, and Tomodactylus. Barycholos more closely resembles the subgenus Adenomera than Eleutherodactylus. Direct development has appeared several times in the course of leptodactylid evolution (for example, Crinia,



the Eleutherodactylini, the subgenus Adenomera of Leptodactylus, and the cycloranine genera Kyarranus and Philoria). The leptodactyline genera Lithodytes and Paratelmatoobius probably exhibit direct development.

The sternal style of Barycholos resembles those of the leptodactyline genera (except Paratelmatoobius) and is very different from the sternal apparatus seen in non-leptodactyline leptodactylid genera. Heyer (1969b) described the style as calcified in contrast to the osseous style seen in Leptodactylus. Histologically, the calcified element is a precursor to an osseous one, and the distinction between a calcified and an osseous element cannot be considered of primary importance. The character of the sternal apparatus which can be considered of primary importance is its shape (style-like or plate-like) because this character is not age or size dependent. Because the sternal style of Barycholos pulcher is style-shaped, I consider Barycholos to be a genus of the Leptodactylinae and to not be closely related to Eleutherodactylus.

The relationships of Barycholos within the Leptodactylinae are not entirely apparent, but I consider the genus most closely related to the subgenus Adenomera (Leptodactylus) and Lithodytes. Osteologically, Barycholos differs from the former in having larger nasals which are in broad median contact and in having smaller prevomers.

Lithodytes has large nasals which look like those of Barycholos but the prevomers of Lithodytes are like those of the Leptodactylus (Adenomera) marmoratus group.

## PHYLOGENY AND RELATIONSHIPS

Ideally, a discussion of the phylogeny of a group of organisms should be based principally on their fossil record. In the absence of such a chronicle of the evolution of the group, systematists turn to study of the living representatives and infer the phylogeny on the basis of primitive and advanced characters. Many fossils from Cretaceous through Pleistocene horizons have been assigned to the Leptodactylidae. Each of these is discussed below; I consider several of the fossils to represent frogs of families other than the Leptodactylidae. The leptodactylid fossils are too recent to be of any significance in determining phylogeny within the family.

My interpretation of the phylogeny of the Leptodactylidae is principally based on comparisons of the characteristics of pelobatid and leptodactylid frogs. The phylogeny is in large measure deduced from a study of evolutionary trends in many characters. Most of these evolutionary trends were noted by earlier authors; the principle difficulty was determination of the directions of the trends.

## The Fossil Record

Pleistocene: Günther (1859b) reported fossils of Ceratophrys aurita (as C. cornuta), Leptodactylus ocellatus, L. pentadactylus, and Leptodactylus sp. (as Cystignathus)

from Lagoa Santa, Minas Gerais, Brasil. Rusconi (1932) named Ceratophrys ensenadensis from a Pleistocene (Ensenadan) locality near Buenos Aires, Argentina. Mecham (1959) reported late Pleistocene cave deposits in central Texas containing Hylactophryne augusti (as Eleutherodactylus latrans). Tihen (1960b) and Lynch (1964) reported middle Pleistocene records for Syrrhophus marnockii from northern Texas. Auffenberg (1958) named some specimens from late Pleistocene cave deposits of Barbuda, British Leeward Islands, as Hyla barbudensis, which Lynch (1966) placed in the genus Eleutherodactylus.

Pliocene: Ameghino (1899) named Ceratophrys prisca from the Upper Pliocene of Monte Hermosa, Argentina.

Miocene: Casamiquela (1963) named Wawelia gerholdi from the Upper Miocene of Río Negro, Argentina, and described additional skeletal remains of Caudiverbera caudiverbera (as Gigantobatrachus parodii) from the same locality and horizon. The type-specimens of Gigantobatrachus were collected from Miocene deposits in Santa Cruz, Argentina (Casamiquela, 1959). Holman (1965) named Leptodactylus abavus from the Arikareean, Lower Miocene, of northern Florida.

Oligocene: Ameghino (1901) listed Teracophrys (a nomen nudum) from the Upper Oligocene of Patagonia. The specimens are now apparently lost (Schaeffer, 1949). Schaeffer (1949) recorded Caudiverbera caudiverbera (as a

new species, Calyptocephallela canqueli), Eupsophus sp., and Neoprocoela edentata from Lower Oligocene deposits in Chubut, Argentina.

Eocene: Schaeffer (1949) named Caudiverbera casamayorensis (as a new genus, Eophractus) from the Lower Eocene of Chubut, Argentina. Hecht (1960) named Eorubeta nevadensis from the Lower Eocene of Nevada. Noble (1930) concluded that Rana pusilla Owen, 1847, from the Eocene (Intertrappean) of peninsular India was a myobatrachine leptodactylid and named a new genus for it (Indobatrachus).

Cretaceous: Estes (1964) reported several bones from the Lance Formation (Upper Cretaceous) of Wyoming as possibly representing leptodactylid frogs; he named none of these. Hecht (1960) suggested that some of the frog fossils from the Trinity Sands (Cretaceous) of Texas were primitive leptodactylids.

The fossil record is summarized in Table 3. Some of these records require special comment, because they are not leptodactylid frogs. The following is a systematic summary (by subfamily) of the fossils I accept as members of the family Leptodactylidae.

Ceratophryinae: Upper Miocene to Recent of South America. Wawelia gerholdi is not distinguishable from either Ceratophrys or Lepidobatrachus but is clearly a member of the subfamily (see generic account, pp. 383-84). Three species of Ceratophrys are known as fossils; two of

Table 3. Geographic and temporal distributions of the fossil frogs currently considered members of the Leptodactylidae.

	NORTH AMERICA	SOUTH AMERICA	OLD WORLD
PLEISTOCENE	<u>Eleutherodactylus</u> <u>barbudensis</u> *	<u>Ceratophrys</u> <u>aurita</u>	
	<u>Hylactophryne</u> <u>augusti</u>	<u>C. ensenadensis</u>	
	<u>Syrrhophus</u> <u>marnockii</u>	<u>Leptodactylus</u> sp.	
		<u>Leptodactylus ocellatus</u>	
		<u>L. pentadactylus</u>	
PLIOCENE		<u>Ceratophrys</u> <u>prisca</u>	
MIOCENE	<u>Leptodactylus</u> <u>abavus</u>	<u>Wawelia</u> <u>gerholdi</u>	
		<u>Caudiverbera</u> <u>caudiverbera</u>	
OLIGOCENE		<u>C. caudiverbera</u>	
		<u>Eupsophus</u> sp.	
		<u>Neoprocoela</u> <u>edentata</u>	
		? <u>Teracophrys</u>	
EOCENE	<u>Eorubeta</u> <u>nevadensis</u>	<u>Caudiverbera</u> <u>casamayorensis</u>	<u>Indobatrachus</u> <u>pusillus</u>
PALEOCENE			
CRETACEOUS	[Lance Formation]		
	[Trinity Sands]		

\* West Indian: Barbuda, Leeward Islands.

these are extinct (C. ensenadensis and C. prisca), the other species still lives in the same area from which the Pleistocene fossils were recovered. Teracophrys may be a ceratophryine, but its taxonomic status must await rediscovery of Ameghino's specimens.

Cycloraninae: No fossil record.

Elosiinae: No fossil record.

Heleophryninae: No fossil record.

Leptodactylinae: Pleistocene to Recent of South America. The three species of Leptodactylus (ocellatus, pentadactylus and sp.) reported by Günther (1859b) are the only fossils known for the subfamily.

Myobatrachinae: Eocene of peninsular India.

Indobatrachus pusillus is very similar to Crinia, and is probably a leptodactylid. However, before the systematic position of Indobatrachus can be fully evaluated, an osteological study must be made of the Arthroleptinae (Ranidae). See the generic account of Indobatrachus for further details (p. 355).

Telmatobiinae: Fossils of three tribes are known.

Telmatobiini: Lower Eocene to Upper Miocene of Patagonia. Caudiverbera is represented in Lower Eocene, Lower Oligocene, and Upper Miocene deposits of south-central Argentina. The Miocene and Oligocene fossils are regarded as identical with the Recent species (Hecht, 1963), but the Lower Eocene fossils are here recognized as specifically

distinct. Neoprocoela edentata, an ancestral stock for Batrachophrynus, is known from the Lower Oligocene of Patagonia. Tihen (1962b) placed it in Bufo, but his action is rejected here (see pp. 414 - 16).

Alsodini: Lower Oligocene of Patagonia. Schaeffer's (1949) Eupsophus sp. is the only fossil record for this tribe. Many specimens of the fossil are available but all are incomplete. Further study of these fossils should be made to assess their specific status. The fossil species differs from all Recent species of the genus in apparently having the nasal bones in median contact.

Eleutherodactylini: Pleistocene of Texas and Barbuda Island, Leeward Islands. Three species of this tribe are known as fossils. The West Indian Eleutherodactylus barbudensis may be extinct or may be identical with E. martinicensis (Schwartz, 1967). The Pleistocene records of Syrrhophus marnockii occur 200 miles north of the present northern limit of the range of the species (Lynch, 1969b). The fossil of Hylactophryne augusti is from a Late Pleistocene cave deposit within the present geographic range of the species.

I do not consider the other species listed in Table 3 to be members of the Leptodactylidae. The fossils here removed from the family have been reported from deposits in North America (Lower Miocene to Upper Cretaceous).



Leptodactylus abavus Holman, 1965: Leptodactylus abavus Holman (Lower Miocene of Florida) is a species of Rana and may not be separable from Rana miccenica Holman of the same horizon and locality. The reasons for placing the species in Rana are presented in the account on pelvic girdles (p. 205).

Eorubeta nevadensis Hecht, 1960. The fossils on this frog are preserved as organic imprints in an oil well core. In this condition, the fossils are badly crushed and must be studied under ultraviolet light. Hecht (1960) considered the presence of maxillary teeth and long transverse processes of the posterior presacral vertebrae as characters adequate to associate the fossil with the advanced frogs (Hylidae, Leptodactylidae, and Ranidae). The Bufonidae were not considered because the fossil has a toothed maxilla. The sacral diapophyses of the fossil are dilated and oriented at right angles to the sagittal line; therefore, Hecht reasoned that the fossil did not belong to the Ranidae.

Hecht then looked for hylid and leptodactylid frogs with long transverse processes of the posterior presacral vertebrae and dilated sacral diapophyses. He characterized hylids as having either somewhat shortened or very thin, needle-like transverse processes of the posterior presacral vertebrae. By process of elimination, Hecht assigned the fossil to the Leptodactylidae. Among the leptodactylids

available to him, he concluded that the fossil was most similar to Mixophyes and Lechriodus, because both genera have dilated sacral diapophyses and long transverse processes of the posterior presacral vertebrae. Hecht stated that Eorubeta differed from both of these genera in having seven instead of eight presacral vertebrae; Eorubeta was further distinguished from Lechriodus, because the latter has transverse processes on the atlas. The "atlas" (in the sense of Hecht) of Lechriodus is the fused cervical and second vertebrae.

Hecht rightfully complained of a lack of skeletons of representative Recent genera in museums and the lack of comparative osteological studies of Recent frog families. With these restrictions, Hecht's action in assigning the fossil to the Australian section of the Leptodactylidae seems capricious. My study of Eorubeta was limited to the description, remarks, and illustrations in Hecht's (1960) paper.

Hecht's description is reasonably accurate. However, I consider the fossil to have eight presacral vertebrae (Hecht recorded seven). Seven presacral vertebrae are clearly evident and all of these bear long transverse processes which are as long as or only slightly shorter than the sacral diapophyses. In all Recent frog genera I have examined, the transverse processes of the second vertebra (first post-cervical) are invariably shorter

than those of the third vertebra. The transverse processes of the third vertebra are as long as, or longer than, those of any other presacral vertebra, and are usually somewhat curved. The transverse processes of the right side of the anterior presacral vertebrae of Eorubeta are concealed beneath matrix except for the leading edge of the vertebra I consider to be the third (Hecht considered this vertebra to be the second). The remains of the skull overlie parts of the vertebral column in this region. It is clearly evident from an examination of Hecht's figures, that the transverse processes of vertebra 2 are very long (as long as the sacral diapophyses) and slightly curved. If this vertebra is the second as Hecht contends, then Eorubeta has a vertebral column like no other in the Anura. It is more reasonable to suggest that this vertebra is the third. Just anterior to the left transverse process of this vertebra and the scapula, is a small area of bone which Hecht tentatively suggested is the coracoid. This structure might be the left transverse process of the second vertebra. Another interpretation is possible for the bones Hecht called the squamosals, occipital condyles, and foramen magnum. If the "occipital condyles and foramen magnum" are the centrum and neural arch of the second vertebra, then the "squamosals" are of the proper shape and length to be considered the transverse processes of the second vertebra. If this

interpretation is correct, then the cervical is not distinguishable from the bones of the posterior part of the skull. The structure designated "atlas" by Hecht is much too small to be this element and is probably not a complete bone. Pending the recovery of additional specimens, I will not offer further interpretation of the osteology of Eorubeta nevadensis.

I concur with Hecht that the fossil does not represent the Ascaphidae, Discoglossidae, Pipidae, or Rhinophrynidae, for his reason (the transverse processes of the posterior presacral vertebrae in the Recent genera of these families are very short and often knob-like). The fossil has dilated sacral diapophyses which are unlike those of any ranid known to me. The Dendrobatidae and leptodactylids of the subfamily Elosiinae have non-dilated sacral diapophyses and short transverse processes on all presacral vertebrae. The pelobatids of the subfamilies Pelobatinae and Pelodytinae have very short transverse processes on the posterior presacral vertebrae, as do some Australo-Papuan leptodactylids, and thus could not be closely related to the fossil frog. The other frog families have dilated sacral diapophyses in some or all of the included genera (Bufonidae, Centrolenidae, Hylidae, Leptodactylidae, Megophryinae, Microhylidae and Pseudidae). The only skeletal elements of Eorubeta nevadensis which are useful in comparisons are those of the vertebral

column, ilium, and maxilla. Eorubeta does not closely resemble any genus in the seven families listed above. Eorubeta has maxillary teeth and therefore is probably not a bufonid, although this character need not completely eliminate the Bufonidae from consideration. The ilium of Eorubeta has little indication of a dorsal protuberance, prominence, or ilial crest; this condition is seen in some leptodactylids, megophryine pelobatids, and microhylids. The ilium is not exposed in lateral aspect and therefore centrolenids and hylids cannot be eliminated from consideration. Eorubeta is not a bufonid, ceratophryine, telmatobiine, leptodactylid, or pseudid because the ilia of Eorubeta lack large ilial prominences and/or dorsal crests.

The vertebral skeletons of the remaining groups (Centrolenidae, Hylidae, Cycloranae, Heleophryinae, Myobatrachinae, Microhylidae, and Megophryinae) are difficult to separate as units when the details of the cervical vertebra are unknown. The cervical cotyles are widely separated medially in the Centrolenidae, Hylidae, Microhylidae, and Myobatrachinae, whereas the cotyles are narrowly separated in the Cycloranae, Heleophryinae, and Megophryinae. The cervical vertebra is not distinguishable in Eorubeta. The only genera of the seven family groups listed above with the transverse processes of the posterior presacral vertebrae as long as the sacral

diapophyses are Hemiphractus and some Hyla (Hylidae), Batrachophrynus, Lechriodus, Limnodynastes, and Mixophyes (Leptodactylidae, Telmatobiinae and Cyclorantinae), and Megophrys (Pelobatidae, Megophryinae). The transverse processes of Batrachophrynus (Fig. 79) are very similar in bulk to those of Eorubeta, but the sacral diapophyses of these two genera are very different from one another. Eorubeta is unique, insofar as I am aware, in having wide, dilated sacral diapophyses. The only comparable sacral diapophyses known to me are those of Atelopus and Rhinoderma.

In summary, Eorubeta does not closely resemble the skeleton of any known modern frog genus and cannot be assigned to any presently recognized family on the basis of its known morphology. Hecht's (1960) assignment of Eorubeta to the Leptodactylidae is not defensible and probably in error. The only reasonable systematic assignment of the fossil is to "Family incertae sedis, Order Salientia".

Estes (1964) described and figured several Upper Cretaceous frog fossils from the Lance Formation of Wyoming. Among the fossils which are of significance to this discussion are the following: "Family ?Pelobatidae; Suborder Neobatrachia, Family incertae sedis, near Hylidae?; and Family incertae sedis, near Leptodactylidae?" (Estes, 1964: 57-61, figs. 30-32). The coccyx described and figured by Estes is unquestionably that of a megophryine

pelobatid, although a generic assignment is not possible at present. The ilium described and figured by Estes is not distinguishable from the ilia of some species of Pelobates and Scaphiopus, but is different from the ilia of the Megophryinae and Pelodytinae; the ilium is that of a pelobatid frog of the subfamily Pelobatinae. The incomplete left maxilla described and figured by Estes resembles those of Pelobates, Scaphiopus, and, insofar as it is known, that of Eopelobates.

Estes tentatively assigned an incomplete right squamosal to the Leptodactylidae. The squamosal does not resemble that of any extant leptodactylid genus but is similar to the squamosals of Scaphiopus (Scaphiopus) and some Pelobates. Estes remarked that the fossil has an "opisthotic articulation surface [which] resembles that of leptodactylids." This cryptic statement implies that there is (or are) a characteristic opisthotic articulation of the squamosal in leptodactylids; the statement is not in agreement with my observations. A complete spectrum of opisthotic articulations can be demonstrated within the Leptodactylidae, ranging from species lacking the dorsal portion of the squamosal (Notaden) to those with the squamosal enclosing much of the crista parotica (Caudiverbera, Ceratophrys). I tentatively assign the fossil squamosal to the Pelobatidae.

The two bones (squamosal, figured; and nasal) which Estes suggested might be from hylids or leptodactylids, could equally confidently be assigned to the Pelobatidae. Until a comprehensive study of the skeletons of all genera of Recent pelobatids and hylids has been made, these bones should not be assigned to any modern family.

The pelobatid centrum from the Middle Eocene of Wyoming figured by Hecht (in McGrew, 1959) is clearly that of a megophryine pelobatid, and as Hecht pointed out, is very similar to that of Eopelobates grandis from the Lower Oligocene of South Dakota. Hecht's fossil is probably generically identical with Eopelobates grandis and may not be specifically distinct. Estes' megophryine coccyx is possibly representative of the same complex.

Hecht (1960:13) referred to some fossil frogs from the Trinity Sands of Texas (early Cretaceous) as "a primitive leptodactylid or some close relative." Until he publishes on them, no further comment will be made, although it should be born in mind that Hecht considered Eorubeta a definite leptodactylid. Hecht and Estes (1960) named a Jurassic frog as Comobatrachus and placed it in Reig's (1958) Neobatrachia. They further suggested that the fossil not be assigned to any recognized family but that "on the basis of probability [no confidence limits are given] a leptodactyloid affinity appears more likely [than a microhylid or hyperoliid affinity]".



The fossil record for the Leptodactylidae can be summarized as follows: fossils of several stocks are known from the Tertiary of southern South America; an Eocene frog from peninsular India seems to be a myobatrachine leptodactylid; and leptodactylids are not known elsewhere in the world until the Pleistocene of the West Indies and Texas.

With the exception of Neoprocoela and Indobatrachus, the fossil record of the Leptodactylidae is of little use in determining the phylogeny and is of limited value in discussing zoogeography.

#### Pelobatid-Leptodactylid Relationships

Some Papuan leptodactylid frogs have been confused with pelobatid frogs. Lechriodus was erroneously believed to be a pelobatid until Noble (1924) demonstrated that the pectoral and thigh musculature were bufonoid, not pelobatoid. In general, however, the two families have always been regarded as being very different from one another. This distinction hinged largely upon a distinction between the Pelobatinae (Pelobates and Scaphiopus) and the Neotropical leptodactylids. In the former, the coccyx is fused to the sacral vertebra, whereas in leptodactylids the two bones are separate.

The Pelobatidae may be separated from the Leptodactylidae by the greater dilation of the sacral

diapophyses in the former, the sacral-coccygeal articulation (fused or with a single condyle in former, double condyle in latter), mid-dorsal cricoid gap in former, single slip to m. depressor mandibulae (pars scapularis) in former, and m. semitendinosus and m. sartorius not separate in former. Two or three subfamilies are recognized depending on the author: Pelobatinae, Megophryinae, and sometimes Pelodytinae.

The Pelobatidae are unquestionably the more primitive group (Griffiths, 1963; Inger, 1967; Kluge and Farris, 1969; Noble, 1922, 1931; and Tihen, 1965), but the distinction between the two families is not so great as has been previously believed, principally because previous authors have tended to ignore the similarities between the Megophryinae and the Australo-Papuan leptodactylids and to stress those features which distinguish the two most abundant and best known groups of the two families (the Pelobatinae and Neotropical leptodactylids).

The amplexic position of the male in the Pelobatidae, Cyclorantinae and Myobatrachinae is inguinal in contrast to the axillary amplexus in almost all advanced frogs. The Megophryinae, Myobatrachinae and Cyclorantinae (part) have free intervertebral discs, a character that has been regarded as pedomorphic or specialized by most authors but which is more likely primitive (Tihen, 1965). Several other characteristics, some heretofore regarded

as of little significance, occur in the primitive families and in some leptodactylids and sporadically, though rarely, in advanced frogs [e.g., absence of an outer metatarsal tubercle; vertical pupil; large, juxtaposed occipital condyles; small transverse processes on the posterior presacral vertebrae; imbricate neural arches; and tadpoles with complete row(s) of labial papillae and high number of anterior tooth rows (3-6)].

Griffiths (1963) contended that ectochordal and stegochordal centra were primitive to holochordal centra; Inger (1967) argued that holochordy is probably primitive since it occurs in most extinct lepospondylous amphibians and that therefore ectochordy and stegochordy are derived. Ectochordy has been termed paedornophic; if so, then any distinction between frog families based on the nature of the coccygeal-sacral articulation cannot be seriously considered in interpreting the macrosystematic evolution of frogs. A full range of variation occurs in the Pelobatidae--the ectochordal megophryines exhibit a monocondylar articulation, the stegochordal pelobatines exhibit a coccygeal-sacral fusion, and the presumably stegochordal pelodytines exhibit a bicondylar articulation. Imbricate neural arches occur in all pelobatids and are found in cyclorranines (but not myobatrachines), in heleophrynines, in ceratophryines, and in some telmatobiines (Odontophrynini and Telmatobiini). The degree of dilation

of the sacral diapophyses in pelobatids exceeds that seen in any leptodactylid except Neoprocoela (Lower Oligocene, Patagonia). Bufonids, which are generally conceded to be leptodactylid derivatines, have broadly dilated sacral diapophyses as well. If Neoprocoela is properly assigned familiarly, then all primitive leptodactylids may have had sacral dilations of the pelobatid degree--those living leptodactylids with sacral dilations do not approach the condition seen in bufonids or pelobatids. The sacral vertebra of Pelodytes is more like that of pipids than other pelobatids.

Hecht (1960) mentioned the lack of moderate to long transverse processes on the presacral vertebrae in primitive frogs. My examination of skeletons of all ascaphid, discoglossid, pipid, and rhinophrynid genera confirms his observation. Among the nine living and three extinct pelobatid genera some variation occurs. The transverse processes of the posterior presacral vertebrae are little more than bosses or are very short in Macropelobates, Pelobates and Scaphiopus. Miopelodytes and Pelodytes have short processes strongly sloped anteriorly as in pipids. In the Megophrys and Eopelobates (Megophryinae), the transverse processes of the posterior presacral vertebrae are of moderate length (Zweifel, 1956a; personal observation) but they are shortened and directed strongly anteriorly in at least one species of

Leptobrachium (Boulenger, 1908), recalling the condition seen in Pelodytes. The anterior presacral vertebrae of all pelobatids have elongate transverse processes (relative to the widths of the sacral diapophyses) as well as in some primitive leptodactylids (Ceratophryinae). This same condition appears in some bufonids and is variable within Bufo. Several groups of leptodactylids have relatively short transverse processes on the posterior presacral vertebrae. This is most pronounced in Neobatrachus and Notaden (Fig. 30) but is also found in several Neotropical groups (e.g., Telmatobiini, Odontophrynini, and Grypiscini) as well as in Heleophryne and most Myobatrachinae and Cyclorantinae.

The presence of postzygapophyses on the sacrum and prezygapophyses on the coccyx must be considered primitive. The zygapophyses are not present in Pelodytes, and their presence is obliterated by sacral-coccygeal fusion in the Pelobatinae; they are found in the Megophryinae but not consistently in any leptodactylid. McDowell (in litt.) observed sacral postzygapophyses and coccygeal prezygapophyses in Metacrinia and in the enigmatic Sooglossus, but I have seen them only in Batrachophrynus and Megophrys. Zweifel (1956a) described coccygeal zygapophyses in Eopelobates.

The tadpoles of pelobatids and leptodactylids, as well as of all advanced frogs (except the microhylids

whose relationships are obscure), are Type IV of Orton (1953). Admittedly, use of gross tadpole morphology as a basis of macrosystematic (interfamilial) classification is hazardous (e.g., Inger, 1967), but an examination of intrafamilial variation can be useful in determining intrafamilial evolutionary trends. Inger (1967) characterized the Pelobatidae and Leptodactylidae as having tadpoles with median vents. Orton (1952) characterized the pelobatid tadpoles as follows: vent median, beak present, tooth rows usually divided with one complete short row anteriorly and two complete rows posteriorly, and labial papillae complete except for a narrow median interruption anteriorly. The data for pelobatids, insofar as is known, are summarized in Table 4.

Only half of the pelobatid genera (and species) have median vents; the temperate Himalayan genera have dextral vents as does the subtropical and tropical Leptobrachium. Inger's (1966:25) statement that a complete row of papillae across the upper lip is characteristic of pelobatids is in error. Insofar as I am aware, it is true for only L. gracilis and L. pelodytoides, although some Oreolalax have large, widely scattered papillae across the upper lip (Liu, 1950). The uppermost tooth row is complete in all pelobatids (if teeth are present) and is very short in the Pelobatinae and Megophryinae. In Pelodytes this row is almost as wide as the mouth,

Table 4. Characteristics of Recent pelobatid genera--tadpoles <sup>1</sup>

Genus	Vent median	Labial papillae complete anteriorly	Tooth formula (Low - High)
<u>Scaphiopus</u> <sup>2</sup>	X	O	II:1-1/2-2:II -- I:4-4/4-4:II
<u>Pelobates</u>	X	O	I:3-3/3-3:II
<u>Pelodytes</u>	X	O	I:3-3/3-3:II
<u>Mesobla</u>	?	?	?
<u>Megophrys</u>	X	A <sup>3</sup>	O
<u>Leptobrachium</u>	O	V	O -- I:7-7/5-5:I
<u>Oreolalax</u>	O	O	I:4-4/4-4:I -- I:7-7/7-7:I
<u>Scutiger</u>	O	O	I:3-3/4-4:I -- I:6-6/6-6:I
<u>Vibrissaphora</u>	O	O	I:5-5/4-4:I

<sup>1</sup> Data from Boulenger (1897), Inger (1966), Liu (1950), Orton (1952), Popo (1931), and Stebbins (1951).

<sup>2</sup> Including Spea.

<sup>3</sup> Absent.

recalling the condition seen in most tadpoles. The Pelobatinae and Pelodytinae differ from the Megophryinae in having two complete tooth rows across the fully papillate lower lip; only a single complete row is found in megophryines. Most tooth rows are divided medially by the upper beak in pelobatids. This feature in combination with the usually high tooth formula characterizes most pelobatids. This is not to say that this condition is not duplicated elsewhere; for example, Neobatrachus has a dental formula of I:2-2/1-1:II to I:3-3/1-1:II, Mixophyes has a II:4-4/1-1:II with three other very short lateral divided rows posteriorly and Heleophryne has a IV/1-1:XII to IV/1-1:XVI formula; most bufonoids exhibit a I:1-1/III tooth formula.

The tadpoles of pelobatids suggest a closer relationship between the European and North American genera than either group has to the Megophryinae. However, the variation within the Megophryinae suggests that the tadpole can be a hazardous source for definitive statements about relationships. Among bufonoid frogs the high tooth formulae in cycloranine and heleophrynine leptodactylids is suggestive of the pelobatid condition in distinction to the relatively dissimilar mouthparts seen in other bufonoid frogs. Tadpole morphology represents perhaps one of the most useful and most misused of the available character complexes to be used in frog classification.



A major problem to be overcome is the descriptive formulae applied to the mouth parts. Many authors use the most simple, least informative system of arabic numerals separated by a solidus (i.e., 2/3) for tadpoles with all of the rows complete or some of them divided. Using various systems, the dental formula for Vibrissaphora liui could be presented as:

(A)	6/5	(B)	$\begin{array}{r} 1 \\ 5-5 \\ \hline 4-4 \\ 1 \end{array}$
(C)	I:5-5/4-4:I	(D)	1C, 1D, 4L/1L, 3D, 1C

The formula with the greatest information content is the last (D), in which the arabic numeral preceding the letters C, D, and L refers to the number of complete, divided (but not lateral), and lateral (and divided) rows of teeth respectively. Lateral rows are separated by the beak. This system differs from that of Liu (1950) in distinguishing between divided and lateral rows and does not require the use of Roman numerals. Liu's system is preferable to the 4-layered formula (B) in requiring less space on a printed page. The four-layered formula likewise does not distinguish divided from strictly lateral rows although this distinction can be demonstrated to be two ends of a continuum.

There can be little argument against the statement that the Pelobatidae is the most primitive of the frog families excepting the archaic Ascaphidae, Discoglossidae, Pipidae, and Rhinophrynidae (Tihen, 1965). An appropriate test of which of the advanced families is most closely related to the Pelobatidae would be to compare them relative to the number of primitive characters shared. The selection of characters and determination of evolutionary direction was made on the following bases: (1) characters shared between the Pelobatidae and some or all of the archaic frog families were regarded as unquestionably ancestral; and (2) those characteristics which occur in these archaic families but also occur in some of the bufonoid families were selected as being useful in measuring the relative primitiveness of each of the bufonoid families and subfamilies (and tribes of the leptodactylid subfamily Telmatobiinae).

The family or subfamily with the lowest sum of values is judged to be most primitive, and the higher the sum of values, the greater is the divergence of that group from the ancestral stock. These primitive characters are (I) large, closely approximated occipital condyles--Types II or III; (II) imbricate neural arches; (III) anterior presacral vertebral transverse processes elongate and posterior presacral vertebral transverse processes shortened; (IV) diapophyses of sacral vertebrae broadly

dilated; (V) post-zygapophyses on sacral vertebra and prezygapophyses and/or transverse processes present on anterior end of coccyx; (VI) intervertebral discs free; (VII) ilium lacking dorsal crest, ilial prominence or protuberance; (VIII) all skull bones present; maxillaries, premaxillaries, and prevomers toothed; (IX) phalangeal formulae 2-2-3-3 and 2-2-3-4-3; (X) pupil vertical; (XI) outer metatarsal tubercle absent; (XII) amplexus inguinal; (XIII) eggs small, laid in water, tadpole free-living; (XIV) tadpole vent median; (XV) tadpole dental formula including at least three or four rows above and three rows below beak; and (XVI) pectoral girdle arciferal. Each of these 16 characters or character complexes was assigned a value from 0 to 2 for each of the 25 bufonoid and pelobatid taxa. The character states and values are summarized in Table 5 and the scores and sums for 35 family groups of "non-archaic" frogs in Table 6.

A value of 0 indicates that the primitive condition is uniform within the group; a value of 1 indicates the group exhibits an intermediate condition or is variable with more than one-half of the included taxa exhibiting the primitive state; and a value of 2 indicates that a majority of or all of the included taxa share the (or a) derived state for the character. The sum of the values for the 16 characters is an index of how far removed a given taxon is from the basal stock of the Bufonoidea--the Pelobatoidea.

Table 5. Sixteen phylogenetically significant characters and the character states and their values.

- I. Cervical type II = 0  
Cervical type I = 2
- II. Neural arches imbricate = 0  
Neural arches open = 2
- III. Transverse processes of anterior presacral vertebrae expanded, those of posterior presacral vertebrae shortened = 0  
All transverse processes as long as sacral diapophyses or all transverse processes shorter than sacral diapophyses = 2
- IV. Sacral diapophyses dilated = 0  
Sacral diapophyses rounded = 2
- V. Sacral vertebra bearing postzygapophyses and/or coccyx bearing prezygapophyses = 0  
Sacral vertebra lacking postzygapophyses and coccyx lacking prezygapophyses = 2
- VI. Intervertebral discs free = 0  
Intervertebral discs fused to centrum = 2
- VII. Ilium without dorsal crest or dorsal protuberance = 0  
Ilium with dorsal crest and/or dorsal protuberance = 2

- VIII. All skull bones present, premaxillae and maxillae bearing teeth = 0  
 Some skull bones lost and/or premaxillae and maxillae toothless = 2
- IX. Phalangeal formulae normal = 0  
 Intercalary element present or phalanges lost = 2
- X. Pupil vertical = 0  
 Pupil horizontal or round = 2
- XI. No outer metatarsal tubercle = 0  
 Outer metatarsal tubercle present = 2
- XII. Amplectic position inguinal = 0  
 Amplectic position axillary = 2
- XIII. Eggs small, usually pigmented, larvae aquatic = 0  
 Eggs large, development abbreviated or direct = 2
- XIV. Tadpole vent median = 0  
 Tadpole vent dextral = 2
- XV. Larval tooth formula at least  $3/3$  = 0  
 Larval tooth formula less than  $3/3$  = 2
- XVI. Pectoral girdle arciferal = 0  
 Pectoral girdle firmisternal = 2

Table 6. Values for each of the sixteen phylogenetically significant characters in non-archaic frog groups.

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	Sum
<b>Pelobatidae</b>																	
Megophryinae	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	2
Pelobatinae	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	3
Pelodytinae	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	4
<b>Leptodactylidae</b>																	
Heleophryinae	0	0	1	2	2	1	0	0	0	0	0	?	0	0	0	0	6
Cyclorantinae	0	0	1	1	2	1	1	0	0	1	0	0	0	1	1	0	9
Myobatrachinae	2	2	1	1	1	0	1	1	0	2	2	0	0	2	2	0	17
Ceratophryinae	0	0	0	2	2	2	1	0	0	1	1	2	0	0	1	0	12
Telmatobiini	0	0	1	1	2	2	1	0	0	1	1	2	0	0	2	0	13
Alsodini	1	1	1	1	2	2	1	0	0	2	2	1	0	0	2	0	16
Odontophrynini	1	0	2	2	2	2	1	0	0	2	2	2	0	0	2	0	18
Leptodactylinae	2	1	2	2	2	2	2	0	0	2	2	2	0	1	2	0	22
Elosiinae	2	2	2	2	2	2	2	1	0	2	2	2	0	2	2	0	25
Grypiscini	2	2	2	2	2	2	2	0	0	2	2	2	1	2	2	0	25
Eleutherodactylini	2	2	2	2	2	2	2	0	0	2	2	2	2	2	2	0	26
Bufonidae	0	1	2	1	2	2	2	2	0	2	2	2	0	1	2	1	22
Rhinodermatidae	0	2	2	1	2	2	2	2	0	2	2	2	2	0	2	2	25
Centrolenidae	2	2	2	1	2	2	2	1	2	2	2	2	1	0	2	0	25

## Hylidae

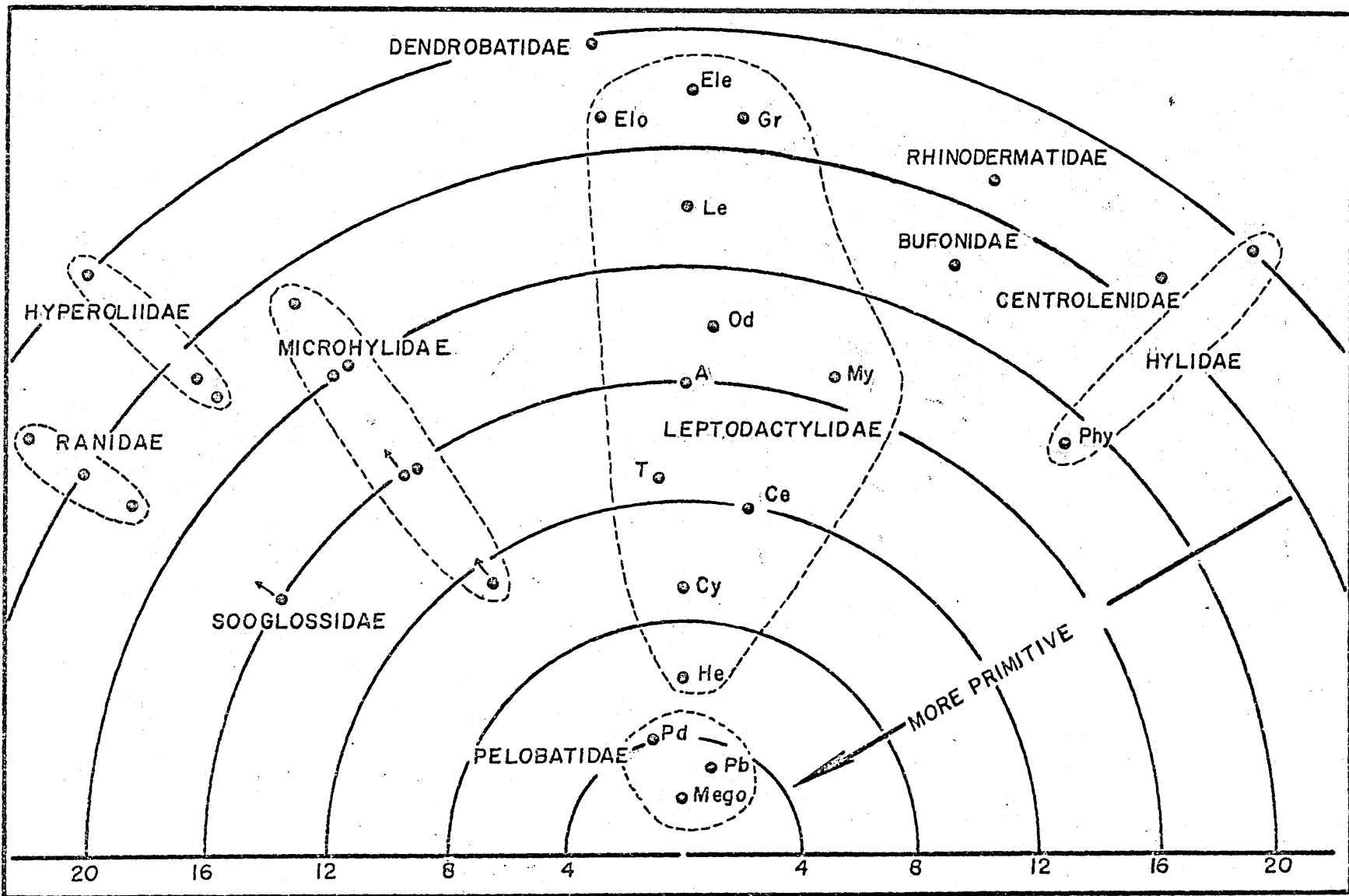
Phyllomedusinae	2	0	2	0	2	2	2	0	1	0	2	2	1	1	2	0	19
other Hylidae	2	2	2	2	2	2	2	1	1	2	2	2	2	2	2	0	28
Dendrobatidae	2	2	2	2	2	2	2	2	0	2	2	2	1	1	2	2	28
Pseudidae	2	2	2	2	2	2	2	0	2	2	2	2	2	2	2	0	28
Sooglossidae	2	2	2	2	0	0	?	?	0	2	0	?	2	0	2	2	16+
Ranidae																	
Raninae	2	2	2	2	2	2	2	0	0	2	2	2	0	2	0	2	24
Rhacophorinae	2	2	2	2	2	2	2	0	2	2	1	2	1	2	0	2	26
Petropedetinae	2	2	2	2	2	2	2	0	0	2	0	2	0	2	0	2	22
Hemisinae	?	?	?	2	2	2	?	2	2	0	0	2	0	2	0	2	16+
Hyperoliidae																	
Astylosterninae	2	2	2	2	2	2	2	0	2	1	0	2	0	2	0	2	23
Hyperoliinae	2	2	2	2	2	2	2	0	2	0	0	2	0	2	0	2	22
Arthroleptinae	2	2	2	2	2	2	2	0	2	2	2	2	2	0	2	2	28
Microhylidae																	
Dyscophinae	?	0	?	0	2	2	0	0	0	1	0	2	0	0	2	2	11+
Brevicipinae	?	0	?	0	2	2	?	2	0	2	2	0	2	0	2	2	16+
Asterophryinae	2	0	2	0	2	2	0	2	0	2	0	2	2	0	2	2	20
Microhyliinae	2	0	0	0	2	2	1	1	0	2	0	2	0	0	2	2	16
Cophylinae	2	2	2	0	2	2	0	0	0	2	0	2	2	0	2	2	20
Phrynomerinae	2	2	2	0	2	2	1	2	2	2	0	2	0	0	2	2	23

All three pelobatid subfamilies exhibit low values--the Megophryinae with 2, the Pelobatinae with 3, and the Pelodytinae with 4. The following leptodactylid groups exhibit values below 14--Heleophryinae, Cyclorantinae, Ceratophryinae, and Telmatobiini (Telmatobiinae). The Heleophryinae are only slightly removed from the pelobatid zone and are considerably more primitive than any other group of the "higher frogs." The Cyclorantinae are well removed from the pelobatid zone but less than one-half as far removed as are the Myobatrachinae. The leptodactylids of southern South America (Ceratophryinae and telmatobiine and alsodine Telmatobiinae) are more primitive than any other bufonoid groups (excepting the heleophryine and cycloranine leptodactylids). Of the non-leptodactylid bufonoid families and subfamilies, the Phyllomedusinae are least unlike the pelobatoid ancestor. The Bufonidae, which are usually regarded as only slightly advanced over the Leptodactylidae, are the next most primitive group.

The Pelobatidae are intermediate between the primitive (discoglossoid and pipoid) and the advanced (bufonoid and ranoid) frogs. The leptodactylids are the stem bufonoids and are difficult to separate from the pelobatids.



Figure 126. Comparison of the relative primitiveness of 35 groups of non-archaic frogs including the 23 bufonoid and pelobatid subfamilies and tribes. The concentric semicircles are guidelines and are not intended to have a special significance. Families are enclosed in dashed lines. The abbreviations used are as follows: A = Alsodini, Ce = Ceratophryinae, Cy = Cyclorantinae, Ele = Eleutherodactylini, Elo = Elosiinae, Gr = Grypiscini, He = Heleophryinae, Le = Leptodactylinae, Mego = Megophryinae, My = Myobatrachinae, Pb = Pelobatinae, Pd = Pelodytinae, Phy = Phyllomedusinae, and T = Telmatobiini. The separation of taxa by degrees of arc is not intended to reflect relationships.



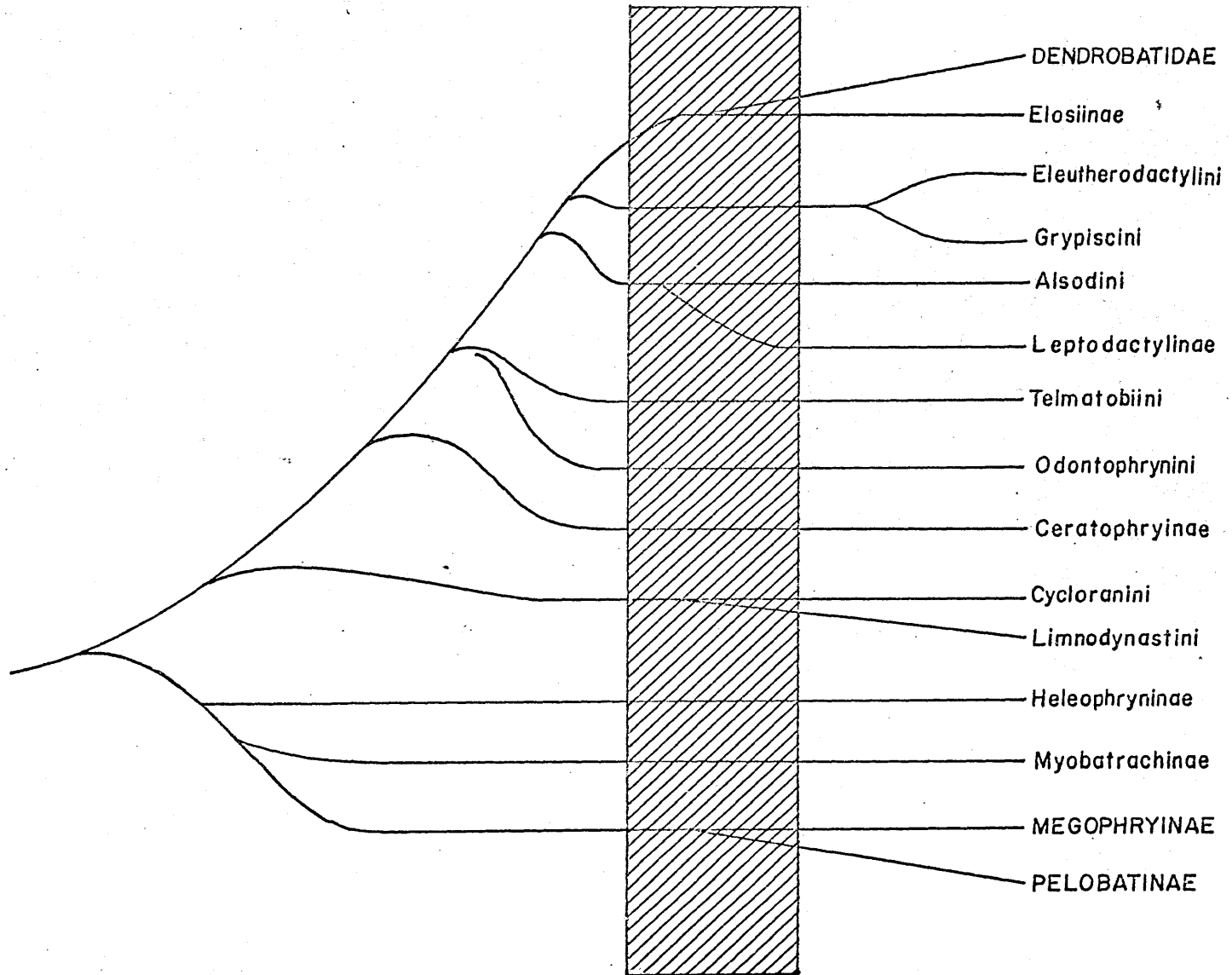
### Intrafamilial Relationships of the Leptodactylidae

Figure 126 reveals that the Leptodactylidae exhibit the greatest range of intrafamilial variability or diversity among the Pelobatoidea, Bufonoidea, and Ranoidea. In part, this diversity represents a finer degree of knowledge about the Leptodactylidae than about some other families, but the diversity is also real. The Leptodactylidae have been the convenient "catch-all" for genera of bufonoid frogs with obscure relationships, and can be defined as "those bufonoid frogs that are not members of the Bufonidae, Centrolenidae, Dendrobatidae, Hylidae, Pseudidae, or Rhinodermatidae." The intrafamilial relationships of the Leptodactylidae are schematically summarized in Fig. 127.

The Leptodactylidae can be viewed as a series of increasingly more specialized subfamilies and tribes which bridge the morphological and behavioral gaps between the Pelobatidae and the smaller families of the Bufonoidea and the Ranoidea. The least specialized subfamilies and tribes of leptodactylids occur in southern Africa and the Australo-Papuan region. Other, only slightly more specialized, groups occur in temperate South America, and the very specialized groups occur in the subtropical and tropical zones of South America and Middle America.

The subfamily Heleophryninae contains one genus and is restricted in distribution to southern Africa.

Figure 127. Dendrogram illustrating proposed relationships of the leptodactylid subfamilies and tribes and derived families. The hatched zone is Cretaceous time during which decreasing equability occurred. The vertical scale is not intended to indicate the duration or age of any group.



Heleophryne is the most primitive leptodactylid genus in terms of its degree of divergence from the pelobatids. In some characters, Heleophryne resembles some of the genera of Australo-Papuan leptodactylids (Heleioporus, Neobatrachus, Notaden, and Mixophyes) of the subfamily Cyclorantinae, but the Australo-Papuan genera are closely interrelated, and none shows any evidence of a close relationship with Heleophryne. The characteristics shared by Heleophryne, some of the Cyclorantinae, the Ceratophryinae, and the Telmatobiini reflect those of the ancestral stock(s) of the Leptodactylidae and may be used to demonstrate a close relationship among these eleven genera; however, with the exception of Heleophryne and the ceratophryines, the other genera are the primitive members of larger groups. Heleophryne may represent an independent line of pelobatid derivatives which has achieved the leptodactylid or bufonoid grade.

The Myobatrachinae are a relatively compact group of Australo-Papuan genera with one Eocene fossil genus from peninsular India. Although sympatric with the Cyclorantinae, the Myobatrachinae are not closely related to the Cyclorantinae. Other than the characteristics of leptodactylid frogs, the two subfamilies have one unifying character (inguinal amplexus), but this is shared with ascaphids, discoglossids, pipids, rhinophryniids, pelobatids, and Batrachyla (Telmatobiinae, Leptodactylidae). I consider

it likely that two other genera of leptodactylids will be found to exhibit inguinal amplexus--Heleophryne and Thoropa. The tadpole mouthparts of the Myobatrachinae are unlike those of all other leptodactylids but are very similar to those of the bufonids. It must be stressed that the Myobatrachinae and Bufonidae share few other characters and that the similarity in tadpole mouthparts may well be convergent or parallel. The species of most myobatrachine genera are toothless, but the species of some genera have teeth on the maxillary arch. The myobatrachines have type I cervical cotylar arrangement and widely separated occipital condyles in contrast to the type II cervical cotylar arrangement and narrowly separated occipital condyles of bufonids. Further study must be made to evaluate the closeness of the relationship between these two groups although among the extant leptodactylids, I consider the myobatrachines least unlikely to be the ancestors of the nearly cosmopolitan Bufonidae.

The Cyclorantinae are restricted to the Australo-Papuan region, as are the Myobatrachinae. Parker (1940) suggested that with further study, the two subfamilies would be shown to be less distinctive than he had characterized them. However, the additional osteological and tadpole characters utilized here have amplified the distinction between these two subfamilies. As pointed out above, the two Australo-Papuan subfamilies share only one significant

character. I consider the community of ancestry of these two groups to be very ancient if it existed at all. The Cyclorantinae share some characters with the Telmatobiini, Alsodini, and Ceratophryinae, but are not closely related to any of these groups. The tribe Cycloranini is less unlike the Neotropical subfamilies than is the Limnodynastini which are more specialized than the Cycloranini.

I consider each of the three subfamilies discussed above to have evolved independently from a megophryine ancestor. One could therefore argue that the Leptodactylidae are polyphyletic. The Cyclorantinae appear to be ancestral to the Neotropical leptodactylids, but the Heleophryinae and Myobatrachinae are apparently not involved in the phylogeny of the Neotropical leptodactylids. As stressed above, the Megophryinae and Australo-Papuan leptodactylids are similar in most character complexes. Taken in combination, the Cyclorantinae, Heleophryinae, and Myobatrachinae form an evolutionary grade between the Megophryinae and the Neotropical leptodactylids. However, I am reluctant to accord both the Heleophryinae and Myobatrachinae familial status and consider equally unrealistic the idea of considering either or both subfamilies of the Pelobatidae. The Myobatrachinae could be more reasonably distinguished familiarly from the Pelobatidae than could the Heleophryinae. From an evolutionary standpoint, the Heleophryinae are a relict of the Megophryine stock which gave rise to the



Cyclorantinae (see below, pp. 725-31). The Myobatrachinae probably evolved from a contemporaneous megophryine. Whether this megophryine was subfamilially distinct from the group which gave rise to the Cyclorantinae cannot be known in the absence of fossils. I doubt that these two megophryines were subfamilially distinct and therefore consider the Leptodactylidae monophyletic following the reasoning of Simpson (1961:124).

The subfamilies discussed below seem to have a common ancestry within the Leptodactylidae. This common ancestor was probably a cycloranine which was not unlike the modern Cycloranini.

The subfamily Ceratophryinae contains only two extant genera and is a morphologically isolated group. This isolation has been described by several workers who consider the subfamily to be a family more closely allied to the Bufonidae than to the Leptodactylidae (Cei, Limeses, Reig). In spite of the morphological isolation of the Ceratophryinae there are some striking similarities between the Ceratophryinae and the Odontophrynini. Boulenger (1882), Cochran (1955), Reig (1960b), Reig and Cei (1963), and Reig and Limeses (1963) suggested that Odontophrynus and Stombus auctorum (= Proceratophrys) are very closely related to the ceratophryines. The Odontophrynini may have been derived from a ceratophryine ancestor, but the extant odontophryine genera exhibit fewer primitive

characters than do the genera of the Telmatobiini. The Odontophrynini represent either the first or second divergence from the original stock of the Telmatobiinae. The Ceratophryinae seem to represent the earliest divergence from the Neotropical leptodactylid stock.

The remainder of the early Neotropical leptodactylid stock (after the Ceratophryinae diverged) is represented by the Telmatobiinae and derived subfamilies (Elosiinae and Leptodactylinae). Some of the terrestrial genera of the Telmatobiini resemble the primitive Australo-Papuan Cycloranini (Cycloraninae) but more closely resemble the other tribes of Telmatobiinae.

The Leptodactylinae are derived from the relatively primitive Alsodini (Eupsophus). The most primitive leptodactyline (Pleurodema) is very similar to Eupsophus. The two genera differ in the sternal apparatus, breeding biology, and loss of the quadratojugal. Pleurodema has an osseous sternal style (as do all other leptodactylines) and lays its eggs in a foam nest (like several other leptodactylines); these two characters clearly ally Pleurodema with the Leptodactylinae although its close relationship to Eupsophus is obvious and could be used to support the argument that the Leptodactylinae are only a tribe of the Telmatobiinae.

The Elosiinae are a small, morphologically homogeneous group except for the cranial adaptations of Megaelosia.

The relationships of the subfamily to other leptodactylid groups are unclear and over-shadowed by the relationship between the Elosiinae and the Dendrobatidae. The Elosiinae exhibit many characters in common with the Alsodini, Grypiscini, and Eleutherodactylini, and I consider the elosines to represent an early division from the alsodine stock which later gave rise to the Grypiscini and Eleutherodactylini.

I recognize two tribes in the Cycloraninae, the Cycloranini and the Limnodynastini. Of the two tribes, the Cycloranini are more primitive. The Limnodynastini are specialized in their breeding biology. None of the five limnodynastine genera has vertical pupils and all have free intervertebral discs, the cervical fused to the second vertebrae, and relatively long transverse processes of the posterior presacral vertebrae. Adelotus brevis and one species of Limnodynastes have outer metatarsal tubercles, which are otherwise lacking in the tribe. The foam-nesting habits and the modifications of the fingers in females of the Limnodynastini are considered adequate reasons for separating these five genera from the Cycloranini which do not lay their eggs in foam nests (except Heleioporus) and do not have finger fringes in the females. The foam-nesting habit of Heleioporus is quite different from that of the Limnodynastini but similar to that exhibited by the frogs of the Leptodactylus fuscus

group. Heleioranus, Neobatrachus, and Notaden are closely related. Although their skeletons are similar, the three genera differ in breeding biology and some external characters. Cyclorana and Mixophyes differ from Heleioranus, Neobatrachus, and Notaden in many features of the skull and vertebral column, but do not closely resemble each other. They are derived genera but probably have evolved several characters in a parallel fashion (ankylosis of intervertebral discs to centra, separation of cervical and second vertebrae in adults, long transverse processes on the posterior presacral vertebrae, and lack of a frontoparietal fontanelle). The last character may be primitive to the presence of a fontanelle, but in the leptodactylid groups the primitive genera frequently have a frontoparietal fontanelle.

The Ceratophryinae and Heleophryinae do not exhibit a great amount of intrasubfamilial variability in that they are small groups. The Myobatrachinae are morphologically homogeneous in many characters but are heterogeneous in many others. With the possible exception of bufonid and ranoid derivatives (see below), the myobatrachines do not figure prominently in bufonoid evolution. With respect to the Leptodactylidae, the Myobatrachinae are an evolutionary dead-end.

The Ceratophryinae and Telmatobiinae apparently evolved from cycloranine ancestors. The Ceratophryinae

represent an early divergence of the Neotropical stock and are a morphologically isolated and small group. The Telmatobiinae are a morphologically diverse and large group with one fossil and 24 Recent genera. I divide the Telmatobiinae into five tribes. The Telmatobiini (5 genera) and Odontophrynini (2 genera) are the most primitive tribes and the Alsodini are but slightly more advanced. The former two tribes have apparently not given rise to additional groups and have the bulk of their species in temperate or Andean South America. The Odontophrynini share several characteristics with the Ceratophryinae and may be early derivatives of that group which have paralleled the Telmatobiini. At present, I include the odontophrynines in the Telmatobiinae because they lack the distinctive vertebral column and vertebral shield of the ceratophryines. Cei (1965) demonstrated that the skin proteins of Ceratophrys and Lepidobatrachus set these genera off from the other leptodactylids including Odontophrynus and Proceratophrys. The distinctive ilia of the ceratophryines are identical with those of the odontophrynines and unlike those of all other leptodactylids. The solution of the problem of whether the odontophrynines represent a proto-ceratophryine or a telmatobiine stock will probably require some fossil data.

The Alsodini and their derivatives make up the majority of the Neotropical Leptodactylidae. The Alsodini

occur in temperate and Andean South America, with one genus (Thoropa) endemic to southeastern Brasil. The tribe is somewhat heterogeneous in that two of the genera (Eupsophus and Hylorina) have a type II cervical cotylar arrangement and lay relatively numerous small eggs in aquatic situations. Both of these genera engage in axillary amplexus and have outer metatarsal tubercles. One of them (Hylorina) has vertical pupils. The other two alsodine genera (Batrachyla and Thoropa) have a type I cervical cotylar arrangement and lay relatively few large eggs in moist terrestrial situations. The larvae of both genera become aquatic after the nest is inundated. Both genera have outer metatarsal tubercles and horizontal pupils. Batrachyla engages in inguinal amplexus (Barrio, 1967a), but amplexic behavior has not been observed for Thoropa. As mentioned above, the Leptodactylinae seem to have been evolved from an ancestral stock with the characteristics of Eupsophus. Batrachyla and Thoropa are probably representative of the alsodine stock which gave rise to the Eleutherodactylini, Grypiscini, and Elosiinae. I consider the Elosiinae to represent an early divergence from this stock because the Elosiinae have aquatic larvae. Osteologically, the Elosiinae are isolated from the Grypiscini and Eleutherodactylini. I consider the Grypiscini more primitive than the Eleutherodactylini. The eggs of grypiscine genera are large and deposited in

moist terrestrial situations as is the case in the Alsodini, but in contrast to the Alsodini, the larvae are not aquatic (Lutz, 1944). The eleutherodactyline genera exhibit direct development. Unlike the grypiscine larvae, eleutherodactyline larvae never free themselves from the enclosing egg envelopes. The Grypiscini make up a small group which is restricted in distribution to the coastal ranges of southeastern and southern Brasil. The Eleutherodactylini range over the entire tropical and subtropical zones of the Americas except in the arid regions of Central America, Ecuador, Peru, and Venezuela. The zenith of the Leptodactylidae is Eleutherodactylus which contains probably 400 species and occurs over most of the range of the Eleutherodactylini. Direct development is probably the single adaptive change made by this tribe which permitted the tribe to evolve into such a large group. The success of the genus Eleutherodactylus is measured by its diversity and adaptability. The genus is rich in species throughout the West Indies and occurs in semiarid as well as very moist habitats. Unlike many leptodactylid genera, it is not restricted to lowland situations where there are ponds (a requirement for species with aquatic larvae) but ranges altitudinally to at least 4200 meters in the Andes.

## Extrafamilial Relationships of the Leptodactylidae

I have discussed the relationships between the Pelobatidae and Leptodactylidae and the relationships within the Leptodactylidae above. In some cases, reference was made to the close relationship between a leptodactylid group and the frogs of other families. I consider the close relationship between the Pelobatidae and Leptodactylidae to be established, and also consider the statement "the Leptodactylidae are the stem bufonoid group" to be established. If the Leptodactylidae are the stem bufonoid group, then all other bufonoid families are leptodactylid derivatives or are independently derived from a pelobatid stock. The works of Griffiths (1963), Inger (1967), Kluge and Farris (1969), Noble (1922, 1931), and Tihen (1965) have clearly established that the archaic frog families (Ascaphidae, Discoglossidae, Pipidae, and Rhinophrynidae) did not directly give rise to the "advanced frogs."

These authors agree that these four families are clearly primitive and that the other frog families are advanced. Most consider the Pelobatidae to bridge the gap between "primitive" and "advanced" frogs. There is considerable debate as to whether the Microhylidae are primitive or advanced frogs. The proponents of the primitive position (Hecht, 1963, Inger, 1967, Orton, 1957,



and Starrett, 1968) based much of their argument on the tadpole morphology, whereas the advocates of the advanced, ranoid position (Griffiths, 1963, Noble, 1922, 1931, and Parker, 1934) rely on the pectoral architecture, thigh musculature, and the variable sacral-presacral central articulation. Further discussion of the relationships of the Microhylidae is withheld pending new data and perhaps another monograph of the family. I have plotted values for some of the microhylid subfamilies in the figure illustrating the degree of primitiveness in frog groups (Fig. 126). The subfamily Microhylinae appears to be the most primitive subfamily of this group on the basis of the characters I used. Relatively little data of the breeding biologies of microhylids are available, and I have seen relatively few genera in computing my values of primitiveness for the family. In general the values are in agreement with the idea of the phylogeny of microhylids advanced by Parker (1934)--that the group represents an early ranoid divergence. The data are not in accord with the position taken by Hecht (1963) and Starrett (1968)--that the family represents one of the archaic families. The remaining frog families seem to have some relationship to the varied leptodactylid stocks.

I consider the rhinodermatids to represent a Neotropical bufonid derivative and therefore include that genus in a discussion of the relationships of the Bufonidae

to the Leptodactylidae. As mentioned above, among the extant leptodactylid groups the Myobatrachinae are most like the Bufonidae and are presumably the modern representatives of the proto-bufonid stock. The two groups agree strikingly in the structure of the tadpole mouthparts. All bufonids (and Rhinoderma) lack teeth; few leptodactylids are edentate, but this character-state is most pronounced in the Myobatrachinae. All bufonids and myobatrachines have dilated sacral diapophyses. Myobatrachines have a type I cervical cotylar arrangement (type II in bufonids), free intervertebral discs (procoelous vertebrae in bufonids), and lack Bidder's organ (present in bufonids). Most bufonids lack a prezonal element in the pectoral girdle (omosternum present in Nectophrynoides and at least one Bufo, B. haematiticus), whereas most leptodactylids have a large omosternum and manubrium. The prezonal element in myobatrachines is small in most genera and absent in some. Although the Neotropical bufonids have radiated (7 endemic genera), there is no close relationship between the Neotropical bufonids and leptodactylids.

The relationships of the Centrolenidae are not apparent. Before the significance of the intercalary cartilage was accepted, they were often placed in the Hylidae or Leptodactylidae. Centrolenids are arboreal, have aquatic tadpoles, intercalary cartilages, T-shaped

terminal phalanges, the astragalus and calcaneum fused, and lack a prezonal element in the pectoral girdle. Most authors consider them hylid derivatives (Eaton, 1958). Much of the argument that centrolenids are hylid derivatives rests on a conviction that all Neotropical taxa with intercalary cartilages are related. The hyolarynx of Centrolenella is distinctive (figured by Eaton, 1958) and quite different from that of most bufonoid genera. The variation in the hyolarynx of hylids has not been adequately investigated and until it has, the taxonomic value of the distinctive hyolarynx of Centrolenella remains unknown.

The Dendrobatidae are an elosiine leptodactylid derivative and not ranoid as claimed by Griffiths (1959, 1963). This point was discussed in greater detail in the section of the Elosiinae (pp. 564-67). Griffiths (1963), in arguing in support of his contention that the Dendrobatidae are a subfamily of the Ranidae, cited the apparent parallelisms in the Petropedetinae (African ranids). My study of the group is limited to some dissection and examination of cleared and stained individuals but results in the conclusion that the two groups exhibit considerable similarity in myology and osteology. The similarities are quite striking and probably reflect a community of ancestry rather than parallelism. However, it should be borne in mind that I have not studied the other ranid

subfamilies and genera in detail and cannot therefore convincingly argue that the similarities are not due to parallelism.

The relationships of the Hylidae are not apparent, but the family is usually tacitly considered a leptodactylid derivative. Inger's (1967:Fig. 6) phylogeny suggests that the Hylidae are the sister group (sensu Hennig) of the Ranidae + Rhacophoridae. The suggestion is unique and mentally provocative but needs further investigation. Previous authors were committed to placing the Hylidae and Ranidae in different suborders because of convictions that the pectoral architecture or sacral centrum were characteristic of basic dichotomies. The same convictions required the Microhylidae to be closely related to ranids.

The Pseudidae were considered leptodactylids until Parker (1935) suggested that they were hylids (because of the presence of an intercalary phalanx). The intercalary phalanx of pseudids is elongate and osseous instead of short, disc-like, and cartilaginous as in centrolenids, hylids, hyperoliids, rhacophorine ranids, and some microhylids (Phrynomerus). Savage and Carvalho (1953) named a new family for the Pseudidae (Lysapsus and Pseudis) because they considered the accessory phalanx analogous to the intercalated cartilage. As pointed out by Burger (1954), Savage and Carvalho's "new family" was authored by Fitzinger (1843). Savage and Carvalho (1953) considered Pseudis

more primitive than Lysapsus and suggested that the family was derived from the Leptodactylidae. Burger (1954) considered Lysapsus more primitive than Pseudis and suggested that the group was a hylid subfamily. I have not studied pseudids in detail, and much information is lacking for Lysapsus, but I consider the group more closely allied to leptodactylids than to hylids. The pseudids are not closely related to any leptodactylid group.

The ranoid families (Hyperoliidae, Sooglossidae, Ranidae, and Rhacophoridae) are usually considered remote from leptodactylids. Sooglossus and Nesomantis were included in the Sooglossinae, a pelobatid subfamily with ranoid parallelisms by Noble (1931). The subfamily is restricted to the Seychelles. Darlington (1957) doubted on zoogeographic grounds (with preconceived acceptance of Matthew's conclusions) that the Sooglossinae could be pelobatids, and Griffiths (1960), with similar zoogeographic biases, demonstrated ranoid affinities for the group and elevated the subfamily to family rank. The Sooglossidae have some pelobatid, myobatrachine leptodactylid, and ranoid traits and are conceivably modern representatives of a leptodactylid derivative that gave rise to the Ranidae. Until further study is made of the numerous hyperoliid, ranid, and rhacophorid genera, additional comments on the relationships of these families to leptodactylids are

held in abeyance. Vertical pupils are considered to be primitive by me and vertical pupils do not occur in the Ranidae or Sooglossidae. Vertical pupils are common in the genera of two of the subfamilies of Laurent's (1951) Hyperoliidae (Astylosterninae and Hyperoliinae). Most of these genera also lack outer metatarsal tubercles.

## ZOOGEOGRAPHY

Almost without exception, previous zoogeographic studies utilizing or involving anurans have been Matthewian in analysis and conclusion. Darlington (1957) voiced numerous suggestions concerning anuran zoogeography but lacked an understanding of the relationships of most groups. Noble (1924, 1926c, 1930) attacked many zoogeographic enigmas, but his approach was strictly Matthewian. Many macrosystematic problems of frogs have been studied and solved in the past decade, and the major evolutionary patterns of the Anura are only now beginning to surface. Many problems, principally minor ones, remain to be solved; a major difficulty to be overcome is the relationships of the families assigned to the Ranoidea, especially the Microhylidae. Paleontological work has continued to force biologists to accept the antiquity of frogs; the order had diversified into several families by the Jurassic (Tihen, 1965). As the known antiquity of frogs increases, so must the consideration that continental drift may have played an important role in establishing their present distributions. However, simply because a group is an old one, continental drift need not be invoked to explain distribution patterns (cf. Kluge, 1967).

The present distribution of the Leptodactylidae (Fig. 1) is suggestive of a southern origin and dispersal.

No fossil evidence is available to establish the presence of the family in the northern hemisphere before the late Tertiary except for the Lower Eocene Indobatrachus from peninsular India. Noble (1930) and Darlington (1957) cited the fossil as evidence of a northern occurrence of the otherwise Australo-Papuan Myobatrachinae. Both authors assumed that peninsular India has always been part of the Asian continent or at least has been part of it for sufficiently long that, zoogeographically, India is part of Asia. However, contrary evidence is impressive. Paleomagnetic studies place Bombay at  $40^{\circ}$  S in the Jurassic and record a steady northerly movement of the subcontinent throughout the later Mesozoic and Cenozoic. During the Eocene, Bombay was at  $10^{\circ}$  S (Takeuchi, Uyeda, and Kanamori, 1967), or at about the level of northern Australia, and the present Himalayan region was crossed by the Sea of Tethys.

The frogs of the family Leptodactylidae presently occur in Australia (and New Guinea and Tasmania), in southern Africa, and in the Neotropics from southern Chile and Argentina ( $53 - 54^{\circ}$  S) north to Arizona, Florida, New Mexico, and Texas ( $30 - 33^{\circ}$  N). With the exceptions of a few leptodactyline and telmatobiine genera which range northward into Middle America and the southern United States, no leptodactylid subfamily occurs on two continents. The Cyclorantinae and Myobatrachinae occur



only in the Australo-Papuan Region (two genera reach eastern New Guinea and three reach Tasmania), the Heleophryninae (monotypic) occur only in southern Africa, and the Ceratophryinae, Elosiinae, Leptodactylinae, and Telmatobiinae occur only in South and Middle America. With the exception of Indobatrachus, the fossil record for each subfamily (insofar as it is known) is included in the Recent distribution of the group (on the same continent). Five genera of the Telmatobiinae range outside of South America; four of these (Hylactophryne, Sminthillus, Syrrhophus, and Tomodactylus) do not occur in South America, but the other (Eleutherodactylus) is wide-spread in tropical South America. Sminthillus is a Cuban endemic, and the other three non-South American genera are principally distributed on or around the Mexican Plateau. Three genera of the Leptodactylinae range outside of South America. Pleurodema occurs in the savannas of central Panamá but has its center of distribution in temperate South America. Physalaemus occurs in the Central American lowlands as far northwest as Oaxaca and Veracruz, México, but has its center of distribution in subtropical and tropical Argentina and Brasil. In the case of both genera, only a single species enters Central America. Leptodactylus ranges northwestward through Central America to Texas and Sinaloa but all Central American species are also found in northern South America. Leptodactylus also occurs on

Hispaniola and Puerto Rico and on several islands in the Lesser Antilles, but is not represented by extra-South American endemics. All of the Middle American leptodactylines are South American species which have spread northward since the Late Pliocene closure of the Panamanian portal (Lloyd, 1963). The Telmatobiine genera all belong to the Eleutherodactylini. Three of the extra-South American genera (Sminthillus, Syrrhophus, and Tomodactylus) are derivatives of the alpha division of Eleutherodactylus. The alpha division of Eleutherodactylus is centered in the West Indies (about 100 species) but also occurs in the Andean system in Colombia, Ecuador, Guyana, and Venezuela. The fourth extra-South American eleutherodactyline (Hylactophryne) is not obviously derived from Eleutherodactylus and shows a greater affinity with an Amazonian genus (Ischnocnema). The paleogeographic maps compiled by Harrington (1962), Jacobs et al (1963), and especially Lloyd (1963) strongly suggest that South America was not connected to North America during the Mesozoic and most of the Tertiary. Contact was established in the Pliocene (Lloyd, 1963). Animals could have moved northward across the volcanic island chain in the latter half of the Tertiary but the degree of isolation of animal groups suggests that the terrestrial South American fauna was isolated in South America until the Pliocene. No leptodactylid group reached

North America via a Panamá-Costa Rica route until late in the Tertiary. Some leptodactylids may have reached North America earlier (perhaps Miocene) by way of the Antillean arc. Therefore, until the Middle Tertiary we may ignore North America insofar as leptodactylids are concerned. The history of the family lies in South America and the southern hemisphere. Vinson and Brineman (1963) suggested that Middle and South America were connected by a Late Paleocene land bridge. These authors argued that this is true because of the lack of Danian-Paleocene marine formations in the Isthmian region of Panamá. This land bridge was essential to Savage's (1966) analysis of the history of the Middle American herpetofauna.

The Australo-Papuan and African leptodactylid groups share a few characters but each of the three groups has more characters in common with the pelobatid subfamily Megophryinae. The Megophryinae seem to be ancestral to the Leptodactylidae, and the lack of obvious interrelationships between the Heleophryinae, Cyclorantinae, and Myobatrachinae suggests that each subfamily is an independent derivative of the megophryine stock. The Cyclorantinae and Heleophryinae share one interesting character (the fusion of the cervical and second vertebrae) which does not appear elsewhere in the family. The fusion appears in some African and South American bufonid genera, rhinodermatids, palaeobatrachids,

and pelodytids; the significance of this character distribution is not entirely apparent at present.

The Recent distribution of the Megophryinae is much smaller than its early Tertiary distribution. Eopelobates is known from Europe in the early Miocene and western North America in the Eocene and Oligocene and is probably represented in the late Cretaceous deposits of Wyoming. The Megophryinae are presently restricted to southeastern Asia and the Indo-Australian archipelago west of Wallace's Line but do not occur on Luzon and Masbate (Philippines).

Both the Cyclorantinae (Lechriodus) and Myobatrachinae (Crinia) occur in eastern New Guinea, and Lechriodus also occurs on the Aru Islands. Lechriodus has three endemic species in New Guinea and the Aru Islands, but one other species also occurs in eastern Australia. The single Crinia which occurs on New Guinea is also widespread on the Australian mainland. Each subfamily is distributed over most suitable anuran habitat on the Australian mainland and both are absent over most of the western Eyrean desert.

Among living leptodactylids, the Cycloranini are least unlike the primitive Neotropical leptodactylid genera. The morphological hiatus between the Neotropical leptodactylids and the several pelobatid stocks requires an intermediate stage whose characteristics are like those exhibited by the Cycloranini. Darlington (1957, 1965) considered the temperate South American frog fauna depauperate and thus,

of little zoogeographic importance. Oei (1962a) and Vellard (1957) contended that the fauna is relict. Vuilleumier (1968) analyzed the amphibian fauna of the Nothofagus forests of temperate South America and noted that the present anuran distributional patterns are a result of Pleistocene events but admitted that the high degree of endemism is a consequence of a long history in the Patagonian forests. Vuilleumier (1968) considered the frog fauna of the Nothofagus forests to consist of four elements: (1) leptodactylid stocks which are autochthonous and have not subsequently diversified; (2) autochthonous leptodactylid elements which have subsequently radiated into northern South America; (3) Nothofagus endemics which are derived from tropical South American leptodactylids; and (4) bufonid and leptodactylid stocks which are widespread in South America and have more species outside of the Nothofagus forests than in it. He considered the available data as inadequate to permit determination of whether these groups are secondary or primary inhabitants of southern South America. Vuilleumier's analysis must be rejected because his conclusions are in part based upon the erroneous conclusions of other authors. His second element [(2), above] consisted of Eupsophus. As I pointed out (Lynch, 1969a), Eupsophus (as used by Vuilleumier and many other authors) is a composite of seven genera. Eupsophus is restricted

to western Argentina and Chile, except for three Andean species in southern Ecuador and central Peru. Vuilleumier's third element has been altered taxonomically by Barrio (1967a) and Lynch (1969a). Batrachyla is valid and contains three species (all Nothofagus endemics); the genus is not an Eleutherodactylus derivative but an offshoot of a Eupsophus-Hylorina stock. The fourth element of Vuilleumier was misrepresented in part. Vuilleumier included the genera Bufo and Pleurodema. The former is widespread and species-rich in tropical and subtropical South America but Pleurodema is basically a temperate South American genus (defined on the basis of cool or cold winters and cool summers). The distributions of eight of the ten species of the genus are contained in temperate South America; the other two species range northward into subtropical and tropical areas in Brasil, Colombia, Venezuela, and the Guianas (Fig. 128). Pleurodema is a temperate zone genus which has invaded the tropical zone, whereas Bufo is more a tropical zone genus which enters the temperate zone.

Batrachophrynus, Batrachyla, Caudiverbera, Eupsophus, Hylorina, Pleurodema, Telmatobufo, and Telmatobius are temperate South American leptodactylid genera either wholly or principally restricted to the temperate zone. This list of genera includes most of the primitive Telmatobiinae and the most primitive living Leptodactylinae.

Figure 128. Distribution of leptodactylids in South America. (A) Black areas encompass the range of the Alsodini. Thoropa is restricted to southeastern Brasil. The dotted line encloses the range of the genera Telmatobius and Batrachophrynus. Two other genera of the tribe (Caudiverbera and Telmatobufo) occur in the black area in Chile. (B) Ranges of the genera Limnomedusa and Pleurodema, the most primitive genera of the Leptodactylinae. (C) Range of the Elosiinae. The area in southeastern Brasil encompasses the distribution of Crossodactylus and Megaelosia; the genus Hylodes also occurs on Cerro Duida, Amazonas, Venezuela. The range of the Elosiinae in southeastern Brasil approximates the range of the Grypiscini.

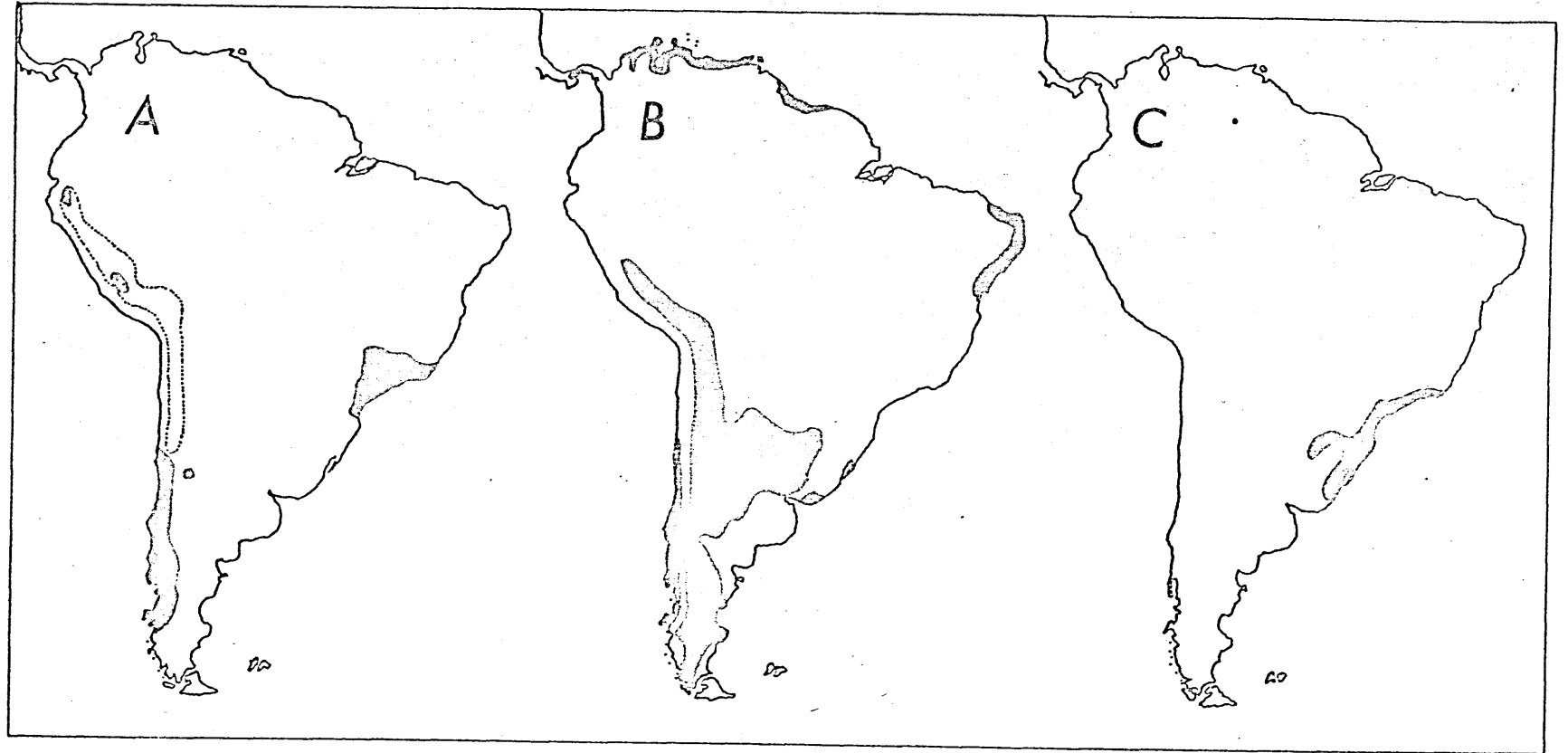
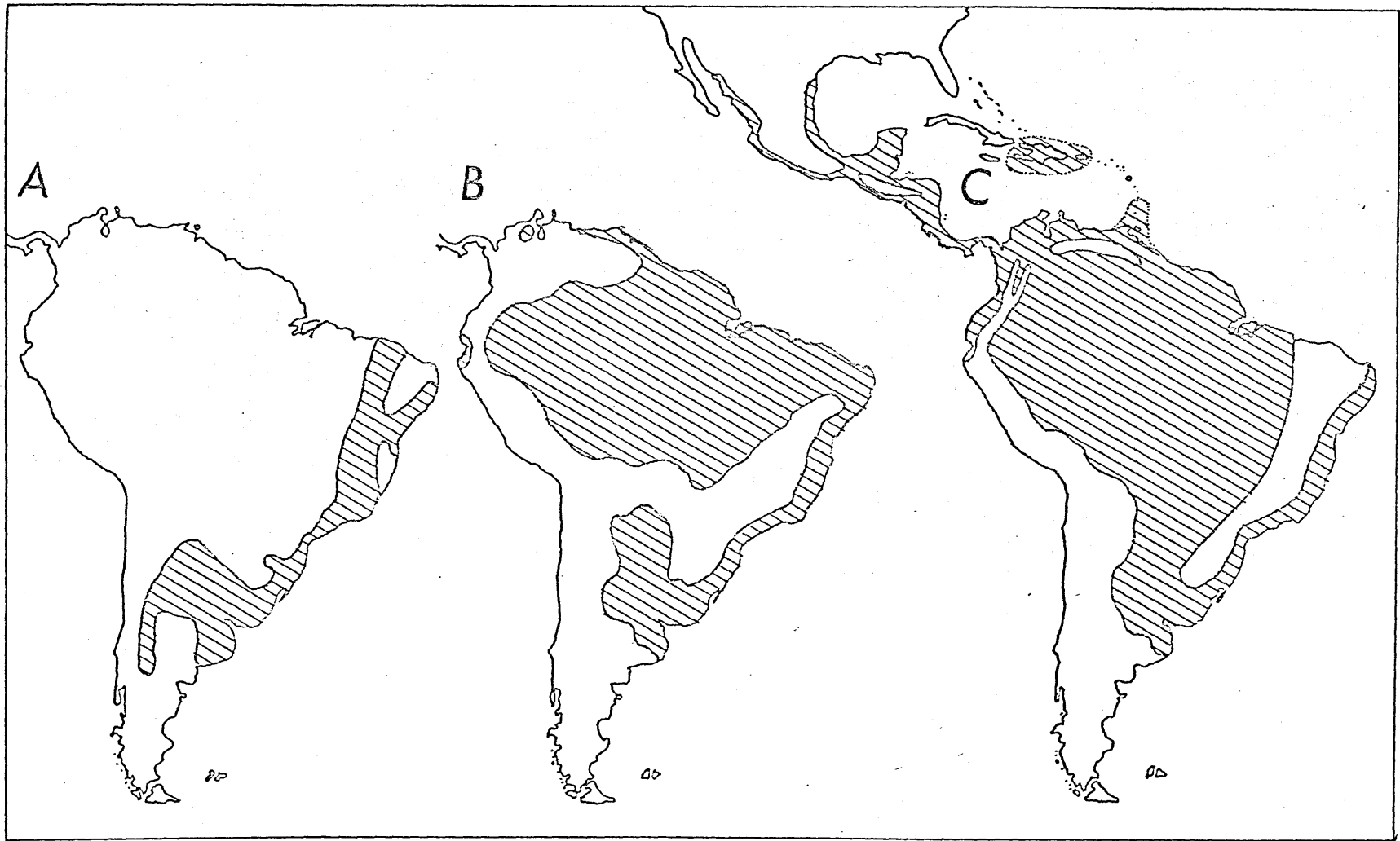




Figure 129. (A) Distribution of the Odontophrynini. (B) Distribution of the Ceratophryinae. (C) Distribution of the Leptodactylinae except for the primitive genera Limnomedusa and Pleurodema.



Ceratophrys, Lepidobatrachus, Limnomedusa, and Thoropa are also considered primitive, and with the exception of Ceratophrys do not range north of the southern subtropical zone.

The primitive Cycloraniini morphologically resemble the primitive Neotropical genera, which are the principally temperate South American genera. These coincidences require that we regard the similarities as convergent or that we consider them products of common ancestry. The latter conclusion further requires some land connection between Patagonia and Australia; the most plausible route is via Antarctica. To conclude that the route involved the Holarctic Region requires a massive extinction of the stocks which passed through the Holarctic and Neotropical regions, and further requires that these stocks survived only in temperate South America from which they gave rise to new groups which then invaded the tropical zone. A possible causative agent for such a mass extinction would be climatic zonation and decreasing climatic equability of the northern hemisphere during Cretaceous time. However, this explanation results in two principle difficulties: (1) why did not leptodactylid stocks survive in areas in the northern hemisphere which retain high equabilities?, and (2) the megophryine pelobatids are probably equally sensitive to low equabilities yet they persisted in North America until the Oligocene and survive

today in southeast Asia.

Equability is a property of climate which expresses departures from  $14.0^{\circ}$  C and thus responds primarily to temperature extremes (Axelrod and Bailey, 1968). High equabilities reflect little variation in temperatures about an annual mean of  $14.0^{\circ}$  C. Equability applies equally well to warm and cold regions. Bailey (1960, 1964) also noted a second aspect of temperature that affects biotic composition--effective temperature, which expresses warmth of the climate in terms of temperature and the duration of the summer (Axelrod and Bailey, 1968). Effective temperature is independent of the mean annual range of temperatures.

Axelrod and Bailey (1968) noted that many areas in the southern hemisphere harbor relicts of the Cretaceous flora (cycads, tree ferns, podocarps, araucarias). It is in some of these regions (south Africa, Australia, southern South America, southeastern Brasil) that primitive leptodactylids (Cyclorantinae, Myobatrachinae, Heleophryninae, Telmatobiini, and Alsodini) occur. These areas are characterized by high climatic equability ( $M = 60 +$ ).

Mesozoic climates were characterized by high equabilities (Axelrod and Bailey, 1968). Equability is increased if the locality is associated with large bodies of water (for example, the equability of localities along the Peruvian coast is higher than might be expected, as

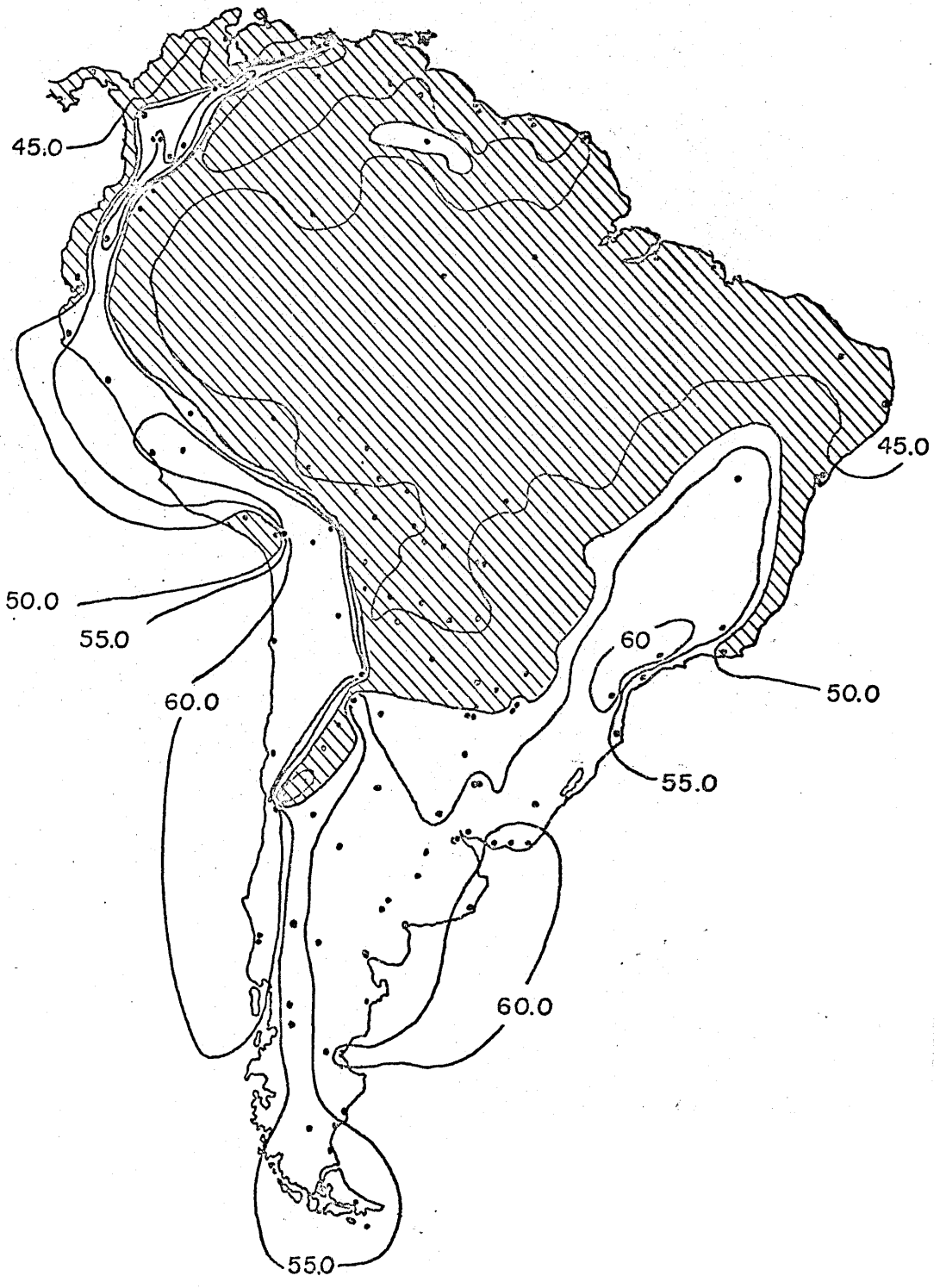
are the equabilities for localities in coastal Uruguay). The broad marine embayments and epeiric seas of Mesozoic landmasses probably contributed to the maintenance of high equabilities in continental situations. Under a temperature regime of high equabilities, the dispersal routes of Mesozoic animals would not be temperature-limited. The southern hemisphere leptodactylid stocks could have invaded the northern hemisphere were land connections available because the northern hemisphere was also under a regime of high equabilities until the Cretaceous. During the Cretaceous many plant and animal groups became extinct or began to flourish. At the same time the earth began to experience a marked climatic zonation. With the development of climatic zonation, broad areas of the world experienced a decrease in equability. Axelrod and Bailey suggested that the primitive faunas and floras presently living in areas of high equability survived in those regions because these groups are, and their ancestors were, adapted to climates of high equability.

The part of South America (Fig. 130) with high equabilities (58+) includes the ranges of almost all of the primitive genera (Batrachophrynus, Batrachyla, Caudiverbera, Eupsophus, Hylorina, Lepidobatrachus, Limnomedusa, Pleurodema, Telmatobius, and Telmatobufo). A few of the species in these genera occur in areas of low equability (for example, Pleurodema brachyops and P.

diplolistris occur in areas with equabilities of 40 - 45). The Leptodactylinae probably evolved in response to the decreasing equability of the Late Cretaceous (see below). Before returning to the history of the Leptodactylidae in South America, it is convenient to review briefly the history of the African and Australo-Papuan groups and the Megophryinae and to discuss the possible role of climatic equability in the establishment of the Recent distributions of these groups.

The Megophryinae have survived in areas with relatively high equabilities. Even the temperate eastern Himalayas have equabilities of 60+. Regardless of which stance (Wegenerian or fixed continents) one wishes to take, the Megophryinae are probably a group which evolved in the northern hemisphere. The Cycloraninae, Heleophryinae, Myobatrachinae, and Pelobatinae are the derivatives of the Megophryinae. Two of these derivatives are Australo-Papuan, one south African, and one Holarctic. The proximity of the present distributions of the Megophryinae, Cycloraninae, and Myobatrachinae tempts one to assume that megophryine stocks crossed the Indo-Australian archipelago into Australia in the early Cretaceous with the Marsupalia and boid and elapid snakes. However, Inger (1954) considered the Megophryinae late invaders of the Philippine Islands. Of further significance in this regard is the wider distribution of the Megophryinae

Figure 130. Map of South America with isoequaphane lines (45, 50, 55, 60 and above) superimposed. All dots on the map represent stations for which equability values (after Axelrod and Bailey, 1968) were computed. The hatched areas have equabilities of 50 or less.

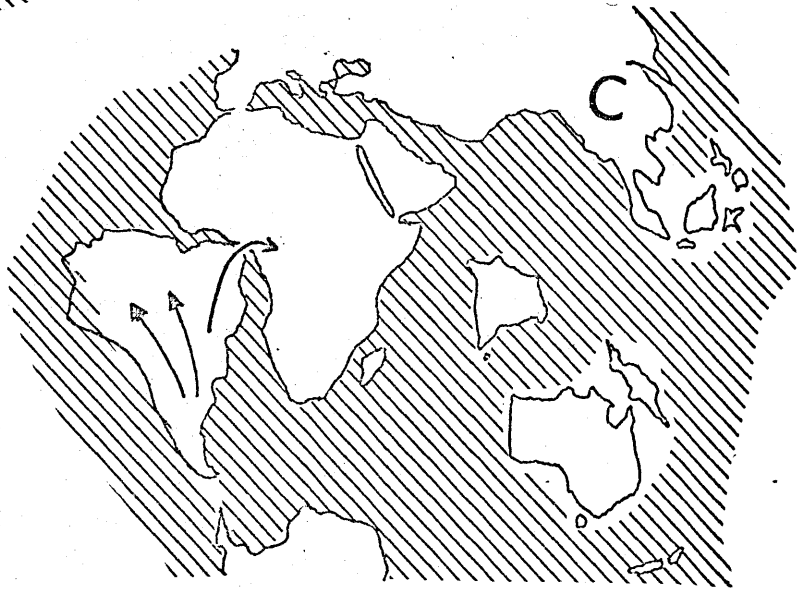
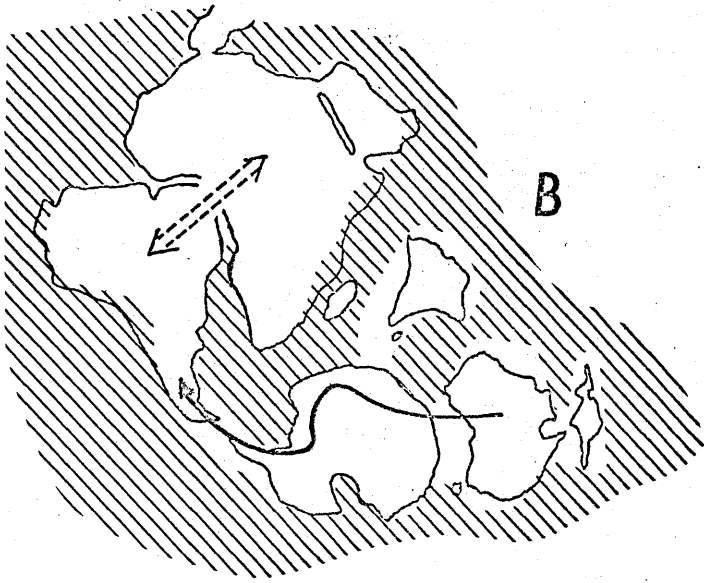
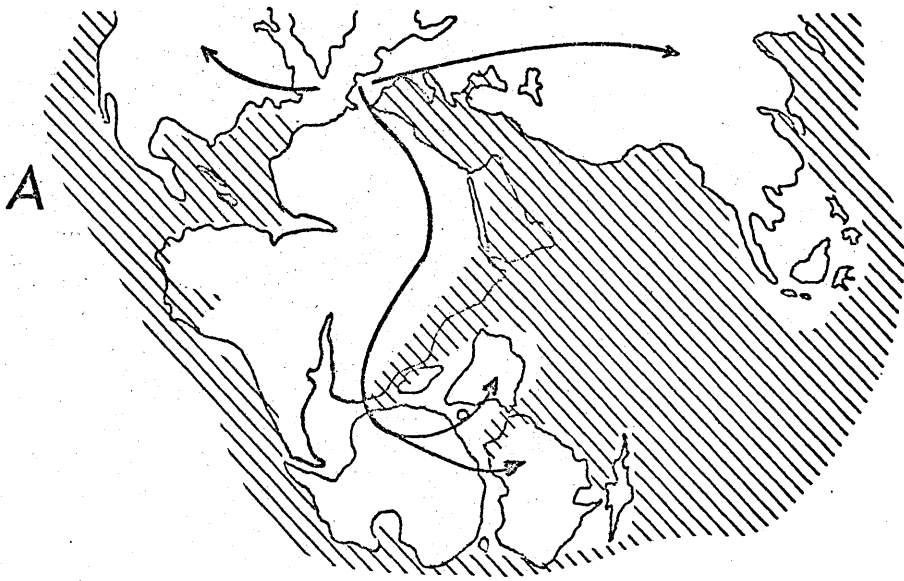




in the Late Cretaceous and early Tertiary of North America and Europe. Proponents of continental drift argue that the proximity of the Sundan shelf and Sahul shelf is a relatively recent phenomenon. The Indo-Australian archipelago is usually cited as the route whereby northern-evolved groups reached Australia in the Cretaceous (Clemens, 1968, Darlington, 1957, 1965). Biologists seeking support for this route have cited Audley-Charles (1966), who after studying the geology of Timor concluded that the relationship between Timor and the Sahul shelf has not changed since the Middle Triassic and that the relationship between Timor and the rest of the archipelago is apparently as ancient. As Hallam (1967) remarked, "...something more than island chain links is required to account for the presence in Australia of the lungfish Neoceratodus and large Jurassic and Cretaceous dinosaurs."

A Jurassic dispersal of megophryine stocks through eastern Africa onto peninsular India, Antarctica, and Australia (Fig. 131) would explain the similarities of the Heleophryninae and some primitive Cycloraniini, but would require that these continental masses be in close proximity instead of being widely separated as they are today. This route also requires that the megophryines not invade South America which was in close proximity with Africa until the Neocomian (Lower Cretaceous). The

Figure 131. Paleozoogeographic maps for three stages of the evolution and dispersal of leptodactylid frogs and for related groups. (A) Jurassic (Callovian)--southerly dispersal of Megophryinae. (B) Late Jurassic or earliest Cretaceous--Africa is isolated from southern masses; climatic equability is beginning to influence dispersal routes. Leptodactylid invasion of South America. The dashed line is the route of free exchange of other vertebrate groups (e.g., characoid fishes and pipid frogs). (C) Middle Cretaceous--Africa-South American connection is tenuous, Neotropical leptodactylids are radiating from Patagonia into low-equability zones. Bufonidae spread into Africa.



megophryine stock probably had the same reproductive biology as do the living pelobatids and the Australo-Papuan leptodactylids. During the Jurassic and early Cretaceous, the Brazilian and Guiana shields must have been formidable barriers to pond-breeding frogs. On the slopes of these uplifted shields, ponds would be rare if they existed at all. In contrast, ponds would be available along the western edge of Africa in the vicinity of the East African Gulf of Tethys sea (Hallam, 1967). If the interior of Antarctica was as formidable to amphibians as Darlington (1965) reasons it must have been, then the only southern route would have been across that part of Antarctica now called Enderby Land and the American Highland. Hallam (1967) suggested that a deep marine sea separated South America and Africa from Antarctica, Australia, and Peninsular India in the Neocomian. Harrington (1962) noted the occurrence of marine facies over the southernmost tip of South America in the Neocomian but the extent of this marine sea was not as great as suggested by Hallam. The leptodactylid stock that did reach southern South America probably entered the continent in Callovian (Upper Jurassic) or Neocomian (Lower Cretaceous) times. Whether dispersal was by a corridor or filter bridge (Darlington, 1957) route is non-consequential; dispersal could even have been via a sweepstakes route. The significant point to be made here is that contrary to Darlington's (1965:38) assertion,

one group of terrestrial vertebrates (leptodactylid frogs) does show special relationships between the southern temperate forms on different continents. Darlington stressed the absence of closely related cold-temperate vertebrates in Tierra del Fuego and Tasmania. However, this absence is explained by increased cold and lowered equabilities in Tierra del Fuego. Once the Australo-Papuan groups reached Peninsular India and Australia, and the Australo-Papuan Cycloraniini spread across Antarctica to Patagonia, continental connections were no longer necessary because each of the subfamilies occupied the appropriate continental masses. The probable time period was [ or perhaps somewhat earlier than] the Neocomian (Lower Cretaceous). After this time, Australia and South America appear to have been completely isolated from all other land masses until the middle Tertiary in the case of Australia (connection via the Indo-Australian archipelago) and the late Tertiary in the case of South America (connection via the Panamanian Isthmus).

The early Cretaceous continental separations were followed by the imposition of a severe climatic regime on the distribution of the early Cretaceous faunas and floras. Insofar as the Megophryinae and their derivatives are concerned, the development of this new climatic regime had several important consequences: (1) evolution of a low-equability adapted group, the Pelobatinae, in the

northern hemisphere; (2) gradual extinction and range restriction of the Holarctic Megophryinae; (3) isolation of the Heleophryinae into a high equability area in south Africa and/or extinction of Heleophryinae or Megophryinae in east Africa; (4) extinction of Myobatrachinae in peninsular India; and (5) evolution of low-equability adapted groups in Australia and South America. The high-equability adapted groups were restricted in geographic distribution to areas of high equability in southern South America and Australia. The development of climatic zonation probably resulted in physiological stresses on the surviving fauna and flora; these stresses forced a concentration of the Cretaceous genera into the remaining areas of high equability and may well have been the principle factors causing a radiation of the Neotropical leptodactylids. The development of foam-nesting habits in the breeding biologies of the Limnodynastini may have been stimulated by decreasing equability. The foam-nesting habit enables the frogs of this group to survive in more xeric, and less equatable, climates than are suitable for the Cyclorani and Myobatrachinae.

The distribution of leptodactylids in South America was greatly restricted during the later Cretaceous, when climatic zonation was developing and equability was decreasing. The fauna probably included only a half dozen genera (Batrachyla, Caudiverbera, Eupsophus, Lepidobatrachus,

Telmatobufo or Neoprocoela, and Thoropa). In response to decreasing equabilities the range of the Alsodini was contracted and probably resulted in the isolation of a relict population on the Brazilian shield. This population probably gave rise to the Elosiinae and Grypiscini. The decreasing equabilities also resulted in the evolution of a group of frogs utilizing foam-nests in their breeding biology. The ancestral stock of this group is Eupsophus which gave rise to Pleurodema and possibly to Limnomedusa. The presence of a foam-nest enabled these frogs to breed in more xeric environments, but presumably the adults were adapted to high equabilities and were therefore unable to successfully invade the tropical zone. New genera evolved to occupy this region (Leptodactylus and Physalaemus). Batrachyla and Thoropa lay their eggs in moist terrestrial situations but require water for their aquatic tadpoles. The Elosiinae represents a derivative of this group which became isolated on the Brazilian and Guiana shields (high equability). The Eleutherodactylini also evolved from an ancestral stock not unlike the Alsodini and Grypiscini. The Grypiscini and Eleutherodactylini evolved direct development, which enabled these groups to invade regions lacking ponds. The evolution of these groups may have been prompted by avoidance of competition in the larval stage. The evolution of Eleutherodactylus is probably partly correlated with the Andean orogeny in

the Mid-Tertiary. The Ceratophryinae and Odontophrynini represent groups that evolved in response to decreasing equability but were adapted to xeric, non-forested habitats. The principle low-equability adaptations of these groups involve a heavier, drier skin.

The Dendrobatidae are the low-equability adapted derivatives of the high-equability adapted Elosiinae. The similarities between the Dendrobatidae and Petropedetinae and the distributions of these two groups are suggestive of their evolution being synchronous with the last stage of separation of eastern Brasil and Africa. The Petropedetinae are low-equability adapted frogs. The radiation of the Dendrobatidae probably occurred during the Andean orogeny; the dispersal of the group into Central America is a Late Tertiary phenomenon (Savage, 1966). The Bufonidae may represent a paedomorphic offshoot of the Telmatobiinae rather than the Myobatrachinae. The heavy, frequently dermostosed skulls and thick, dry-adapted skin of bufonids suggest that this group evolved in response to decreasing equability. The antiquity of the group is not directly known, but the earliest fossils are Lower Miocene (North America and Europe). The most primitive genus is African (Tihen, 1960a), but the remainder of the genera are derived from the widespread Bufo. Among its derivatives are seven Neotropical, seven African, and five Malaysian and Philippine genera. Bufo ranges



over all continents except Australia and Antarctica. The Bufonidae probably originated in Africa and South America when the two continents were connected. The early evolution and dispersal of the Bufonidae is considered syntopic with that of the Pipidae and characoid fishes. The Gymnophiona exhibit a distribution and radiation pattern which is similar to that of the Bufonidae except that there is no caecilian genus which ranges over the Holarctic. The evidence suggesting that the Bufonidae represent an offshoot of the Myobatrachinae is meager. The mouthparts of the tadpoles of the two groups are similar. It is possible that the Bufonidae are a paedomorphic myobatrachine offshoot that invaded South America synchronously with the Telmatobiinae. If Antarctica was under a temperature regime of increasingly lower equability while Australia was under one of higher equability, it is conceivable that a low-equability adapted myobatrachine group evolved in Antarctica and dispersed into South America before the South America-Antarctica land bridge was obliterated in the Cretaceous. One serious objection to this hypothesis is the absence of any high-equability adapted bufonid genera in South America. Rhinoderma is a high-equability adapted genus and is related to the Bufonidae. The Rhinodermatidae may represent this high-equability adapted proto-bufonid. The bufonid genus Melanophryniscus lives in areas of

relatively high equability in northern Argentina and Uruguay but does not range southward into the zone of very high equability (58+). A further difficulty with the hypothesis is the requirement of a low-equability corridor through the high equability zone which presumably covered all of Patagonia during the Late Cretaceous and subsequent Tertiary. A more thorough study of Rhinoderma may prove to be the key in ascertaining the relationships of the Bufonidae to the Australo-Papuan or southern South American leptodactylids.

## SUMMARY AND CONCLUSIONS

Based on the variation of behavioral and morphological characters, 57 Recent and three fossil genera of the Leptodactylidae are recognized. These 60 genera are placed in seven subfamilies, two of which are further subdivided into tribes. Two of the subfamilies (Cyclorantinae and Myobatrachinae) occur only in the Australo-Papuan region, one (Heleophryinae) in southern Africa, and four (Ceratophryinae, Elosiinae, Leptodactylinae, and Telmatobiinae) in the Neotropical realm.

The fossil record of leptodactylid frogs is of little value in deducing macrosystematic phylogeny. Fossils are represented in the Pleistocene of North America, the West Indies, and South America. Fossils of three phyletic lines are preserved in Lower Eocene to Pliocene deposits of Patagonia. All of the above-mentioned fossils are members of genera living in the same regions today or are closely related, extinct genera. The only zoogeographically important fossil is the Lower Eocene Indobatrachus, a myobatrachine from peninsular India. The subfamily Myobatrachinae is presently restricted to the Australo-Papuan region.

In order to determine the evolutionary direction (primitive to advanced) of several evolutionary trends, the following reasoning was used: character states shared by some or all archaic frog families and the other

lissamphibian orders are primitive in the Anura; character states shared by most archaic frogs and most pelobatids are primitive in the Anura; and character states which are rare in the archaic families but always evident in the Pelobatidae are primitive in the pelobatid-bufonoid superfamily complex and may be primitive in all frogs. This analysis resulted in the conclusion that the following character complexes are useful in ascertaining the relative primitiveness of frog groups: (1) type of cervical cotylar arrangement and type of occipital condylar arrangement; (2) neural arches--imbricate or not; (3) relative lengths of transverse processes of presacral vertebrae; (4) extent of dilation of sacral diapophyses; (5) presence of zygapophyses involved in sacral-coccygeal articulation; (6) separation of intervertebral discs from the centra; (7) complexity of the ilium; (8) loss of skull bones and teeth; (9) modifications of phalangeal formulae; (10) shape of pupil; (11) presence of outer metatarsal tubercles; (12) amplexic position; (13) egg size, oviposition site, larval development; (14) tadpole vent position; (15) tooth row formula of tadpole; and (16) architecture of pectoral girdle.

The Megophryinae (Pelobatidae) gave rise to four principle groups: (1) the Pelobatinae, (2) the Heleophryinae, (3) the Cyclorantinae, and (4) the Myobatrachinae. Each of these groups appears to be an independent derivative.

All of the Neotropical leptodactylids are probably descendants of one invasion of a cycloranine stock into South America. The Ceratophryinae and Telmatobiini are the most primitive Neotropical groups. The major leptodactylid radiation occurred within South America and radiated out of southern South America. One primitive tribe of the Telmatobiini (Alsodini) gave rise to the advanced tribes of the subfamily (Grypiscini and Eleutherodactylini) as well as to two additional subfamilies (Elosiinae and Leptodactylinae). The Dendrobatidae are a derivative of the Elosiinae. The Telmatobiini and Odontophrynini are two tribes of the Telmatobiinae which appear to be the most primitive.

The evolution of leptodactylids is best explained on a superstructure involving continental drift. The following paleozoogeographic sequence is proposed: the basal stock, the Megophryinae, originated on northern landmasses from an ascaphid-discoglossid ancestor and dispersed southward in the Middle Mesozoic. A single dispersal corridor was utilized, the area in east Africa to the west of the East African Gulf of Tethys Sea. The megophryine stock could not invade South America because of the lack of a lowland corridor between North and South America or between Africa and the Brazilian shield. The stock passed through south Africa onto the southern landmass composed of peninsular India, Australia, and part of Antarctica. Progressive southerly extension

of the East African Gulf isolated the derived group on India, Australia, and coastal Antarctica. During the Late Jurassic or early Cretaceous, a cycloranine stock dispersed along the coast of Antarctica into southern South America. Concurrently, climatic zonation and the ensuing decrease in climatic equability were bringing about the extinction of many groups of plants and animals. In the northern hemisphere, the Megophryinae gave rise to a low-equability adapted group, the Pelobatinae, and were restricted in distribution to a high-equability zone in southeast Asia. Lowering equability resulted in the isolation of the African megophryine derivative in the high-equability refugium in south Africa. This group is the Heleophryinae. The effect of decreasing equability in Australia was minor. The Cyclorantinae evolved a low-equability tolerant group, the Limnodynastini. Decreasing equabilities with the northward movement of peninsular India during the Cretaceous and Tertiary resulted in the extinction of the myobatrachines living there. In South America, the more primitive leptodactylid genera survive in the area of high equability (often termed temperate South America). Decreasing equability resulted in the evolution of a low-equability adapted group, the Leptodactylinae. The Ceratophryinae and Odontophrynini are arid-adapted frogs and were therefore able to invade the low-equability areas which were arid

or semi-arid. Decreasing equabilities probably initially led to range restrictions which resulted in the isolation of the Elosiinae and Grypiscini in southeastern Brasil (a high-equability zone). The Dendrobatidae are low-equability adapted frogs which evolved from the high-equability adapted Elosiinae. The African ranids of the subfamily Petropedetinae are usually cited as ranids with adaptations paralleling the Neotropical dendrobatids. I have studied briefly the anatomy of Petropedetes and find the similarity to dendrobatids striking. The two family groups may represent remnants of a group once ranging across the South American-African isthmus. However, before the relationship can be established, more study of the ranids needs to be made.

In the course of this study, many taxonomic changes have been proposed. These are summarized below.

1. Geobatrachus Ruthven is removed from the Leptodactylidae and tentatively assigned to the Microhylidae, pending completion of a study of the systematic position of the genus by Dr. Charles F. Walker.

2. Hyloopsis platycephalus Werner is a species of the Hylidae and perhaps not separable from Hyla.

3. Rhinoderma is placed in a monotypic family, the Rhinodermatidae.

4. The subfamily Cyclorantinae is recognized for 10 genera. The subfamily is divided into two tribes:

Cycloranini (Cyclorana, Heleioporus, Neobatrachus, and Notaden) and Limnodynastini new tribe (Adelotus, Kyarranus, Lechriodus, Limnodynastes, and Philoria).

5. The subfamily Myobatrachinae is recognized for one fossil and seven Recent genera (Orinia, Glauertia, Indobatrachus, Metacrinia, Myobatrachus, Pseudophryne, Taudactylus, and Uperoleia).

6. Glauertia mjoebergi is transferred to the genus Uperoleia.

7. Taudactylus diurnus is identical to Orinia acutirostris; the genus Taudactylus is worthy of recognition but the only species in the genus must now be called T. acutirostris.

8. The subfamily Heleophryninae is recognized for the African leptodactylid, Heleophryne. The opinions of some earlier authors that Heleophryne is a ranid or the only genus of a monotypic ranoid family are rejected. The subfamily is similar to megophryine pelobatids but has achieved the leptodactylid grade.

9. The subfamily Ceratophryinae is recognized for two Recent genera (Ceratophrys and Lepidobatrachus). The group is not sufficiently different to be accorded family rank and is not more closely related to the Bufonidae than to other leptodactylids.

10. Chacophrys is considered a synonym of Ceratophrys.

11. Stomabus Gravenhorst, 1825, is a synonym of



Ceratophrys Wied, 1824; Rana cornuta Linné is designated the type-species of Stombus.

12. The Miocene fossil Wawelia gerholdi is a ceratophryine but is not separable from either Ceratophrys or Lepidobatrachus and is therefore tentatively recognized.

13. The subfamily Telmatobiinae is recognized for one fossil and 24 Recent genera of Neotropical leptodactylids. The following family group names are considered synonymous with the Telmatobiinae: Hylodidae Günther, 1859, Alsodina Mivart, 1869, Cacotina Mivart, 1869, Grypiscina Mivart, 1869, Cyclorhamphinae Lutz, 1954, Eleutherodactylinae Lutz, 1954, Calyptocephalellinae Reig, 1960, and Batrachylinae Gallardo, 1965. The subfamily is divided into five tribes: Telmatobiini (Batrachophrynus, Caudiverbera, Neoprocoela, Telmatobius, and Telmatobufo), Alsodini (Batrachyla, Eupsophus, Hylorina, and Thoropa), Odontophrynini new tribe (Odontophrynus and Proceratophrys), Grypiscini (Crossodactylodes, Cycloramphus, and Zachaenus), and Eleutherodactylini (Amblyphrynus, Eleutherodactylus, Euparkerella, Holoaden, Hylactophryne, Ischnocnema, Niceforonia, Sminthillus, Syrrophus, and Tomodactylus). A new genus, Scythrophrys, is named for Zachaenus sawayae Cochran but cannot be confidently assigned to a tribe until osteological data are available.

14. The generic name Caudiverbera is used in preference to Calyptocephalella. Eophractus Schaeffer is placed

in the synonymy of Caudiverbera. Gigantobatrachus parodii (Miocene of Patagonia) and Calyptocephalella canqueli (Oligocene of Patagonia) are placed in the synonymy of Caudiverbera caudiverbera.

15. Neoprocoela is not a synonym of Bufo and is recognized as a genus of leptodactylid frogs which is ancestral to Batrachophrynus.

16. Telmatobufo is not a synonym of Aruncus; Aruncus is a synonym of Bufo.

17. Macrogenioglottus is placed in the synonymy of Odontophrynus.

18. Proceratophrys is the valid generic name for the supraspecific group frequently called Stombus.

19. Craspedoglossa is considered a synonym of Zachaenus.

20. Zachaenus roseus Cope is not a member of the genus Zachaenus and is considered a species inquirenda in the Leptodactylidae, probably in the Telmatobiinae.

21. Noblella is placed in the synonymy of Eleutherodactylus.

22. Pseudohyla, previously considered a hylid genus or a synonym of Hyla, is a synonym of Eleutherodactylus.

23. Eupsophus wettsteini is transferred to the genus Niceforonia.

24. Syrrhophus laplacai is probably a member of the genus Niceforonia.

25. Syrrhophus is not a synonym of Eleutherodactylus, but the separation of Syrrhophus and Tomodactylus is considered tenuous.

26. The subfamily Elosiinae is recognized for three Recent genera (Crossodactylus, Hylodes, and Megaelosia). Hylodes Fitzinger is used in preference to Elosia Tschudi.

27. The subfamily Leptodactylinae is recognized for ten Neotropical genera (Barycholos, Edalorbina, Hydrolaetare, Leptodactylus, Limnomedusa, Lithodytes, Paratelmatoobius, Physalaemus, Pleurodema, and Pseudopaludicola).

28. Paratelmatoobius pictiventris A. Lutz, in Lutz and Carvalho, is a nomen nudum and an obligate synonym of Paratelmatoobius gaiseae (Cochran).

29. Pseudopaludicola boliviana Parker is considered a synonym of P. pusilla (Ruthven).

30. Leptodactylus abavus Holman (Lower Miocene of Florida) is a Rana and questionably separable from Rana miocenica Holman of the same horizon and locality.

31. Eorubeta nevadensis Hecht (Lower Eocene of Nevada) is not a leptodactylid and is considered "Family incertae sedis, Order Salientia".

32. The following new taxa are proposed:  
Limnodynastini new tribe, Odontophrynini new tribe,  
and Scythrophrys new genus (type-species Zachaenus sawayae Cochran, 1953).

## APPENDIX

The following is an alphabetical list of the species and specimens used in formulating the generic accounts for the Leptodactylidae. In addition to the museum abbreviations listed on page 33, the following abbreviations (and the name of the institution) are used below:

CAS	California Academy of Science
LHUBA	Laboratorio Herpetologica Universidad Buenos Aires
MCZ	Museum of Comparative Zoology
NMW	Naturhistorisches Museum zu Wien
WAM	Western Australia Museum

Unless otherwise noted, the specimens listed below are dry skeletons. Specimens which were cleared and stained are indicated by "CS"; those which were studied with stereoradiographs are indicated by "SRG".

Adelotus brevis.-- AMNH 59489-90, KU 56242.

Amblyphrynus ingeri.-- FMNH 54591 (SRG).

Barycholos pulcher.-- UMMZ S-2881 (CS).

Batrachophrynus macrostomus.-- KU 98127-28.

Batrachyla leptopus.-- UMMZ S-2246 (CS).

Batrachyla taeniata.-- UMMZ S-2247 (CS).

Caudiverbera caudiverbera.-- AMNH 23622, 23958, 24016, 51510, FMNH 9703.

Ceratophrys aurita.-- EMT 1415, FMNH 51703-04, KU 98129.

Ceratophrys calcarata.-- KU 69844, JDL S-76, 237-40,  
1189.

Ceratophrys ornata.-- UMMZ 98334 (tadpole, CS),  
109753 (juvenile, CS).

Crinia signifera.-- AMNH 40291, KU 56243-49 (CS),  
56364 (CS).

Crossodactylodes pinto.-- USNM 102611 (CS).

Crossodactylus dispar.-- KU 92753 (CS).

Crossodactylus saudichaudi.-- KU 92759 (CS),  
JDL S-265, 283-84, 417-19.

Crossodactylus grandis.-- KU 92765 (CS).

Cycloramphus asper.-- KU 92773.

Cycloramphus dubius.-- KU 92780.

Cycloramphus eleutherodactylus.-- KU 92785.

Cycloramphus fuliginosus.-- KU 92790-91.

Cycloramphus granulatus.-- KU 92795 (CS).

Cycloramphus ohausi.-- KU 92801 (CS).

Cycloramphus pinderi.-- KU 92807.

Cyclorana australis.-- AMNH 62228, KU 93549 (CS),  
93550.

Cyclorana cultripes.-- AMNH 67232 (CS), KU 110324.

Cyclorana dahli.-- UMMZ 65250.

Cyclorana platycephalus.-- KU 110329.

Edalorhina perez.-- AMNH 52847, KU 124225 (CS),  
124226.

Eleutherodactylus abbotti.-- AS X1795 (CS), X2006 (CS).

Eleutherodactylus achatinus.-- KU 119472 (CS).

Eleutherodactylus antillensis.-- AS 12083 (CS),  
12104 (CS).

Eleutherodactylus areolatus.-- KU 118129 (CS),  
119501 (CS).

Eleutherodactylus armstrongi.-- KU 110347 (CS),  
JDL S-236.

Eleutherodactylus atkinsi.-- AS V6263 (CS).

Eleutherodactylus audanti.-- JDL S-235.

Eleutherodactylus auriculatoides.-- AS X9200 (CS).

Eleutherodactylus barlagnei.-- MCZ 35331.

Eleutherodactylus binotatus.-- KU 92813 (CS).

Eleutherodactylus biporcatus.-- KU 41047, 105903.

Eleutherodactylus bogotensis.-- KU 110408-09 (CS).

Eleutherodactylus bransfordi.-- KU 25217, 41032,  
103036-41 (CS), JDL S-243, 401.

Eleutherodactylus brederi.-- KU 77670 (CS).

Eleutherodactylus brevicrus.-- KU 108982 (CS).

Eleutherodactylus bufoniformis.-- KU 80621.

Eleutherodactylus caryophyllaceus.-- KU 68261 (CS).

Eleutherodactylus cerasinus.-- KU 103026-27 (CS).

Eleutherodactylus chloronotus.-- KU 118130-33 (CS),  
JDL S-247, 260, 335.

Eleutherodactylus cochranæ.-- AS V8014 (CS).

Eleutherodactylus conspicillatus.-- KU 108988 (CS).

Eleutherodactylus coqui.-- KU 79924 (CS), 79947-50 (CS).

Eleutherodactylus crassidigitatus.-- KU 68262 (CS).

Eleutherodactylus croceoinguinis.-- KU 109086 (CS).

Eleutherodactylus cruentus.-- KU 102998 (CS),

107941-41 (CS), 117353-54.

Eleutherodactylus cundalli.-- AS 15128 (CS), 15711 (CS).

Eleutherodactylus curtipes.-- KU 109052-58 (CS),

JDL S-252-54, 261, 310, 337-38, 342-43, 351, 402, 430-31.

Eleutherodactylus devillei.-- UIMNH 55833 (CS).

Eleutherodactylus diastema.-- KU 41033-35, 68263 (CS),

80636 (CS), JDL S-244, 441.

Eleutherodactylus eneidae.-- AS 12637 (CS), 12758 (CS).

Eleutherodactylus encyrtomenum.-- KU 102999-3007 (CS),

117355-57.

Eleutherodactylus fitzingeri.-- KU 77658, 117358-62,

JDL S-407-08.

Eleutherodactylus flavomaculatus.-- KU 119743 (CS).

Eleutherodactylus fleischmanni.-- KU 65790 (CS),

68157-58, 68264-65 (CS).

Eleutherodactylus florulentus.-- KU 102242-46 (CS).

Eleutherodactylus frater.-- KU 80637 (CS).

Eleutherodactylus furcyensis.-- AS X2018 (CS).

Eleutherodactylus gageae.-- KU 106297-98 (CS).

Eleutherodactylus galdi.-- USNM GOV 8944 (CS).

Eleutherodactylus kollmeri.-- KU 41036-37.

Eleutherodactylus gossei.-- AS 13795 (CS), 14464 (CS),

15677 (CS).

- Eleutherodactylus zuentheri.-- KU 92819 (CS).  
Eleutherodactylus haitianus.-- AS X8296 (CS).  
Eleutherodactylus inoptatus.-- AS X2356.  
Eleutherodactylus juxans.-- MCZ 19856 (2) (CS).  
Eleutherodactylus karlschmidti.-- AS 12760 (CS).  
Eleutherodactylus lentus.-- AS V7395 (CS).  
Eleutherodactylus locustus.-- AS 11867 (CS), 11881 (CS).  
Eleutherodactylus longirostris.-- KU 77671 (CS).  
Eleutherodactylus macdougalli.-- UIMNH 40941 (CS).  
Eleutherodactylus martinicensis.-- MCZ 35321.  
Eleutherodactylus melanostictus.-- KU 107943 (CS).  
Eleutherodactylus mexicanus.-- KU 55592-95 (CS),  
55596-98, 55599-600 (CS), 55622, 103008-15 (CS), JDL S-1261-62.  
Eleutherodactylus minutus.-- AS X8939 (CS).  
Eleutherodactylus molinoi.-- KU 80635 (CS).  
Eleutherodactylus montanus.-- AS X8313 (CS), X8479 (CS).  
Eleutherodactylus nasutus.-- KU 92822 (CS).  
Eleutherodactylus nigriventris.-- KU 92739 (CS).  
Eleutherodactylus nigrovittatus.-- USNM GOV 8108 (CS).  
Eleutherodactylus nubicola.-- AS 12891 (CS), 12898 (CS).  
Eleutherodactylus occidentalis.-- KU 102598 (CS),  
104101 (CS).  
Eleutherodactylus octavioi.-- KU 92828 (CS).  
Eleutherodactylus orcutti.-- AS 13373 (CS).  
Eleutherodactylus ornatissimus.-- KU 119749 (CS).  
Eleutherodactylus palmatus.-- KU 41038.



Eleutherodactylus palmeri.-- KU 110913 (CS), 110923 (CS), JDL S-242, 397.

Eleutherodactylus pantoni.-- AS 13494 (CS), 13747 (CS).

Eleutherodactylus parvus.-- KU 92834 (CS).

Eleutherodactylus patriciae.-- KU 79770-71 (CS), 79794 (CS).

Eleutherodactylus peruvianus.-- (paratype of Sminthillus peruvianus) AMNH not catalogued (CS).

Eleutherodactylus pictissimus.-- AS X2750 (CS), X2813 (CS).

Eleutherodactylus planirostris.-- KU 92656 (CS), JDL S-230, 245, 1068.

Eleutherodactylus podociferus.-- KU 41049, 68266 (CS), 80644 (CS), 103017-24 (CS).

Eleutherodactylus portoricensis.-- AS 11710 (CS).

Eleutherodactylus punctariolus.-- KU 117363.

Eleutherodactylus pygmaeus.-- KU 103025 (CS), JDL S-15, 25, 1311, UIMNH 15141 (CS), 16132 (CS), 40335 (CS), 49268 (CS), 49275 (CS).

Eleutherodactylus rhodopis.-- UIMNH 14729 (CS), 47996 (CS), 49192 (CS), 49194 (CS), 49211 (CS).

Eleutherodactylus richmondi.-- AS 12623 (CS).

Eleutherodactylus ricordi.-- AMNH 63439 (CS), 63450 (CS).

Eleutherodactylus ridens.-- KU 102996-97 (CS).

Eleutherodactylus rugulosus.-- KU 59877-79, 84891,

JDL S-17, 67, 1006, 1238-51, UIMNH 14756 (CS).

Eleutherodactylus ruthae.-- AS V4237 (CS).

Eleutherodactylus spatulatus.-- KU 87781 (CS).

Eleutherodactylus sulcatus.-- KU 100355,  
124227 (CS).

Eleutherodactylus surdus.-- JDL S-268, 357-58, 360.

Eleutherodactylus talamancae.-- KU 68267-68 (CS),  
117364.

Eleutherodactylus trepidotus.-- KU 118134-35 (CS),  
UIMNH 55874 (CS).

Eleutherodactylus unistrigatus.-- KU 111136-37 (CS),  
JDL S-263, 269, 332, 340, 392-95, 530-31.

Eleutherodactylus variabilis.-- KU 109094 (CS).

Eleutherodactylus venancioi.-- KU 92839 (CS).

Eleutherodactylus weinlandi.-- AS V1718 (CS),  
V2466 (CS).

Eleutherodactylus whympersi.-- JDL S- 248-51, 270,  
446.

Eleutherodactylus wighmanae.-- AS 12704 (CS),  
12739 (CS).

Eleutherodactylus w-nigrum.-- KU 119857 (CS).

Eleutherodactylus zugii.-- AMNH 63269-70 (CS).

Euparkerella brasiliensis.-- KU 93192 (CS).

Eupsochus juninensis.-- MCZ 24360 (CS).

Eupsochus roseus.-- AMNH 22104, KU 84731 (CS).

Glauertia russelli.-- WAM R22920 (CS).

Heleioporus albopunctatus.-- UMMZ not catalogued.

Heleioporus australiacus.-- AMNH 59491.

Heleioporus eyeri.-- UMMZ 124504.

Heleophryne natalensis.-- KU 105925 (CS).

Holoaden bradei.-- KU 92868 (CS), 107087-88 (CS).

Hydrolaetare schmidti.-- KU 110613.

Hylactophryne augusti.-- KU 56187, 56192 (CS), UMMZ

S-2695.

Hylodes aspera.-- KU 92870 (CS), 92875.

Hylodes lateristrigata.-- KU 92878 (CS).

Hylodes magalhaesi.-- KU 92887 (CS).

Hylodes nasus.-- KU 74209 (CS), 92893-94, JDL

S- 255-56, 258, 282.

Hylodes pulcher.-- KU 92899 (CS), 92900.

Hylorina sylvatica.-- FMNH 7102 (SRG), 7107 (SRG).

Ischnocnema quixensis.-- KU 104388, UIMNH 59643 (CS).

Kyarranus sohagnicola.-- AMNH 64294, KU 110331 (CS).

Lechriodus fletcheri.-- AMNH 59488, OAS 82221 (CS).

Lepidobatrachus asper.-- KU 80783.

Leptodactylus albilabris.-- UMMZ S-166.

Leptodactylus bolivianus.-- KU 41026.

Leptodactylus bufonius.-- KU 92905.

Leptodactylus chaguensis.-- KU 80795.

Leptodactylus gracilis.-- KU 92913-14.

Leptodactylus hylaedactylus.-- KU 119387-88 (CS).

Leptodactylus labialis.-- KU 41027, 68273-74 (CS).

Leptodactylus macrosternus.-- KU 92919-20.

Leptodactylus melanonotus.-- KU 68275-76 (CS), JDL  
S- 1252-58, UMMZ S-858, 1045.

Leptodactylus mystaceus.-- KU 92932.

Leptodactylus mystacinus.-- KU 92925-26.

Leptodactylus pentadactylus.-- KU 41028-29, 68159,  
84981-82, 117366-68.

Leptodactylus podicipinus.-- KU 92938.

Leptodactylus prognathus.-- KU 80824 (CS), 92944.

Leptodactylus pustulosus.-- KU 92947.

Leptodactylus quadrivittatus.-- KU 41030.

Leptodactylus syphax.-- KU 92951.

Leptodactylus wagneri.-- KU 104389-90.

Limnodynastes dorsalis.-- KU 93553, UMMZ S-165.

Limnodynastes fletcheri.-- KU 93559 (CS).

Limnodynastes peronii.-- KU 93566 (CS).

Limnodynastes tasmanensis.-- AMNH 60589, KU  
93573-74 (CS).

Limnomedusa macroglossa.-- KU 92960 (CS), 92961.

Lithodytes lineatus.-- KU 104340 (CS).

Megaelosia goeldi.-- KU 92965-66, 106271.

Metacrinia nichollsi.-- KU 110332 (CS).

Mixophyes fasciolatus.-- KU 56627.

Myobatrachus gouldii.-- KU 110333 (CS).

Neobatrachus centralis.-- KU 93578.

Neobatrachus pictus.-- FMNH 97281, KU 69278 (CS).

Niceforonia festae.-- KU 118137 (CS), USNM 160944 (CS), 160950 (CS).

Niceforonia montia.-- MCZ 24352 (CS).

Niceforonia wettsteini (paratypes of Eupsophus wettsteini).-- MNW 15846:1-2 (SRG).

Notaden bennetti.-- FMNH 97658.

Notaden nichollsi.-- KU 93580 (CS), 93582 (CS).

Odontophrynus americanus.-- KU 92968, 100437.

Odontophrynus carvalhoi.-- KU 100441-42.

Odontophrynus cultripes.-- KU 92975.

Odontophrynus occidentalis.-- LHUBA 1200, 1218.

Paratelmatoebius lutzi.-- KU 92981 (CS), 107089 (CS).

Philoria frosti.-- KU 50699 (CS).

Physalaemus albonotatus.-- KU 92987 (CS).

Physalaemus biligonigerus.-- KU 84768-76.

Physalaemus centralis.-- KU 92993 (CS).

Physalaemus cuvieri.-- KU 92999 (CS).

Physalaemus ehippifer.-- KU 93005 (CS).

Physalaemus fuscomaculatus.-- KU 80811 (CS), 93010 (CS), URMZ S-2357 (CS).

Physalaemus gracilis.-- KU 93016 (CS).

Physalaemus maculiventris.-- KU 93022 (CS).

Physalaemus nanus.-- KU 93025 (CS).

Physalaemus nattereri.-- KU 92844 (CS), 92845.

Physalaemus petersi.-- KU 120290 (CS).

Physalaemus pustulatus.-- KU 118136 (CS).

- Physalaemus pustulosus.-- KU 41031, 68269-72 (CS),  
JDL S-1204.
- Physalaemus signiferus.-- KU 93033 (CS).
- Pleurodema bibroni.-- FMNH 3746-47, 3758.
- Pleurodema brachyops.-- AMNH 69754, KU 96159, 104318  
(CS), UIMNH WLB-725.(CS).
- Pleurodema cinerea.-- KU 80836, 93038.
- Pleurodema diplolistris.-- KU 93044 (CS), UMMZ  
108521 (CS), 108395 (6) (CS).
- Proceratophrys appendiculata.-- KU 93070.
- Proceratophrys boiei.-- KU 93076.
- Proceratophrys cristiceps.-- KU 106273, UMMZ 115658.
- Pseudopaludicola ameghini.-- KU 93050 (CS).
- Pseudopaludicola falcipes.-- KU 93056 (CS).
- Pseudopaludicola pusilla.-- UMMZ 54589(2) (CS);  
boliviana topotypes, UMMZ (2), not catalogued (CS).
- Pseudopaludicola saltica.-- KU 93068 (CS).
- Pseudophryne bibroni.-- KU 93588 (CS).
- Pseudophryne corroborae.-- AMNH 64510-12.
- Scythrophrys sawayae.-- USNM 125530 (holotype), not  
a skeletal preparation; some skeletal features were observed  
through slits in the skin.
- Sminthillus limbatus.-- KU 68684 (CS).
- Syrhophus guttilatus.-- JDL S-1215.
- Syrhophus leprus.-- JDL S-992, UIMNH 27130 (CS).
- Syrhophus marnockii.-- JDL S-214.

- Syrrhophus pallidus.-- KU 80320 (CS).
- Syrrhophus pipilans.-- KU 59950 (CS).
- Syrrhophus rubrimaculatus.-- UIMNH 55313-16 (CS).
- Taudactylus acutirostris.-- KU 124233 (CS).
- Telmatobius hauthali.-- KU 72879 (CS), UMMZ S-164.
- Telmatobius marmoratus.-- UMMZ 68179 (2).
- Telmatobius patagonicus.-- KU 80781 (CS).
- Telmatobufo bullocki.-- FMNH 23842 (SRG).
- Thoropa lutzi.-- KU 92850 (CS), 92908 (CS).
- Thoropa miliaris.-- KU 92855 (CS), 92856.
- Thoropa petropolitana.-- KU 92862 (CS).
- Tomodactylus albolabris.-- KU 87780 (CS).
- Tomodactylus grandis.-- UMMZ S-963.
- Tomodactylus nitidus.-- KU 102649 (CS), JDL S-1308,  
UIMNH 7830 (CS), 7832-34 (CS), UMMZ S-2225.
- Uperoleia rugosa.-- AMNH 13336, KU 109861 (CS).
- Zachaeus parvulus.-- KU 93082 (CS), 107090 (CS),  
107091.
- Zachaeus roseus.-- USNM 15126 (holotype).
- Zachaeus stejnegeri.-- KU 92742 (CS), 92747.

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Plate 1. Amplexing pairs of Pseudophryne australis (top) and Physalaemus pustulosus (bottom); the latter also illustrates a foam nest. Photo of Pseudophryne courtesy of John A. Moore; that of Physalaemus courtesy of William E. Duellman.



