

1999

# Chondrocranial and oral morphology of Leptodactylid larvae

William Hagood Turner

Follow this and additional works at: <https://scholarship.richmond.edu/masters-theses>



Part of the [Biology Commons](#)

---

## Recommended Citation

Turner, William Hagood, "Chondrocranial and oral morphology of Leptodactylid larvae" (1999). *Master's Theses*. 1349.  
<https://scholarship.richmond.edu/masters-theses/1349>

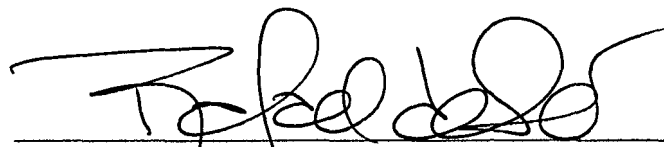
This Thesis is brought to you for free and open access by the Student Research at UR Scholarship Repository. It has been accepted for inclusion in Master's Theses by an authorized administrator of UR Scholarship Repository. For more information, please contact [scholarshiprepository@richmond.edu](mailto:scholarshiprepository@richmond.edu).

Chondrocranial and Oral Morphology of  
Leptodactylid Larvae

by

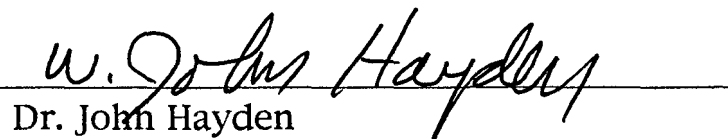
William H. Turner Jr.

I certify that I have read this thesis and find that, in scope and  
quality, it satisfies the requirements for the degree of Master of  
Science.



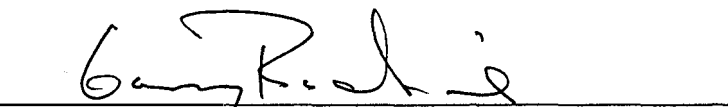
---

Dr. Rafael O. de Sá, Thesis Advisor



---

Dr. John Hayden



---

Dr. Gary Radice

Other Faculty Members:

|                       |
|-----------------------|
| Peter D. Smallwood    |
| Toni J. Krey          |
| John Reynolds         |
| Krista Fisher Stenger |
| John W. [Signature]   |
|                       |
|                       |
|                       |
|                       |

# CHONDROCRANIAL and Oral Morphology of Leptodactylid Larvae

William H. Turner Jr.

Masters of Science in Biology

University of Richmond, 1999

Thesis Director: Rafael O. de Sá

Abstract. Leptodactylidae is a diverse assemblage of anurans that varies in their life history, ecology, and morphology. Little is known about the chondrocranial anatomy of this family. Current knowledge of the evolutionary relationships of the family does not include chondrocranial data. The present paper focuses on understanding the larval chondrocranial morphology and internal oral anatomy of Leptodactylidae. Chondrocranial morphology and internal oral anatomy correlate with ecology and life history. A phylogenetic analysis of the family was executed based on 28 chondrocranial characters using *Hyla lanciformis* as the outgroup. The phylogenetic analysis resulted in two clades within Leptodactylidae: the Leptodactylinae-*Odontophrynus* clade and the Telmatobiinae-Hylodinae-Ceratophryinae clade. Analyses of chondrocranial and internal oral morphology can provide useful phylogenetic information for members of Leptodactylidae.

Chondrocranial and Oral Morphology of Leptodactylid Larvae

By

William H. Turner Jr.  
B.S., University of Richmond, 1997

A Thesis

Submitted to the Graduate<sup>†</sup> Faculty

of the University of Richmond

in Candidacy

for the degree of

MASTER OF SCIENCE

in

Biology

April, 1999

Richmond, Virginia

## Acknowledgements

I would not have been able to complete this degree were it not for the support, tutelage, and emotional backing of several people. I am indebted to Dr. Rafael O. de Sá for taking me into his lab, assisting me financially (NSF#BIR-9510228), guiding me mentally, and putting his foot down when he saw me straying from the academic path. I am grateful to the Graduate School of Arts and Sciences for providing me with research and travel grants, and academic scholarships. I am also grateful to Dr. John Hayden and Dr. Gary Radice who taught me scanning electron microscope procedures. I would like to thank the Biology department faculty, staff, and students, especially Chris Swart, who offered me many smiles and much encouragement.

None of this could have been possible without my mom, my brothers, my dogs, and the rest of my family and friends. I dedicate this work in memory of my father, William H. Turner Sr.; thanks for everything.

| Table of Contents  | page |
|--|------|
| List of Figures . . . . .  | i.   |
| List of Appendices . . . . .   | ii.  |
| Introduction . . . . .   | 1.   |
| Background on Chondrocranial Studies . . . . .   | 11.  |
| Background on Internal Oral Anatomy Studies. . . . .   | 15.  |
| Materials and Methods. . . . .   | 17.  |
| Results  |      |
| Chondrocranium of <i>Adenomera marmorata</i> . . . . .   | 22.  |
| Chondrocranium of <i>Edalorhina perezii</i> . . . . .  | 31.  |
| Chondrocranium of <i>Limnomedusa macroglossa</i> . . . . .   | 40.  |
| Chondrocranium of <i>Physalaemus gracilis</i> , <i>P. henselii</i> , and<br><i>P. pustulosus</i> . . . . . | 49.  |
| Chondrocranium of <i>Pleurodema brachyops</i> , <i>P. brachyops2</i> , and<br><i>P. tucumana</i> . . . . . | 59.  |
| Oral Morphology of <i>Limnomedusa macroglossa</i> . . . . .  | 68.  |
| Oral Morphology of <i>Physalaemus gracilis</i> . . . . .   | 74.  |
| Oral Morphology of <i>Physalaemus henselii</i> . . . . .   | 80.  |
| Larval Characters for phylogenetic analysis . . . . .  | 86.  |

|   | page |
|---|------|
| Discussion  |      |
| Chondrocranial Morphology and skeletogenesis. . . . . | 94.  |
| Internal Oral Anatomy. . . . .                        | 104. |
| Phylogenetic Analysis . . . . .                       | 105. |
| Literature cited . . . . .                            | 117. |
| Appendix . . . . .                                    | 139. |
| Vita . . . . .  | 142. |



| List of Figures:  | Page |
|---|------|
| Figure 1. Chondrocranium of <i>Adenomera marmorata</i> at stage 36 .  | 26.  |
| Figure 2. Chondrocranium of <i>Adenomera marmorata</i> at stage 36 .  | 28.  |
| Figure 3. Chondrocranium of <i>Edalorhina perezii</i> at stage 36 . .   | 34.  |
| Figure 4. Chondrocranium of <i>Edalorhina perezii</i> at stage 36 . .   | 36.  |
| Figure 5. Chondrocranium of <i>Limnomedusa macroglossa</i> at stage 34  | 44.  |
| Figure 6. Chondrocranium of <i>Limnomedusa macroglossa</i> at stage 34  | 46.  |
| Figure 7. Chondrocrania of <i>Physalaemus gracilis</i> at stage 40, <i>P. henselii</i><br>at stage 39, and <i>P. pustulosus</i> at stage 38 . . | 54.  |
| Figure 8. Chondrocrania of <i>Physalaemus gracilis</i> at stage 40, <i>P. henselii</i><br>at stage 39, and <i>P. pustulosus</i> at stage 38 . . | 56.  |
| Figure 9. Chondrocranium of <i>Pleurodema brachyops</i> at stage 35,<br><i>P. brachyops2</i> at stage 37, and <i>P. tucumana</i> at stage 35    | 63.  |
| Figure 10. Chondrocranium of <i>Pleurodema brachyops</i> at stage 35,<br><i>P. brachyops2</i> at stage 37, and <i>P. tucumana</i> at stage 35   | 65.  |
| Figure 11. Scanning electron microscope photograph of buccal floor of<br><i>Limnomedusa macroglossa</i> at stage 37 . . .                       | 71.  |
| Figure 12. Scanning electron microscope photograph of buccal roof of<br><i>Limnomedusa macroglossa</i> at stage 37 . . .                        | 73.  |

|  |      |
|--|------|
| Figure 13. Scanning electron microscope photograph of buccal floor of<br><i>Physalaemus gracilis</i> at stage 37 . . . . . | 77.  |
| Figure 14. Scanning electron microscope photograph of buccal roof of<br><i>Physalaemus gracilis</i> at stage 37 . . . . .  | 79.  |
| Figure 15. Scanning electron microscope photograph of buccal floor of<br><i>Physalaemus henselii</i> at stage 31 . . . . . | 83.  |
| Figure 16. Scanning electron microscope photograph of buccal roof of<br><i>Physalaemus henselii</i> at stage 31 . . . . .  | 85.  |
| Figure 17. Phylogenetic trees . . . . .  | 109. |
| Figure 18. Consensus trees . . . . .   | 113. |

LIST OF TABLES:

|   |      |
|---|------|
| Table 1. Data matrix of phylogenetic characters . . . . .   | 93.  |
| Table 2. Ossification sequence for the specimens of <i>Physalaemus</i><br><i>gracilis</i> and <i>P. pustulosus</i> used in this work. . . . . | 101. |

LIST OF APPENDICES:

|   |      |
|---|------|
| Appendix 1. Stages, measurements, and status of specimens used<br>in this work. . . . . | 139. |
|---|------|

## INTRODUCTION

The word amphibian comes from the Greek amphi, meaning “on both sides,” and bios, meaning “life” or “mode of life.” Anurans most accurately define the word amphibian because considering their larval and adult forms, they live a dual lifestyle, aquatic and terrestrial. These two stages of their life cycle are connected by an intricate metamorphic event that morphologically, ecologically, behaviorally, and physiologically transforms the tadpole into the adult frog (Orton, 1953). Any shift in the timing or rate of the metamorphic events would be an example of heterochrony, and heterochronic mechanisms have been shown to be driving forces in amphibian evolution (Gould, 1977; Wassersug, 1980; Trueb and Alberch, 1985; Davies, 1989; Richardson, 1995; Haas, 1996b; Wakahara, 1996). An increase in the ways anurans have diversified results from heterochronic mechanisms acting on the larval stage of the life cycle and selective pressures acting on both the larva and the adult.

The diversity of anurans is not reflected in their overall simple body plan (Sokol, 1975). Anurans have achieved high levels of

specialization yet the anatomical differences across frogs are subtle. This constancy of form presents a challenge to studies of anuran evolution and systematics. Consequently, a variety of data sets must be used to decipher anuran evolution (Duellman and Trueb, 1994; Kluge, 1989; Brooks and McLennan, 1991).

In fact, anuran research has expanded into a diverse field of study incorporating a variety of data sets. Osteological studies have been useful in diagnosing species and determining anuran relationships (Cope, 1865, 1889; Noble, 1922, 1931; Parker, 1927; Lynch, 1970, 1971; Trueb, 1973). More recently, many studies have included additional characters such as: karyotype (Barrio and Rinaldi de Chieri, 1970; Bogart, 1970; Veloso et al., 1973; Duellman and Veloso, 1977; King, 1990; Green and Sessions, 1991), behavior (Wells, 1977; Greer and Wells, 1980; Martins, 1989; Cardoso and Heyer, 1995), diet (Premo and Atmowidjojo, 1987; Toft, 1995; Kovács and Török, 1997; Howard et al., 1997), call analysis (Barrio, 1964; Duellman, 1973; Duellman and Veloso, 1977; Ryan and Rand, 1995), development (Wassersug and Hoff, 1982; Trueb and Hanken, 1992) and molecular data (Hillis and Davis, 1987; Maxson and

Heyer, 1988; de Sá and Hillis, 1990; Hillis et al., 1993; Hay et al., 1995; Ruvinsky and Maxson, 1996).

Anuran research has also focused on larval characters. Research on the structure of the head in anuran larvae and studies of their internal oral anatomy date back to the early 19<sup>th</sup> century (Martin St. Ange, 1831; Schulze, 1870, 1892). These initial studies are characterized by inconsistent terminology and varied thoroughness of their descriptions. De Beer (1937) summarized what was known about the development of the vertebrate skull through detailed descriptions and illustrations of four anuran taxa.

The use of larval characters in systematics began in the 1950s when a comparative study of tadpoles at similar stages of development was undertaken (Orton 1953, 1957). Orton (1957) grouped tadpoles into four major categories based on external morphology. Subsequently, Orton's data were combined with other larval characters such as larval musculature and chondrocranial data (Starrett, 1973; Sokol, 1975, 1977).

Larval chondrocranial descriptions exist for less than 5% of known species (Haas, 1996a). Few chondrocranial studies place

their results in a phylogenetic context (Sokol, 1977, 1981; de Sá and Trueb, 1991; Haas, 1995, 1996a, 1997). Furthermore, only recently has chondrocranial variation been analyzed in closely related species to understand its utility in phylogenetic studies (Larson and de Sá, 1998). Still, there is a lack of baseline comparative data that precludes the use of chondrocranial characters in anuran phylogenetics and systematics.

Another relatively recent systematic tool is the analysis of the characteristics of the internal oral anatomy of anuran larvae. Wassersug (1976) examined the oral morphology of species representing six anuran families. Detailed analyses, illustrations, and descriptions, showed the usefulness of these characters in species identification (Wassersug, 1980). Additionally, Wassersug and Heyer (1988) surveyed the internal oral anatomy of species from three anuran families and concluded that these characters are phylogenetically informative at both the generic and specific levels. However, the inclusion of internal oral characters in anuran phylogenetics and systematics is also hindered by a lack of baseline comparative intrageneric data.

The Leptodactylidae are placed in the superfamily Bufonoidea (Reig, 1958; Lynch, 1973, Duellman, 1975; Laurent, 1979, 1986; Ford and Cannatella, 1993). However, Bufonoidea lack synapomorphies uniting them and are grouped together because they lack characters that would place them in any other group (Ford and Cannatella, 1993).

The family Leptodactylidae is a strictly new world assemblage. Their distribution extends from Southern United States and the Antilles south to southern South America (Frost, 1985). Leptodactylidae is considered “grossly paraphyletic” (Ford, 1989). There are no synapomorphies defining the Leptodactylidae; in other words, the group is based on their lack of the characteristics that unite other Bufonoid families (Lynch, 1971; Ford and Cannatella, 1993).

The evolution of the family has hinged on the ability to adapt to forests, stream habitats, and increasingly xeric conditions correlated with continental drift (Lynch, 1971). The fossil history of the family dates to the Eocene of Argentina (*Caudiverbera casamayorensis*, Telmatobiinae) (Lynch, 1971). There is no fossil

record for any members of Hylodinae (Duellman and Trueb, 1994); yet, Ceratophryinae dates to the Miocene (Lynch, 1971), and Leptodactylinae dates to the Pleistocene (Heyer, 1979).

The family Leptodactylidae consists of 54 genera and over 840 species distributed into four subfamilies--Ceratophryinae, Hylodinae, Leptodactylinae, and Telmatobiinae (Frost, 1985; Duellman, 1993). Leptodactylidae has been the focus of extensive systematic and phylogenetic studies both intergenerically (Bogart, 1970; Lynch, 1971; Heyer, 1975) and intragenerically (Heyer, 1969a, 1970, 1973, 1974, 1977, 1978, 1979, 1984, 1994; Bogart, 1974; Duellman and Veloso, 1977; Heyer and Maxson, 1982; Lavilla, 1983, 1988; Cannatella and Duellman, 1984; Lobo, 1995; Cannatella et al., 1998; Larson and de Sá, 1998).

The systematic and phylogenetic reviews of Leptodactylidae have resulted in varied degrees of resolution (Boulenger, 1882; Lynch, 1971; Heyer, 1975, Hay et al., 1995; Ruvinsky and Maxson, 1996). Two of the four subfamilies, Hylodinae and Ceratophryinae, are well supported. However, results from the examination of adult and larval external morphology, myology, life history, behavior,



osteology, and cytogenetics of Telmatobiinae and Leptodactylinae are not as definitive (Lynch, 1969, 1971; Barrio, 1971; Barrio and Rinaldi de Chieri, 1971; Formas, 1975, 1976; Heyer, 1975; Lavilla, 1983, 1988).

The members of the subfamily Leptodactylinae are prime candidates for larval evolutionary study because they represent the extremes in reproductive biology; some species are completely aquatic while others are completely terrestrial (Heyer, 1969b; Langone and Prigioni, 1985; De la Riva, 1995). The existing diversity of reproductive modes would be expected to have a direct effect on tadpole diversity. Furthermore, morphological differences that correlate with different larval ecologies could reveal taxonomic information on the group.

Leptodactylinae is divided into 11 genera (*Adenomera*, *Edalorhina*, *Hydrolaetare*, *Leptodactylus*, *Limnomedusa*, *Lithodytes*, *Paratelmatus*, *Physalaemus*, *Pleurodema*, *Pseudopaludicola*, and *Vanzolinius*) and over 120 species (Frost, 1985; Duellman, 1993). Four of these genera are monotypic, and the larvae of some are only

known from a few specimens or not at all (Frost, 1985; Heyer, pers. comm.).

Leptodactylinae has been defined by the presence of an osseous sternal plate although this character is not a synapomorphy for the group (Noble, 1931; Lynch, 1971). Lynch (1971) suggested a close relationship between *Physalaemus* and *Pseudopaludicola*, Heyer (1974) supported this conclusion. Alternate arrangements have been proposed for *Paratelmatoebius* and *Limnomedusa*, the latter of these being the most controversial (Heyer, 1975; Lynch, 1978).

Heyer (1975) suggested that *Edalorhina* and *Pseudopaludicola* are sister taxa. *Limnomedusa* and *Hydrolaetare* also formed a sister clade within Leptodactylinae. Furthermore, the clade comprised of *Adenomera*, *Leptodactylus*, *Lithodytes* and *Vanzolinius* was consistent with Heyer's arrangement (Heyer, 1974). Although it shared a majority of characters with *Physalaemus*, *Pleurodema* presented confusing results in its relationships with the rest of Leptodactylinae (Heyer, 1975).

Heyer (1975) excluded *Paratelmatobius* from Leptodactylinae. Instead, he suggested that *Paratelmatobius* should be included in a clade with *Cycloramphus*, *Crossodactylus*, and *Hylodes* (Heyer, 1975). The latter share a large number of derived character states and were sister taxa in Heyer's (1975) study. Another highly derived clade corresponded to the carnivorous *Ceratophrys* and *Lepidobatrachus* (Heyer, 1975).

The relationships of *Limnomedusa* are controversial. Barrio (1971) and Barrio and Rinaldi de Chieri (1971) showed that *Limnomedusa* possess  $2n = 26$ , departing from the standard 22 chromosome number for Leptodactylinae, and based on these data they suggested that *Limnomedusa* is a telmatobiine. However, Bogart (1973) showed that *Adenomera* also diverges in chromosome number ( $2n = 26$ ). Lynch (1978) used *Limnomedusa* and *Pleurodema* as outgroups in an osteological study of Telmatobiinae. *Limnomedusa* and *Pleurodema* did not group together in his analysis, and consequently, he suggested that *Limnomedusa* should be assigned to the Telmatobiinae (Lynch, 1978). Neither Frost (1985) nor Duellman (1993) accepted Lynch's (1978) arrangement.

However, Lavilla (1985, 1988), Langone and Prigioni (1985), and Lavilla and Scrocchi (1986) did recognize that arrangement.

These examples illustrate the ongoing debate over the systematics of Telmatobiinae and Leptodactylinae and the need for further analysis utilizing new characters.

I focused my research on Leptodactylidae in order to determine the usefulness of chondrocranial and internal oral characters in systematic and phylogenetic studies of this anuran family. To achieve this goal, I examined the chondrocrania of eight species of the Leptodactylinae: *Adenomera marmorata*, *Edalorhina perezii*, *Limnomedusa macroglossa*, *Physalaemus gracilis*, *P. henselii*, *P. pustulosus*, *Pleurodema brachyops*, and *P. tucumana*. Furthermore, I analyzed and described the internal oral anatomy of *Physalaemus gracilis*, *P. henselii*, and *Limnomedusa macroglossa* and the skeletogenesis of *P. gracilis* and *P. pustulosus*. Subsequently, I integrated these data with all available data on the larval chondrocrania and internal oral anatomy of the family Leptodactylidae.

## BACKGROUND ON CHONDROCRANIAL STUDIES

Within the Leptodactylidae, the larval chondrocrania have been reported for the following 39 taxa: *Caudiverbera caudiverbera* (Reinbach, 1939), *Lepidobatrachus laevis* (Ruibal and Thomas, 1988), *Cycloramphus stejnegeri* (Lavilla, 1991), *Alsodes barrioi* (Lavilla, 1992), *Lepidobatrachus llanensis*, *Ceratophrys cranwelli* (Lavilla and Fabrezi, 1992), *Telmatobius ceiorum*, *T. laticeps*, *T. pisanoi* (Fabrezi and Lavilla, 1993), *T. bolivianus* (Lavilla and De la Riva, 1993), *Odontophrynus americanus*, *O. lavillai*, *Physalaemus biligonigerus*, *P. cuqui*, *Pleurodema borellii*, *P. tucumana* (Fabrezi and Vera, 1997), *Ceratophrys cornuta* (Wild, 1997) and 22 species of *Leptodactylus* (Fabrezi and Vera, 1997; Larson and de Sá, 1998). Additionally, osteological development within Leptodactylidae has only been reported for *Ceratophrys cornuta* (Wild, 1997).

There are no chondrocranial synapomorphies uniting the Leptodactylidae. However, Lavilla and Fabrezi (1992) suggested two synapomorphies for the Ceratophryinae: (1) fused suprarostrals with no distinction between each corpus and ala and (2) fused infrarostrals. Data on other ceratophryine species support these

synapomorphies (Ruibal and Thomas, 1988; Wild, 1997). The chondrocrania of all Ceratophryinae described so far lack the following characters: a commissura quadratoorbitalis, a processus pseudopterygoideus, spiculae, and a processus branchialis (Ruibal and Thomas, 1988; Lavilla and Fabrezi, 1992, Wild, 1997).

The chondrocrania of eight species representing five genera of Telmatobiinae have been described (Reinbach, 1939; Lavilla, 1991, 1992; Fabrezi and Lavilla, 1993; Lavilla and De la Riva, 1993; Fabrezi and Vera, 1997). *Caudiverbera caudiverbera* has a commissura quadratoorbitalis, commissura quadratoethmoidalis, processus lateralis trabeculae, and a well-developed crista parotica, which bears a processus anterolateralis and processus posterolateralis. The cornua trabeculae of *C. caudiverbera* are equal to about 12% of the total chondrocranial length.

*Telmatobius* larvae are characterized by unfused suprarostrals and corpora. In addition, members of this genus lack both a commissura quadratoorbitalis and a closed processus branchialis. The posterior curvature of the palatoquadrate in these species extends past the anterior margin of the capsulae auditivae. The

processus ascendens has an intermediate attachment to the braincase in *Telmatobius pisanoi* and *T. bolivianus*, and a low attachment in *T. ceiorum* and *T. laticeps* (Sokol, 1981).

Furthermore, a well-developed processus urobranchialis and two parietal fenestrae are present in the chondrocrania of *Telmatobius*. (Fabrezi and Lavilla, 1993; Lavilla and De la Riva, 1993).

Lavilla (1991) described the chondrocrania of *Cycloramphus stejneri*. This species also lacks a commissura quadratoorbitalis and a closed processus branchialis. However, the processus ascendens has a high attachment to braincase. Additionally, the chondrocranium of *C. stejneri* exhibits fused infrarostrals, ventral fusion of the suprarostrals corpus and ala, an undivided frontoparietal fontanelle, and extreme reduction of both the cornua trabeculae and the processus muscularis quadrati (Lavilla, 1991).

The chondrocrania of two *Odontophrynus* have been described, *O. americanus* and *O. lavillai*. The presence of a commissura quadratoorbitalis, a processus pseudopterygoideus, an open processus branchialis, and an undivided frontoparietal fontanelle characterize *Odontophrynus* larvae. Moreover, the

suprarostrals and alae are fused dorsally, and the cornua trabeculae equal approximately 22% of the total chondrocranial length (Fabrezi and Vera, 1997).

*Alsodes barrioi* also possesses a commissura quadratoorbitalis and an undivided frontoparietal fontanelle. However, *Alsodes barrioi* is the only telmatobiine species described to exhibit a larval processus oticus. In addition, the processus ascendens has a low attachment to the braincase (Lavilla, 1992).

The earliest references to leptodactyline chondrocrania were those of Sokol (1981) for *Leptodactylus chaquensis* and *Pleurodema bibroni*. However, this was a review of tadpole chondrocrania comparing distantly related taxa. Wassersug and Hoff (1982) illustrated the chondrocrania of *Pleurodema borellii* and *Leptodactylus wagneri* in their analysis of the developmental changes in jaw suspensorium. Fabrezi and Vera (1997) provided a complete description of *P. borellii*.

Larson and de Sá (1998) examined chondrocrania from 22 species of *Leptodactylus* in a phylogenetic context. The results of that study showed that the members of *Leptodactylus* examined



share the following characters: (1) quadripartite suprarostrals fused to each other and to the alae; (2) processus posterior dorsalis present on the suprarostal alae; (3) larval crista parotica present; (4) larval processus oticus absent; (5) commissura quadratoorbitalis present; (6) processus quadratoethmoidalis present; (7) processus dorsomedialis, processus ventromedialis, and processus retroarticularis of cartilago Meckeli present; (8) proximal ends of all ceratobranchials fused to hypobranchial plate; (9) spiculae present on ceratobranchials I, II, and III; (10) processus anterior branchialis present; (11) palatoquadrate wide and outwardly rounded; and (12) capsulae auditivae ovoid and representing approximately 30% of the length of the chondrocranium. Larson and de Sá (1998) also illustrated *Crossodactylus gaudichaudii* and *Hylodes nasus* (Hylodinae) and used them as outgroups.

#### BACKGROUND ON INTERNAL ORAL ANATOMY STUDIES

Wassersug and Heyer (1988) reported the internal oral anatomy of species representing Leptodactylidae. Leptodactylid larvae are characterized by the presence of four lingual papillae.

The species studied correspond to larvae that range in a variety of larval ecologies. The internal oral anatomy correlated well with differing habitats. For instance, *Cycloramphus stejnegeri* has non-feeding tadpoles that survive solely off of yolk reserves, consequently, it exhibits a reduction in the size and number of feeding structures, such as infralabial papillae and secretory ridges. *Lepidobatrachus* larvae are macrophagous and carnivorous (Cei, 1968), and their internal oral anatomy lacks the mucous-entrapment surfaces typical of pond dwelling tadpoles (Wassersug and Heyer, 1988). As previously mentioned, internal oral features do not help to resolve intergeneric relationships, but these characters can provide information intragenerically or at the species level.

## MATERIALS AND METHODS

### CHONDROCRANIAL DESCRIPTIONS

All specimens used in this study were measured with a Mitutoyo Digimatic caliper and staged according to Gosner's (1960) table. Collection numbers, measurements, status, and stages of all specimens examined are given in Appendix 1. Chondrocranial descriptions are based on specimens that were cleared and double-stained (Alcian blue and Alizarin red) for cartilage and bone following Dingerkus and Uhler (1977). Chondrocrania were observed through a Wild M3C stereomicroscope. Illustrations were done with a camera lucida attachment. Chondrocranial terminology follows de Beer (1937), De Jongh (1968), Haas (1995, 1996), and Sokol (1981); osteological terminology follows Trueb (1973). Where more than one species is described for a genus, the chondrocranial description is representative for the genus and interspecific differences are described.

## SCANNING ELECTRON MICROSCOPY

In preparation for scanning electron microscopy, specimens were dissected following Wassersug (1976). These were then ultrasonically cleaned, fixed in 10% glutaraldehyde for 2 hours, and washed in three changes of 0.1 M phosphate buffer for 15 minutes each. The specimens were then fixed for an hour in 4% osmium tetroxide and again washed in three changes of the phosphate buffer. They were then dehydrated through increasing concentrations of ethanol for 15 minutes each: 35, 50, 70, 80, 95, and 3 changes of 100%. The specimens were critical point dried with CO<sub>2</sub> in an EMS 850, mounted on aluminum stubs and sputter coated with gold/palladium (35 nm) using a Hummer VII sputtering system. Two of the specimens required 23 nm of additional coating. All specimens were examined with an Hitachi S-2300 scanning electron microscope at 15kV, and images were captured using Polaroid type 55 positive/negative film (de Sá and Lavilla, 1997). Descriptions of the internal oral anatomy of *Adenomera marmorata*, *Crossodactylus gaudichaudii*, *Cycloramphus stejnegeri*, *Lepidobatrachus laevis*, *Leptodactylus chaquensis*, *L. gracilis*,

*Odontophrynus americanus*, *Physalaemus pustulosus*, *Pleurodema borellii*, and *P. brachyops* (Wassersug and Heyer, 1988) were synthesized with new data on *Physalaemus gracilis*, *P. henselii*, and *Limnomedusa macroglossa*.

#### SPECIMENS EXAMINED

*Adenomera*, *Edalorhina*, and *Pleurodema* larvae were loaned from the National Museum of Natural History, Smithsonian Institution. Chondrocranial descriptions are based on stage 36 of *Adenomera marmorata* (USNM 209363), stage 36 of *Edalorhina perezi* (USNM 342752), stages 35-37 of *Pleurodema brachyops* (USNM 302093), and stages 31, 34, and 35 of *P. tucumana* (USNM 307190). Significant differences in the chondrocrania of *Pleurodema brachyops* specimens were noted after clearing and staining, therefore, the chondrocrania of *P. brachyops* is illustrated and referenced in the chondrocranial description as *P. brachyops* and *P. brachyops*<sup>2</sup>.

*Limnomedusa macroglossa* larvae that were used in this study were wild caught and fixed in 10% formalin by R. O. de Sá and A.

Gehrau, Pajas Blancas, Montevideo, Uruguay, July 3, 1978. Six individuals were cleared and double-stained, and one was dissected and prepared for scanning electron microscopy of internal oral anatomy. Chondrocranial descriptions are based on a stage 34 specimen, and descriptions of internal oral anatomy are based on a stage 37 specimen.

*Physalaemus pustulosus* larvae used in this study were captive bred. The ossification sequence is based on 73 cleared and double-stained larvae, while the chondrocranium is described and illustrated at stage 38.

*Physalaemus gracilis* larvae used in this study were wild caught and fixed in 10% formalin by R. O. and N. de Sá, Atlantida, Uruguay, July 26, 1993. The ossification sequence is based on 66 cleared and double-stained larvae, and the chondrocranium illustrated for a stage 40 individual. Two stage 37 individuals were dissected and prepared for scanning electron microscopy of internal oral anatomy.

*Physalaemus henselii* larvae used in this study were wild caught and fixed in 10% formalin by A. Gehrau, Barra de Valizas,

Depto. de Rocha, August 17, 1981. Seventeen individuals were cleared and double-stained, and the chondrocranial description is based on a stage 39 specimen. One stage 31 individual was dissected and prepared for scanning electron microscopy of internal oral anatomy.

#### PHYLOGENETIC ANALYSIS

Phylogenetic analyses were performed under maximum parsimony using PAUP version 3.1.1 (Swofford, 1993). Characters were run unordered and were polarized using *Hyla lanciformis* as the outgroup. Character coding is summarized in Table 1. The chondrocrania of *Caudiverbera caudiverbera* and *Pleurodema bibroni* were excluded from this analysis because many character states could not be determined based on the illustrations and descriptions available. Additionally, *Telmatobius laticeps* and *T. ceiorum* exhibited identical characteristics, consequently only *T. ceiorum* is included in the analysis.

## RESULTS

### CHONDROCRANIAL DESCRIPTIONS

#### *ADENOMERA MARMORATA*

The chondrocranium of *Adenomera marmorata* is ovoid (Fig. 1). Its greatest width corresponds to 80% of the total length, while the greatest depth is only about 40% of the total length.

The quadripartite suprarostrals, composed of the central corpora and the lateral alae, support the keratinized beak and serve as the larval upper jaw. The ventromedially directed corpora are shaped like an inverted-T; they are continuous medially, and a lateral protrusion exists along their ventral margin. Each corpus is dorsally fused with the ventromedially directed ala. The ventral tip of the ala is rounded, and the dorsal margin is concave (Fig. 2). This concavity exists between the well-developed processus posterior dorsalis and the point of articulation of the suprarostrals with the cornua trabeculae.

The cornua trabeculae are concave anteroventral extensions of the planum trabeculare anticum. They are about 10% of the total chondrocranial length (Fig. 1). The margins of the cornua



trabeculae are medially convex with their anterior tips expanded laterally. A processus lateralis trabeculae is absent (Fig. 2).

Posterior to the divergence of the cornua trabeculae, the anterior wall of the braincase is occupied by the large foramina olfactoria (Fig. 2). These foramina are delimited by the septum nasi medially, by the preoptic root of the cartilago orbitalis laterally, by the taenia ethmoidalis dorsally, and by the planum ethmoidale ventrally. The brain is enclosed laterally by the cartilago orbitalis, which bears 3 foramina: the trochlear, otic, and oculomotor. At the confluence of the commissura quadratocranialis anterior and the cartilago orbitalis, a lamina orbitonasalis projects laterally.

Posterior to the lamina orbitonasalis a fourth foramen is visible on the cartilago orbitalis. The foramen prooticum is found between the posterior margin of the cartilago orbitalis and the capsula auditiva; it is delimited dorsally by the taenia tectum marginalis.

The floor of the braincase is perforated by two pairs of foramina, the foramina craniopalatina anteriorly and the foramina carotica primaria posteriorly (Fig. 1). The roof of the braincase is divided into three fenestrae. The anterior fenestra is limited

laterally by the taeniae tecti marginales and posteriorly by the taenia tectum transversalis. Posteriorly, the taenia tectum transversalis is continuous with the taenia tectum medialis, which in turn contacts the tectum synoticum, creating two posterior parietal fenestrae.

The tectum synoticum bridges the two ovoid capsulae auditivae and serves as the dorsal margin of the foramen magnum. Each arcus occipitalis is continuous with the tectum synoticum dorsally and the planum basale ventrally forming the foramen magnum and foramen jugulare. The capsulae auditivae are about one-third of the total chondrocranial length. They form the lateral margin of each foramen jugulare. A small crista parotica extends laterally from the capsulae auditivae. Beneath the crista parotica a large fenestra ovalis is found, but it lacks an operculum (Fig. 2).

The palatoquadrate has two attachments to the braincase, anteriorly, the commissura quadratocranialis anterior, and posteriorly, the processus ascendens. The rod-like processus ascendens has an intermediate attachment to the braincase

Fig. 1. Chondrocranium of *Adenomera marmorata* at stage 36 (USNM 209363). A. Dorsal view. B. Ventral view. ca = capsula auditiva, ci = cartilago infrarostralis, cm = cartilago Meckeli, cqa = commissura quadratocranialis anterior, ct = cornu trabecularum, fca = foramen caroticum primarium, fcp = foramen craniopalatinum, fh = facies hyoidis, fj = foramen jugulare, fo = fenestra ovalis, lon = lamina orbitonasalis, pa = pars articularis quadrati, pal = processus anterolateralis, pao = processus antorbitalis, paq = processus ascendens quadrati, pm = processus muscularis quadrati, ppl = processus posterolateralis of the crista parotica, pq = palatoquadrate, pqe = processus quadratoethmoidalis, pra = processus retroarticularis, sa = suprarostr al ala, sc = suprarostr al corpus, tm = taenia tectum marginalis, ts = tectum synoticum, ttm = taenia tectum medialis, ttt = taenia tectum transversalis. Bar = 1.0 mm.

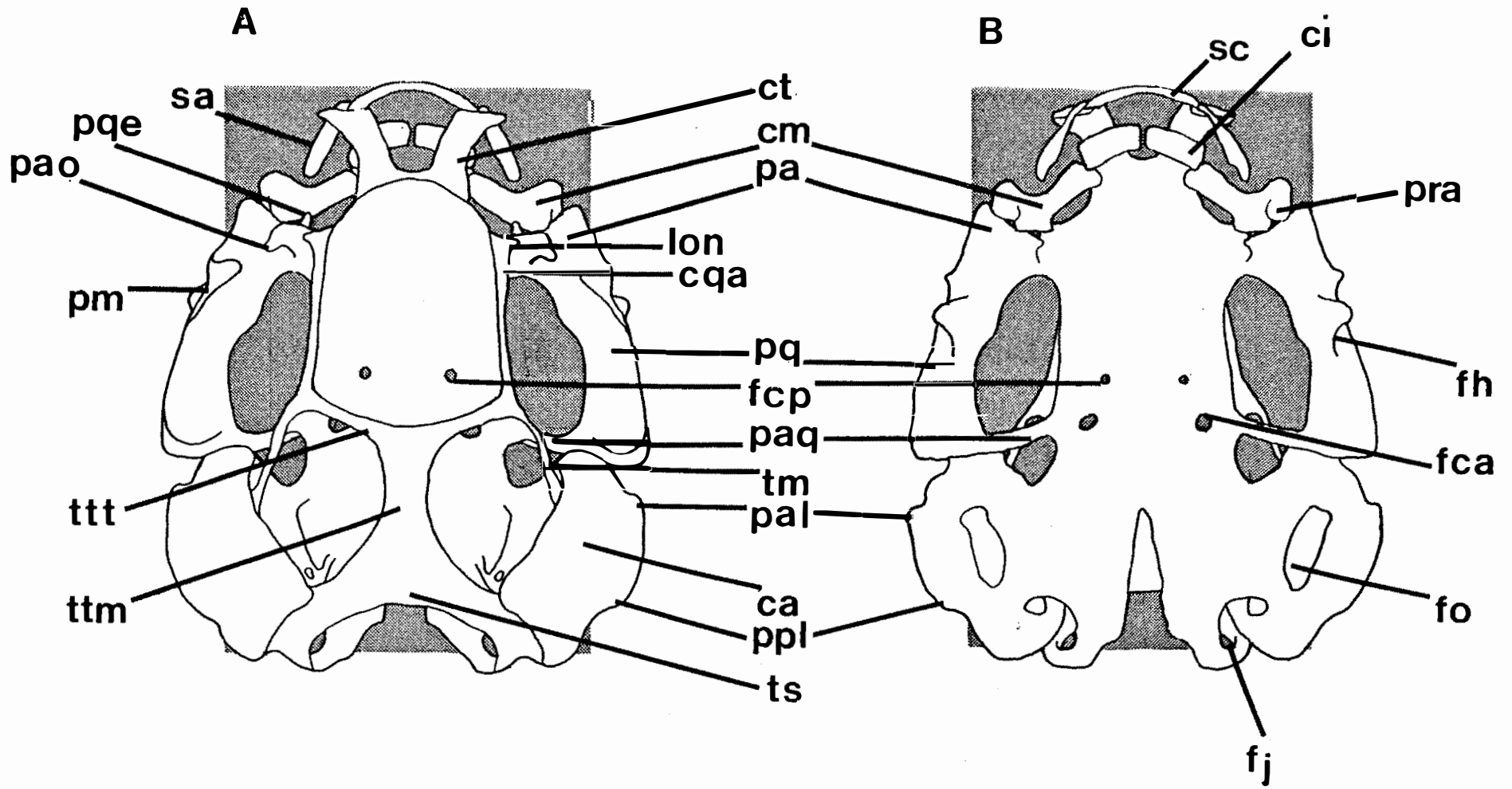
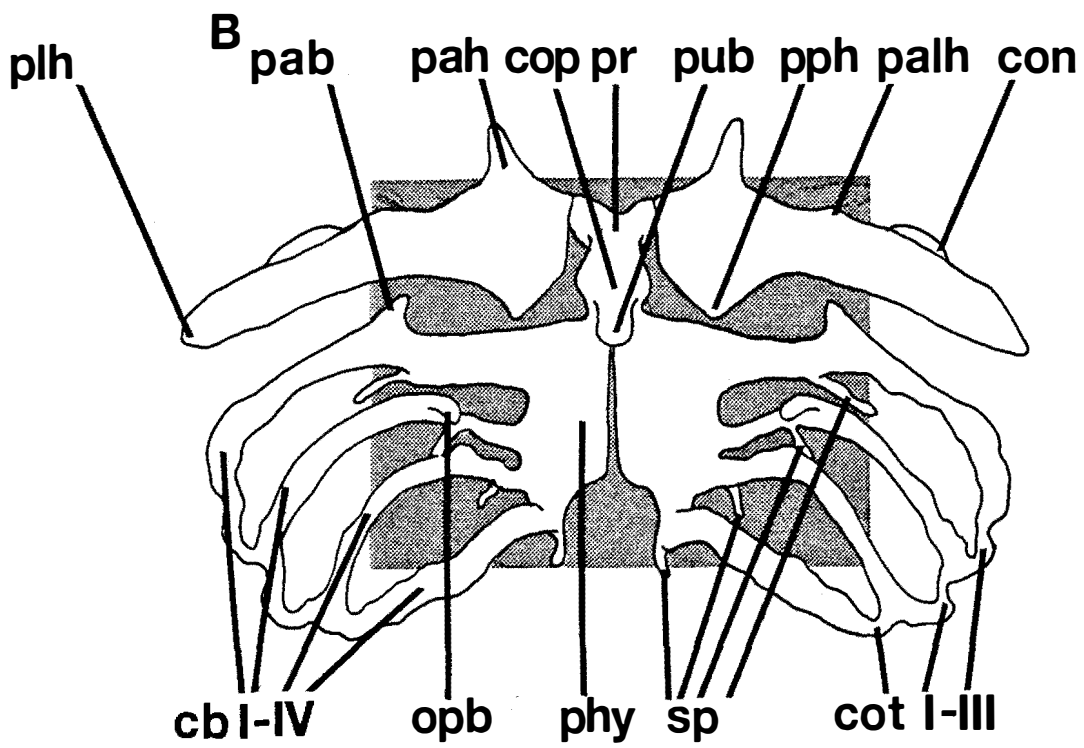
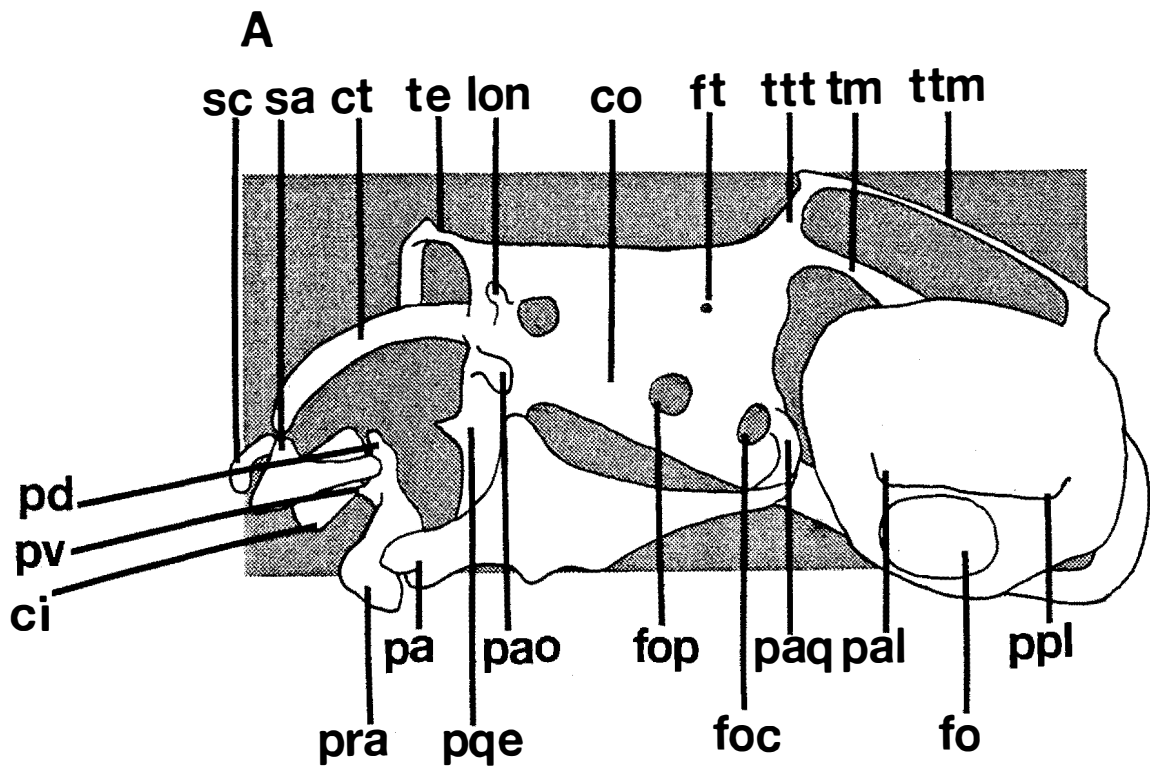


Fig. 2. Chondrocranium of *Adenomera marmorata* at stage 36 (USNM 209363). A. Lateral view. B. Ventral view of hyobranchial apparatus. cb I - IV = ceratobranchials I - IV, co = cartilago orbitalis, con = condylus articularis, cop = copula II, cot I - III = commissurae terminales I - III, foc = foramen oculomotorium, fop = foramen opticum, ft = foramen trochleare, opb = open processus branchialis, pab = processus anterior branchialis, pah = processus anterior hyalis, palh = processus anterolateralis hyalis, pd = processus dorsomedialis, phy = planum hypobranchiale, plh = processus lateralis hyalis, pph = processus posterior hyalis, pr = pars reuniens, pra = processus retroarticularis, pub = processus urobranchialis, pv = processus ventromedialis, sp = spiculae, te = taenia ethmoidalis. Bar = 1.0 mm. Other labels as in Fig. 1.



(sensu Sokol, 1981). The lateral margin of the palatoquadrate curves dorsally. The confluence of the palatoquadrate with the processus ascendens forms a pocket-like depression. Anteriorly, the processus muscularis quadrati projects dorsally from the lateral margin of the palatoquadrate at the level of the posterior margin of the commissura quadratocranialis anterior. However, the processus muscularis quadrati is reduced in *Adenomera marmorata*. Ventral to the processus muscularis quadrati is the facies hyoidis, which articulates with the ceratohyal. There is a well-developed processus antorbitalis, but a commissura quadratoorbitalis is lacking in *A. marmorata*.

The commissura quadratocranialis anterior is a ventrolateral extension of the braincase. Its anterior margin possesses a blunt and triangular commissura quadratoethmoidalis that serves as the posterior point of attachment for the ligamentum quadratoethmoidale. *Adenomera marmorata* lacks a processus pseudopterygoideus. The pars articularis quadrati is a poorly-developed anterior extension of the palatoquadrate; it articulates broadly with cartilago Meckeli.

Cartilago Meckeli is unipartite, but consists of three regions. Laterally, the processus retroarticularis extends beneath the pars articularis quadrati. The body of cartilago Meckeli is in the same plane as the palatoquadrate and has a small knob posteromedially. The largest region of cartilago Meckeli is an anteromedial extension composed of the processus dorsomedialis and processus ventromedialis. The cartilagine infrarostrales articulate with cartilago Meckeli between these processes (Fig. 2). The cartilagine infrarostrales are angled ventromedially. They are overall rectangular in ventral view and anteriorly U-shaped (Fig. 1).

The hyobranchial apparatus has a V-shaped pars reuniens that unite the ceratohyals medially (Fig. 2). The broad ceratohyals bear two processes, the processus anterior hyalis and the processus posterior hyalis. The processus anterolateralis hyalis is also present along the anterior margin of the ceratohyal, but it is extremely reduced. *Adenomera marmorata* lacks copula I. The condylus articularis is produced dorsally from the processus lateralis hyalis and articulates with the palatoquadrate. The pars reuniens is



posteriorly continuous with copula II, which bears a thick and round, posteroventrally directed, processus urobranchialis.

Posterolaterally, the copula I is continuous with the planum hypobranchiale. The plana hypobranchiales do not contact each other medially, but they are continuous with the four ceratobranchials and their corresponding dorsal spiculae laterally. The dorsally concave ceratobranchials are united posteriorly by the commissurae terminales, each of which bears a small posterior process. *Adenomera marmorata* lacks an extensive cartilaginous network within the ceratobranchials. Ceratobranchial I, the widest of the four, possesses the processus anterior branchialis along its anterior margin. Ceratobranchials II and III bear opposing but non-continuous, poorly chondrified, processes that form an open processus branchialis.

#### *EDALORHINA PEREZI*

The chondrocranium of *Edalorhina perezii* is circular in dorsal view (Fig. 3). Its greatest width is about 90% of the total length,

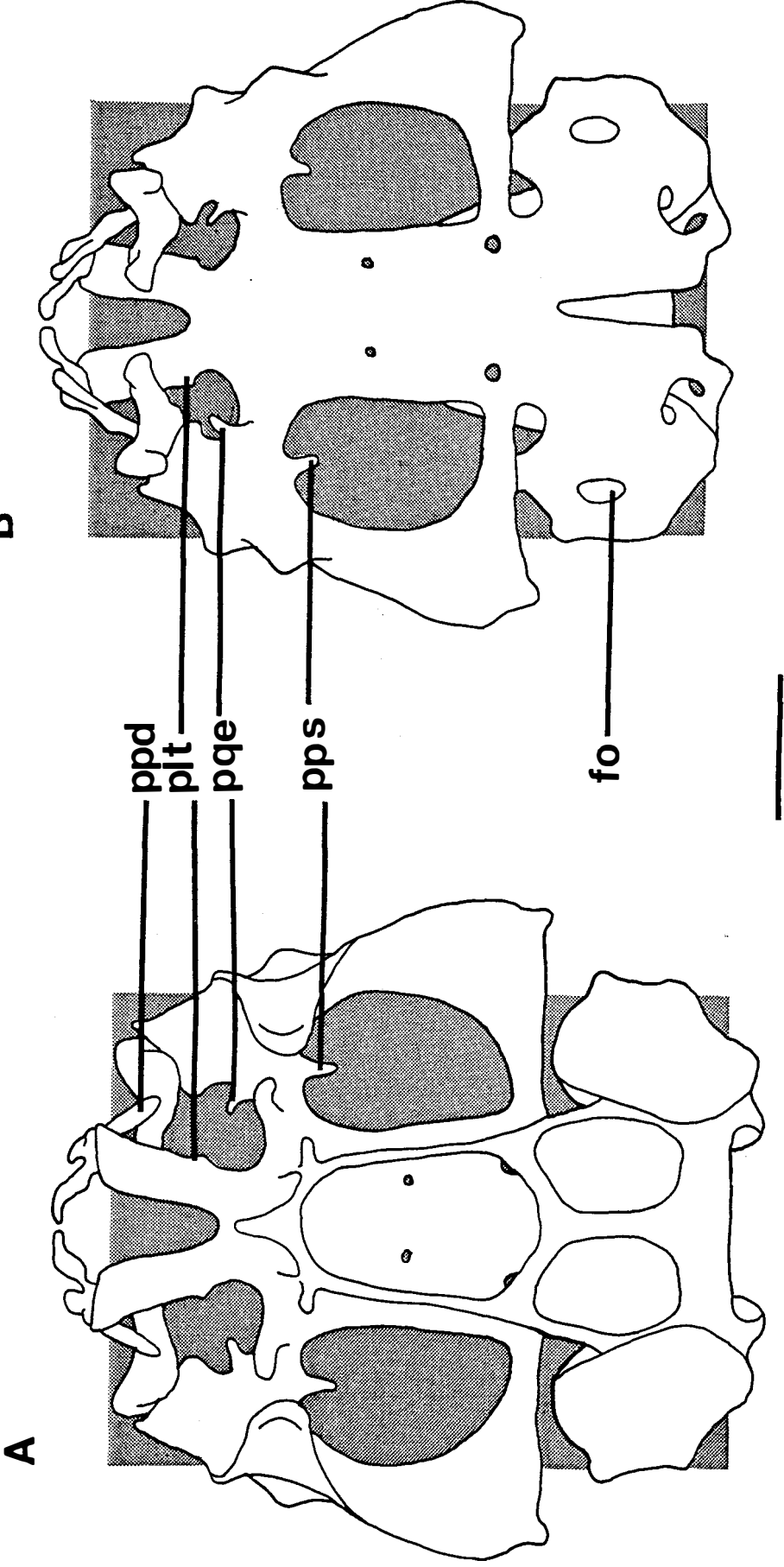
while its greatest depth is about 31% of its total length. The specimen examined did not have cartilagine infrarostrales.

Anteriorly, the suprarrostral corpora and alae are fused dorsally. The L-shaped corpora are ventromedially angled. Each corpus has a small medial process along the ventral margin, but they are not continuous. The semicircular alae possess the processus posterior dorsalis, which reaches over the horizontal body of cartilago Meckeli (Fig. 4). The point of articulation of the suprarostrals with the cornua trabeculae is knob-shaped.

The cornua trabeculae are about 15% of the total chondrocranial length (Fig. 3). They are ventrally concave and V-shaped. A processus lateralis trabeculae is present proximally from their lateral margin (Fig. 4). It serves as the anterior point of attachment for the ligamentum quadratoethmoidale.

The cartilago orbitalis forms the braincase laterally. The lamina orbitonasalis projects anterolaterally from the braincase at the junction with the commissura quadratocranialis anterior. The cartilago orbitalis has three foramina. The smallest is the foramen

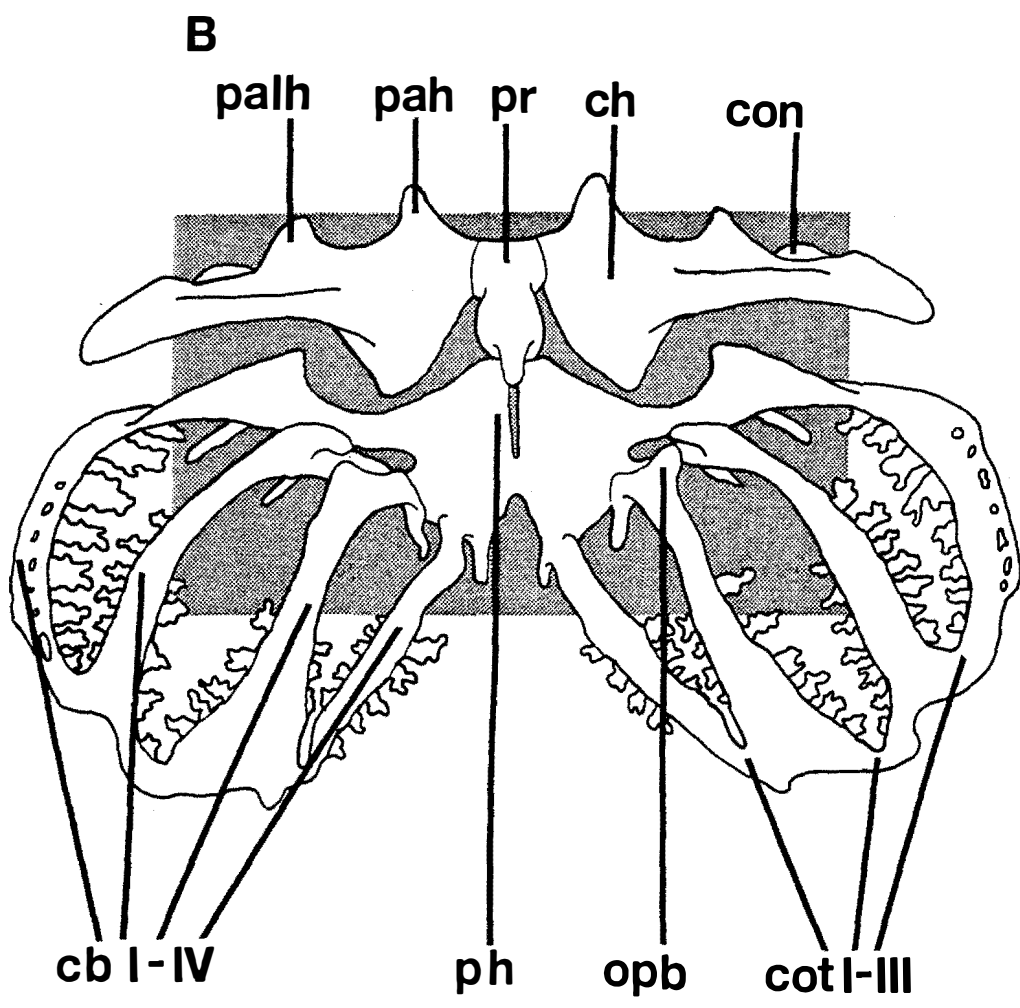
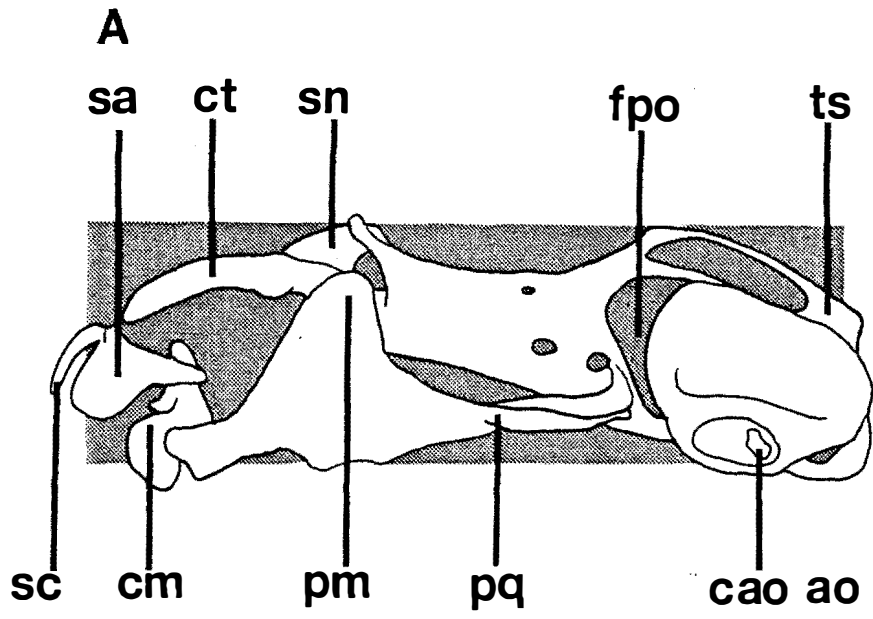
Fig. 3. Chondrocranium of *Edalorhina perezii* at stage 36 (USNM 342752). A. Dorsal view. B. Ventral view. plt = processus lateralis trabeculae, ppd = processus posterior dorsalis, pps = processus pseudopterygoideus. Bar = 1.0 mm. Other labels as in Figs. 1 and 2.



**B**

**A**

Fig. 4. Chondrocranium of *Edalorhina perezii* at stage 36 (USNM 342752). A. Lateral view. B. Ventral view of hyobranchial apparatus. ao = arcus occipitalis, cao = cartilaginous operculum, ch = ceratohyal, fpo = foramen prooticum, sn = septum nasi, Bar = 1.0 mm. Other labels as in Figs. 1 and 2.



trochleare, which is dorsal to the foramen opticum. Posterior to the foramen opticum is the foramen oculomotorium.

The roof of the braincase is divided into three fenestrae, an anterior frontal fenestra and two posterior parietal fenestrae (Fig. 3). The floor of the braincase has two pairs of foramina: craniopalatina and carotica primaria. The planum basale serves as the floor of the braincase between the capsulae auditivae and diverges posteriorly forming the otic notch.

The tectum synoticum bridges the capsulae auditivae dorsally. Each capsula auditiva is slightly more than 25% of the total chondrocranial length and slightly less than 25% of the total chondrocranial width. A small processus anterolateralis projects from the crista parotica of the capsula auditiva. Ventral to the crista parotica, the fenestra ovalis is partially occluded by a cartilaginous operculum (Fig. 4). A larval processus oticus is absent in *Edalorhina perezii* larvae.

The palatoquadrate of *Edalorhina* is broad (Fig. 3). A large fenestra subocularis is located between the medial margin of the palatoquadrate and the braincase. A small rounded posterior

protrusion is on the posterolateral margin of the palatoquadrate. The posterior curvature does not extend past the level of the intermediate attachment of the processus ascendens to the braincase (sensu Sokol, 1981) (Figs. 3, 4).

The commissura quadratocranialis anterior has three processes: the commissura quadratoethmoidalis anteriorly, the processus pseudopterygoideus posteriorly, and the processus antorbitalis dorsally (Fig. 3). A commissura quadratoorbitalis is lacking.

At the level of the commissura quadratocranialis anterior, the broad processus muscularis quadrati is a dorsal outgrowth of the lateral edge of the palatoquadrate. Ventral to the processus muscularis quadrati is the facies hyoidis.

The pars articularis quadrati is slightly angled medially and articulates broadly with cartilago Meckeli. The anterolateral margin of the pars articularis quadrati has a rounded protrusion that is the posterior point of attachment for the ligamentum cornu quadratum laterale.



Cartilago Meckeli is sigmoid in shape and thus divided into three regions. Laterally, the processus retroarticularis curves ventrally, around, and under the pars articularis quadrati. The horizontal part of cartilago Meckeli is its largest component; it has a convex posterior margin that overlaps the pars articularis quadrati. The processus ventromedialis and processus dorsomedialis are distinct on the medial region of cartilago Meckeli (Fig. 4). The posteromedial margin of cartilago Meckeli is slightly enlarged (Fig. 3).

The broad ceratohyals are united medially by the pars reuniens (Fig. 4). Anteriorly, each ceratohyal has a well-developed processus anterior hyalis and a less developed processus anterolateralis hyalis. Laterally, the ceratohyals are thicker at the level of the condylus articularis, which articulates dorsally with the palatoquadrate. The processus posterior hyalis is large and triangular. Posterior to the pars reuniens, copula II bears a large and rounded posteroventral processus urobranchialis. Copula I is lacking. The plana hypobranchiales articulate with copula II anteriorly and are fused medially along the posterior half of their

length. The plana hypobranchiales are continuous with the four dorsally concave ceratobranchials and their corresponding dorsal spiculae. At the confluence of the planum hypobranchiale with ceratobranchial I, a processus anterior branchialis is found. The ceratobranchials are united distally by the commissurae terminales; the commissura terminalis III between ceratobranchials III and IV bears a small rounded posterior process. A cartilaginous network is present among the ceratobranchials. Ceratobranchial I is perforated. Proximally, ceratobranchials II and III each bear ventral opposing non-continuous processes forming an open processus branchialis.

#### *LIMNOMEDUSA MACROGLOSSA*

Overall the chondrocranium of *Limnomedusa macroglossa* is ovoid (Fig. 5). The widest portion of the chondrocranium is approximately 80% of the total length, and the maximum chondrocranial height is approximately 33% of the total length.

The suprarostrals are fused ventromedially forming a continuous broad sheet of cartilage. The dorsal margin of the

corpora is widely V-shaped, and their ventral margin is horizontal. The corpora are not continuous laterally with the semicircular alae. The dorsal margin of each ala is slightly concave between the processus posterior dorsalis and the well-developed and knob-like point of articulation of the suprarostrals with the cornua trabeculae (Fig. 6).

The cornua trabeculae are slightly more than 20% of the total length of the chondrocranium (Fig. 5). They are deeply V-shaped and anteriorly expanded. They have a well-developed and triangular-shaped processus lateralis trabeculae.

The brain is enclosed laterally by the cartilago orbitalis (Fig. 6). The lamina orbitonasalis is present as a dorsolateral outgrowth of the anterior region of the cartilago. Posteriorly, the foramen trochleare, foramen opticum, and foramen oculomotorium are seen on the cartilago orbitalis. A thin ventromedial bar of cartilage connects the anterior margin of the foramen oculomotorium with the floor of the braincase. The oculomotor nerve exits the braincase dorsal to this bar, and the ophthalmic artery leaves the braincase ventral to this bar (Sokol, 1981).

The anterior wall of the braincase is perforated by the foramina olfactoria. In dorsal view, the braincase has an anterior frontal fenestra and two posterior parietal fenestrae (Fig. 5). The floor of the braincase is pierced by two pairs of foramina: the foramina carotica primaria and the foramina craniopalatina.

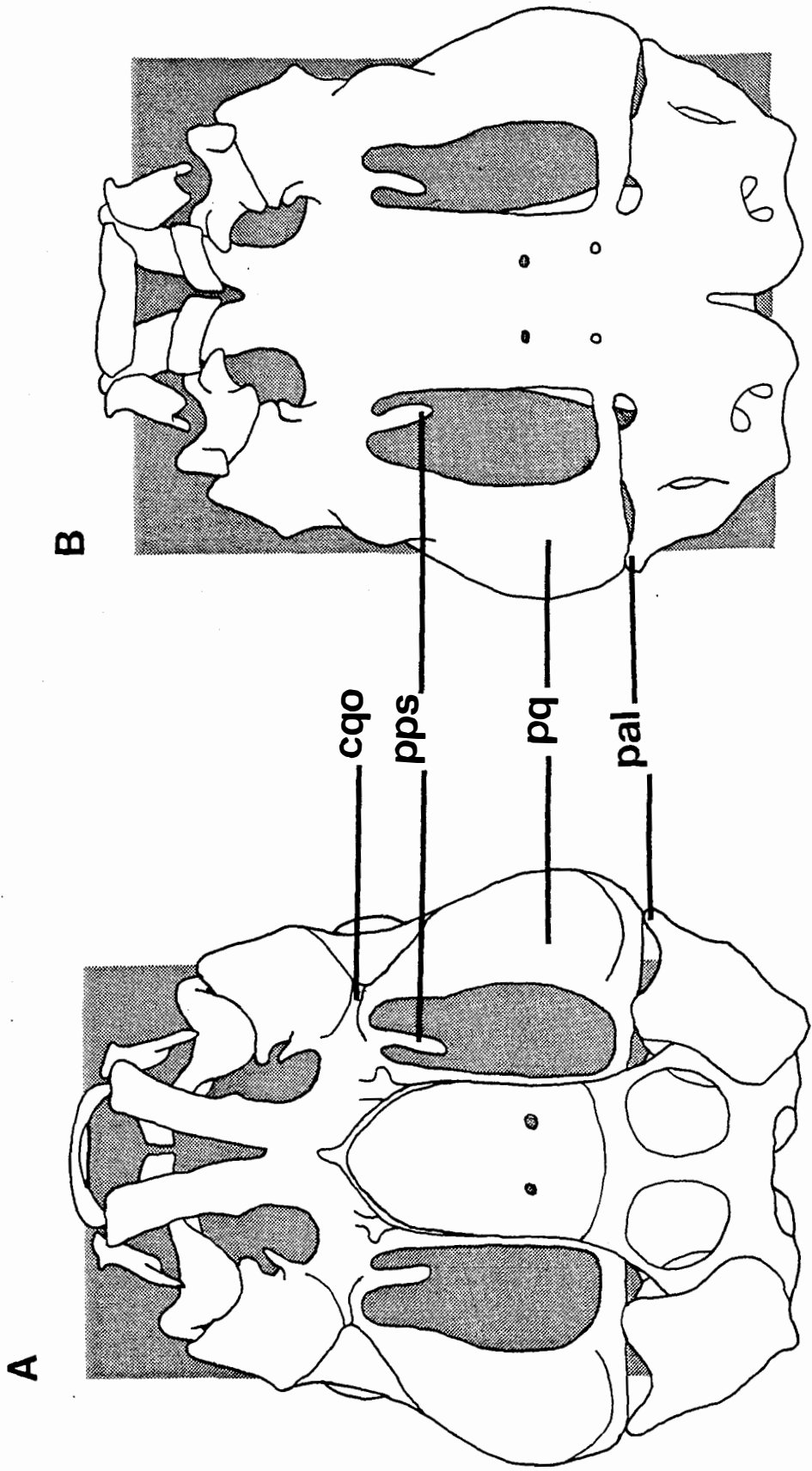
The tectum synoticum bridges the capsulae<sup>s</sup> auditivae dorsally. The capsulae auditivae are overall diamond-shaped, and they are 25% of the total chondrocranial length. The width of each capsula auditiva is about 80% of their length and accounts for 25% of the total width of the chondrocranium. Each capsula auditiva has a well-developed and finger-like processus anterolateralis of the crista parotica that contacts, but is not continuous with, the posterior curvature of the palatoquadrate. However, these will fuse by stage 40. Ventral to the crista parotica is the fenestra ovalis, which is occluded by a large cartilaginous operculum (Fig. 6).

The palatoquadrate of *Limnomedusa* is wide and the posterior curvature extends past the anterior margin of the capsula auditiva (Fig. 5). The posterior and lateral margins of the palatoquadrate curve dorsally forming a concavity at the confluence of the

Fig. 5. Chondrocranium of *Limnomedusa macroglossa* at stage 34.

A. Dorsal view. B. Ventral view. cqo = commissura

quadratoorbitalis. Bar = 1.0mm. Other labels as in Figs. 1 and 2.

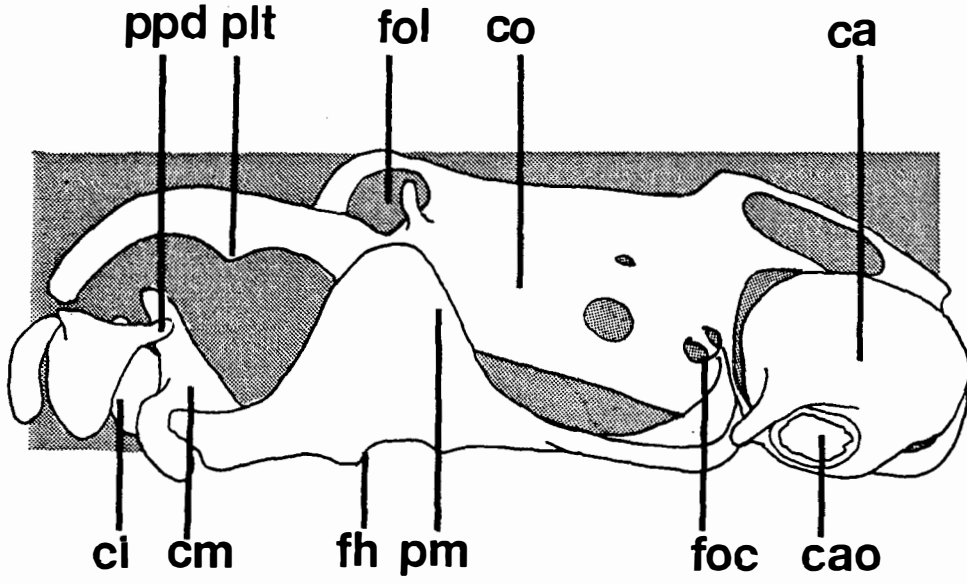


A

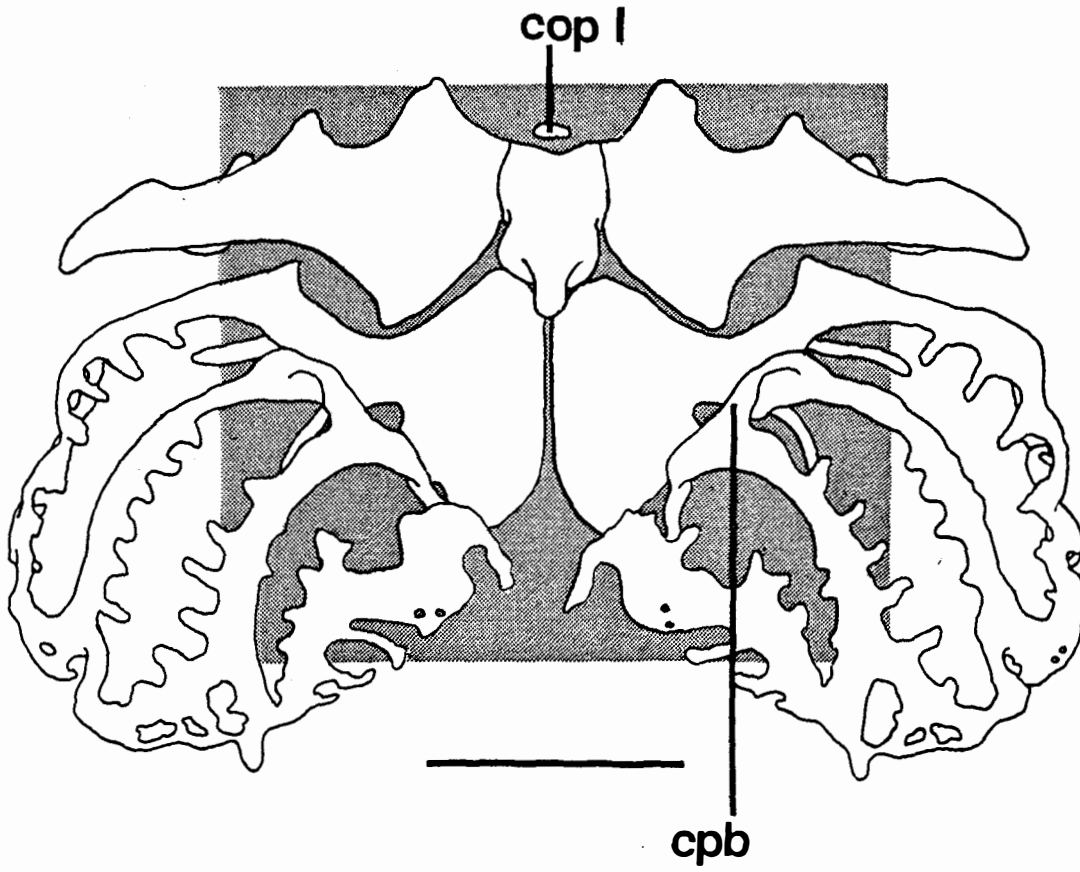
B

Fig. 6. Chondrocranium of *Limnomedusa macroglossa* at stage 34. A. Lateral view. B. Ventral view of hyobranchial apparatus. cop I = copula I, cpb = closed processus branchialis, fol = foramina olfactoria. Bar = 1.0mm. Other labels as in Figs. 1 and 2.

**A**



**B**





palatoquadrate with the processus ascendens. The processus ascendens has an intermediate attachment to the braincase (sensu Sokol, 1981) (Fig. 6).

The confluence of the commissura quadratocranialis anterior with the palatoquadrate is about twice as wide as its confluence with braincase (Fig. 5). The commissura quadratocranialis anterior bears a processus quadratoethmoidalis and a well-developed and finger-like processus pseudopterygoideus. The commissura quadratoorbitalis is present, fused to the tip of the processus muscularis quadrati.

A laterally concave processus muscularis quadrati extends dorsally from the lateral margin of the palatoquadrate at the level of the commissura quadratocranialis anterior. The dorsally concave anterior margin of the pars articularis quadrati articulates broadly with cartilago Meckeli.

Cartilago Meckeli is sigmoid in shape and bears three processes: the processus retroarticularis, the processus ventromedialis, and the processus dorsomedialis. A distinct medial process also extends from the posteroventral margin of cartilago

Meckeli. Each cartilago infrarostralis articulates posteriorly with cartilago Meckeli between the processus ventromedialis and the processus dorsomedialis. The lateral margins of the cartilagine infrarostrales are thicker than the medial margins, which accentuates the ventromedial slope of the cartilages.

The hyobranchial apparatus has a poorly chondrified pars reuniens, which unites the broad ceratohyals and the copula II posteriorly (Fig. 6). Anterior to the pars reuniens, a small elliptical copula I is present. The anterior margin of each ceratohyal bears the processus anterior hyalis and the processus anterolateralis hyalis. The posteromedial margin of the ceratohyal has a broad, flat, laterally concave processus posterior hyalis. The lateral region of the ceratohyal bears the dorsally protruding condylus articularis. A long and round posteroventral processus urobranchialis is located on copula II, which articulates posteriorly with the plana hypobranchiales.

The plana hypobranchiales are not continuous medially; furthermore, they are only continuous with ceratobranchials I and IV and their corresponding spiculae. An extensive network of

poorly chondrified cartilage exists among the ceratobranchials. The four ceratobranchials are united distally via fenestrated commissurae terminales. Commissurae terminales II and III bear posterodorsal processes. At the confluence of ceratobranchial I with the planum hypobranchiale, a processus anterior branchialis is present. Ceratobranchials I and IV are fenestrated. A processus lateralis hypobranchialis forms on the lateral margin of the planum hypobranchiale and articulates with ceratobranchials II and III. A closed processus branchialis is found between ceratobranchials II and III.

*PHYSALAEEMUS: P. GRACILIS, P. HENSELII, P. PUSTULOSUS*

Overall, the chondrocrania of *Physalaemus* larvae are ovoid (Fig. 7). The greatest width being about 87% of the total length, while the greatest height is about 33% of the total length.

Anteriorly, the suprarostrals are rectangular and unite ventrally by a thin cartilaginous commissura. In *Physalaemus pustulosus*, the corpora are narrow, therefore, the ventral cartilaginous commissura uniting them is longer. Each corpus is

continuous dorsolaterally with the ala. The semicircular alae are thin broad sheets of cartilage that bear the processus posterior dorsalis and articulate with the cornua trabeculae dorsally. The processus posterior dorsalis is reduced in *P. henselii* (Fig. 8).

The cornua trabeculae are approximately 20% of the total length of the chondrocranium (Fig. 7). Overall, the cornua trabeculae are U-shaped in *Physalaemus pustulosus* and *P. henselii*, while in *P. gracilis* these form a V. Each cornu trabecularum bears a blunt, triangular, processus lateralis trabeculae.

The foramina olfactoria are large perforations in the anterior wall of the braincase. These foramina are reduced in *Physalaemus henselii*, and they are not visible in lateral view (Fig.8). The braincase is enclosed laterally by the cartilago orbitalis. Anteriorly, a lamina orbitonasalis protrudes laterally from the cartilago orbitalis. In *Physalaemus pustulosus* and *P. gracilis*, the foramen orbitonasalis is visible on the proximal portion of this outgrowth. The foramen oculomotorium, foramen opticum, and foramen trochleare perforate the cartilago orbitalis. The latter is not distinguishable in *P. pustulosus*.

The roof of the braincase is subdivided into a large anterior frontal fenestra and two smaller posterior parietal fenestrae (Fig. 7). However, the taenia tectum transversalis and taenia tectum medialis are absent in *Physalaemus henselii* leaving a large frontoparietal fontanelle delimited posteriorly by the tectum synoticum. The taeniae tecti marginales are absent in *Physalaemus* larvae, therefore, the dorsal margin of the cartilagine orbitales is not continuous with the capsulae auditivae. Ventrally, the braincase bears the foramina carotica primaria and the foramina craniopalatina.

The capsulae auditivae are bridged dorsally by the tectum synoticum. Each capsula auditiva is overall ovoid and is about 33% of the total chondrocranial length. However, in *Physalaemus gracilis*, the capsulae auditivae are smaller, about 25% of the total length of the chondrocranium. The width of each capsula auditiva is about 80% of its length; however, in *P. gracilis*, the width is slightly more than 90% of the length. Laterally, beneath the crista parotica, the fenestra ovalis is partially occluded by a cartilaginous operculum. The cartilaginous operculum is less-developed in *P.*

*henselii* (Fig.8). Each crista parotica has a processus anterolateralis; this process is best-developed in *P. pustulosus*. A larval processus oticus is absent in *Physalaemus*.

The posterior curvature of the palatoquadrate is the broadest point in the chondrocranium (Fig. 7). The processus ascendens has an intermediate attachment to the braincase (sensu Sokol, 1981) (Fig. 8). An orifice exists at the confluence of the processus ascendens with the palatoquadrate in *Physalaemus gracilis*. In *P. henselii*, a ventral depression is present in this region of the palatoquadrate, and this depression is accented by dorsal curving of the posterior and lateral margins of the palatoquadrate. An orifice is variably present here during earlier stages of development in the *P. henselii* specimens examined.

The commissura quadratocranialis anterior is wider towards the palatoquadrate (Fig. 7). The well-developed commissura quadratoethmoidalis and the processus pseudopterygoideus are found on the commissura quadratocranialis anterior. In *Physalaemus gracilis*, the processus pseudopterygoideus is a well-developed process, however, it is lacking in *P. henselii*. It is a

Fig. 7. Dorsal and ventral view of chondrocranium. A. *Physalaemus gracilis* at stage 40. B. *P. henselii* at stage 39. C. *P. pustulosus* at stage 38. Bar = 1.0mm.

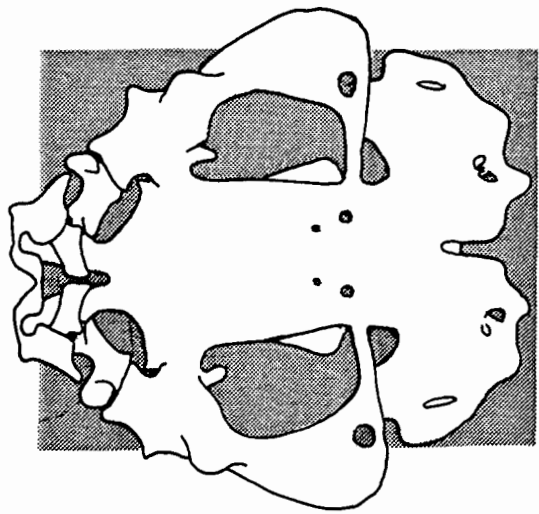
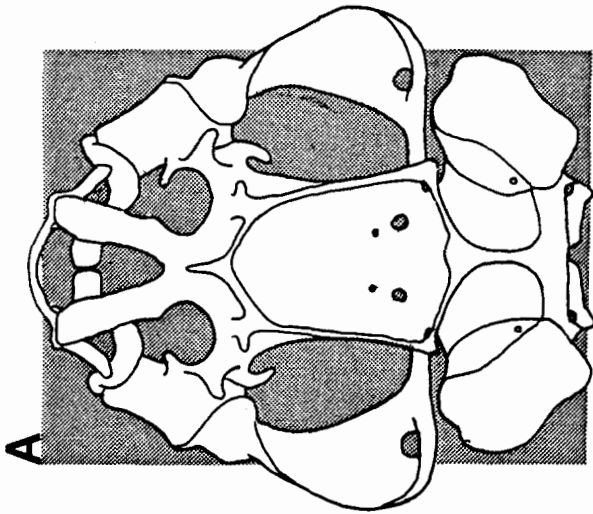
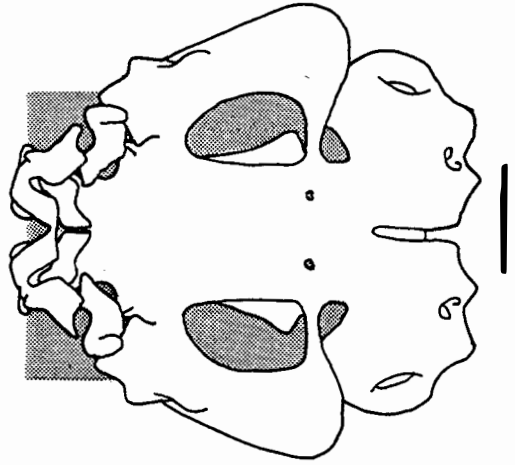
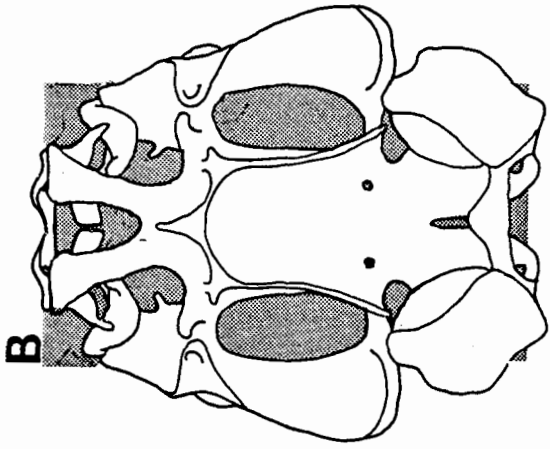
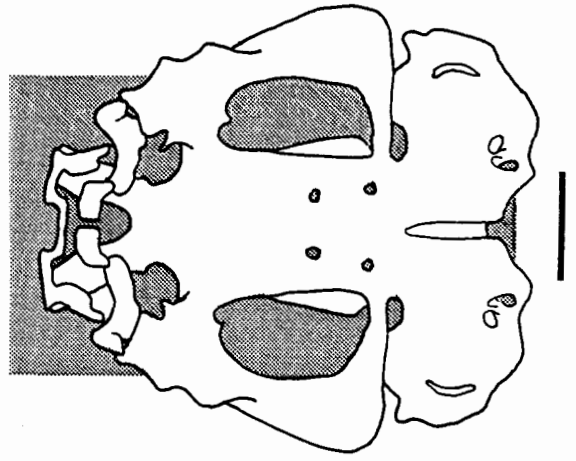
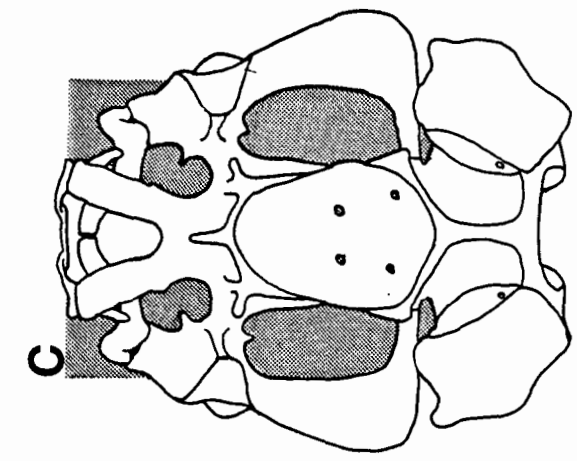
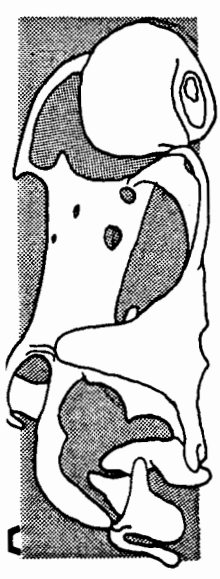
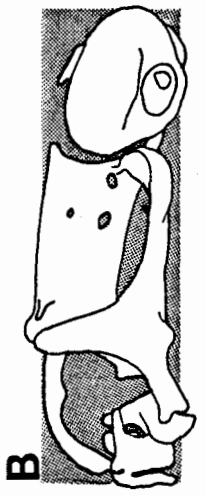
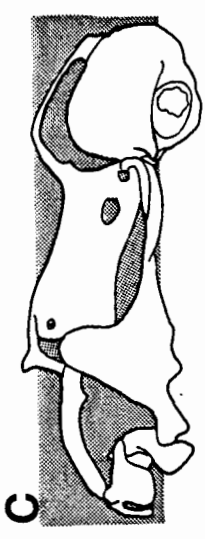
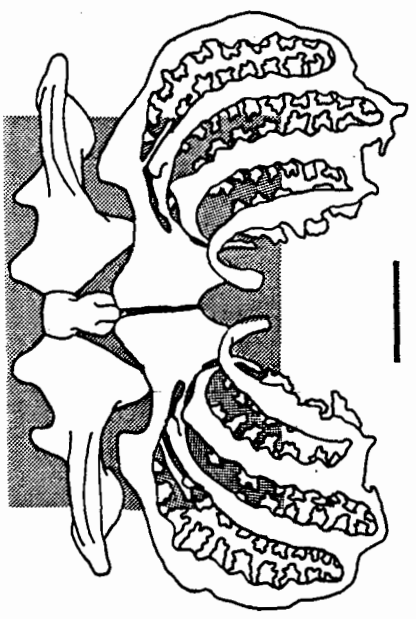
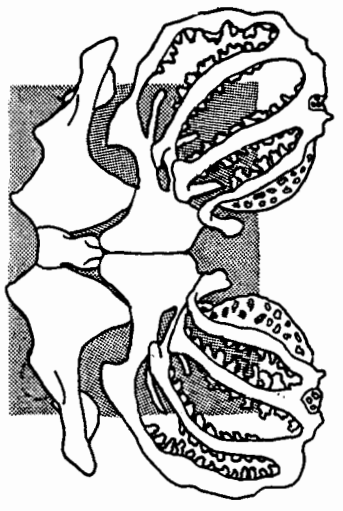
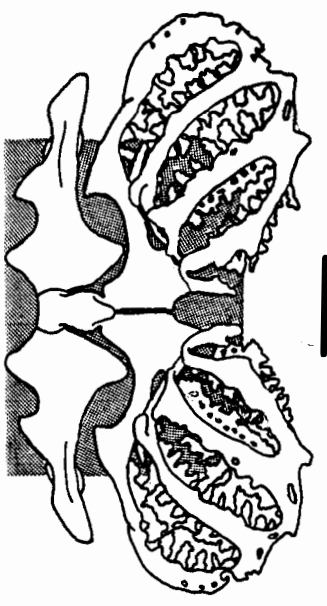




Fig. 8. Lateral view of chondrocranium and ventral view of  
hyobranchial apparatus. A. *Physalaemus gracilis*<sup>†</sup> at stage 40. B. *P.*  
*henselii* at stage 39. C. *P. pustulosus* at stage 38. Bar = 1.0 mm.



defined process in stage 31 of *P. pustulosus*, but it is reduced by stage 38. The processus antorbitalis is well-developed in *P. henselii* and *P. gracilis*; these species lack a commissura quadratoorbitalis. In *P. pustulosus*, a commissura quadratoorbitalis is present.

The processus muscularis quadrati is a well-developed dorsomedial extension of the lateral margin of the palatoquadrate at the level of the commissura quadratocranialis (Fig. 8). This process is thin in *Physalaemus henselii*. Ventral to the processus muscularis quadrati is the facies hyoidis. *Physalaemus henselii* has a small facies hyoidis.

The pars articularis quadrati articulates broadly with the convex posterior margin of cartilago Meckeli (Fig. 7). Cartilago Meckeli is sigmoid in shape and bears three processes: the processus retroarticularis, the processus ventromedialis, and the processus dorsomedialis; the latter is most distinct in *Physalaemus henselii* (Fig. 8). A slight ventral swelling is noticeable on the posteromedial margin of cartilago Meckeli. Each cartilago infrarostralis articulates with cartilago Meckeli between the processus dorsomedialis and processus ventromedialis. Overall, the cartilagine infrarostrales are

dorsally concave and ventromedially directed. In *P. gracilis*, the dorsolateral tip of each cartilago infrarostralis almost reaches the cornua trabeculae.

The pars reuniens of the hyobranchial apparatus unites the wide ceratohyals and copula II. Copula I is absent. A processus anterior hyalis and a processus anterolateralis hyalis are present. These processes are poorly developed in *Physalaemus henselii*. The tip of the processus posterior hyalis, a broad triangular outgrowth of the ceratohyal, is dorsal to the planum hypobranchiale in *P. henselii* and *P. gracilis*. A condylus articularis is present on the dorsolateral region of the ceratohyal. The pars reuniens is continuous posteriorly with the copula II, which bears a long and rounded posteroventral processus urobranchialis. Copula II is continuous posteriorly with the plana hypobranchiales in *P. pustulosus*. The plana hypobranchiales are broad sheets of cartilage that are continuous with Ceratobranchials I and IV and their corresponding spiculae. The plana hypobranchiales are not fused medially. The processus lateralis hypobranchialis of each planum hypobranchiale articulates with ceratobranchial II. An extensive

network of poorly chondrified cartilage exists among the four dorsally concave ceratobranchials. Distally, the commissurae terminales unite the ceratobranchials, and commissurae terminales II and III each bear a posterodorsal process. The processus branchialis is open. The processus anterior branchialis is a medially concave process of ceratobranchial I, the widest of the four ceratobranchials. In *P. pustulosus*, ceratobranchial I and the commissurae terminales are fenestrated.

*PLEURODEMA: P. BRACHYOPS, P. BRACHYOPS2, P. TUCUMANA*

The chondrocrania of *Pleurodema* tadpoles are overall ovoid (Fig. 9). The width of the chondrocrania is approximately 85% of the total length, while the height is about 30% of the total length.

The I-shaped suprarostrals are continuous ventrally by a cartilaginous commissura. Each corpus is continuous dorsolaterally with the semicircular ala. This continuity is not evident until stage 35 in *Pleurodema tucumana*. Ventral fusion between the corpus and the ala exists in *P. brachyops2* and in later stages of *P. tucumana*. The broad alae are concave between the

processus posterior dorsalis and the point of articulation with the cornua trabeculae. These two protrusions of the alae are poorly developed in *P. brachyops*<sup>2</sup>, however, overall, the ala in *P. brachyops*<sup>2</sup> is broader (Fig. 10). Posterior to the tip of the processus posterior dorsalis, cartilaginous adrostrals are present. *Pleurodema brachyops* lacks adrostrals.

The V-shaped cornua trabeculae are about 20% of the total chondrocranial length (Fig. 9). In *P. brachyops*<sup>2</sup>, the cornua trabeculae are not as long, only about 15% of the total chondrocranial length. They are broad and thinly U-shaped. The proximal lateral margin of each cornu trabecularum bears a processus lateralis trabeculae. The processus lateralis trabeculae is poorly-developed in *P. brachyops*.

The anterior wall of the braincase is perforated by the large foramina olfactoria. A lamina orbitonasalis protrudes anterolaterally from the cartilago orbitalis. The cartilago orbitalis has three foramina: the foramen trochleare, the foramen opticum, and the foramen oculomotorium (Fig. 10). *Pleurodema tucumana* lacks foramina olfactoria, a taenia ethmoidalis, a lamina

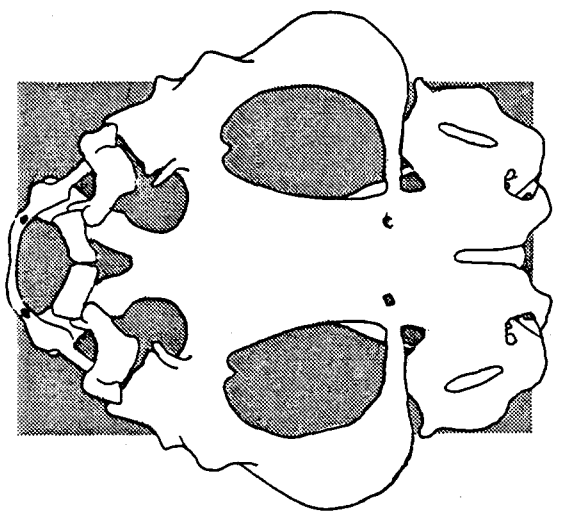
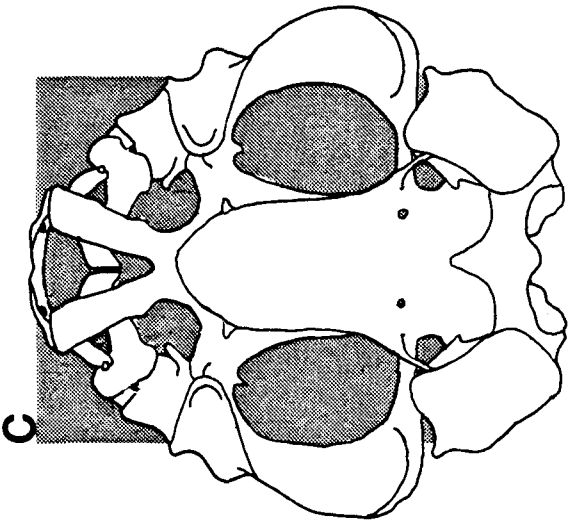
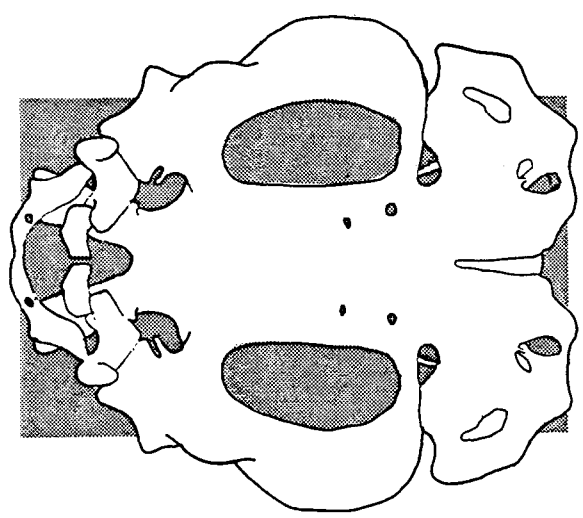
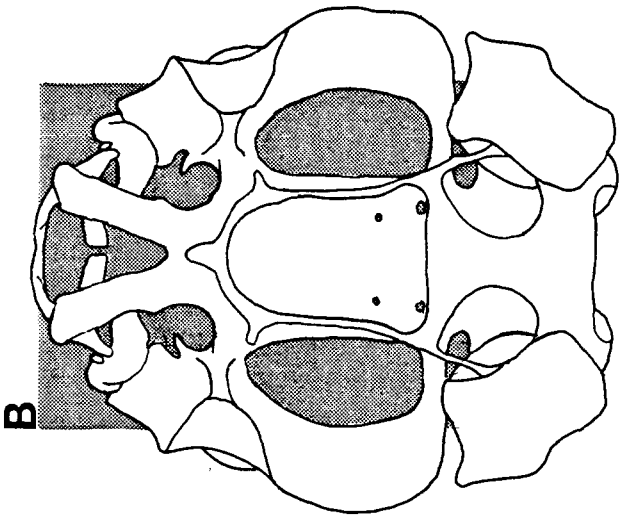
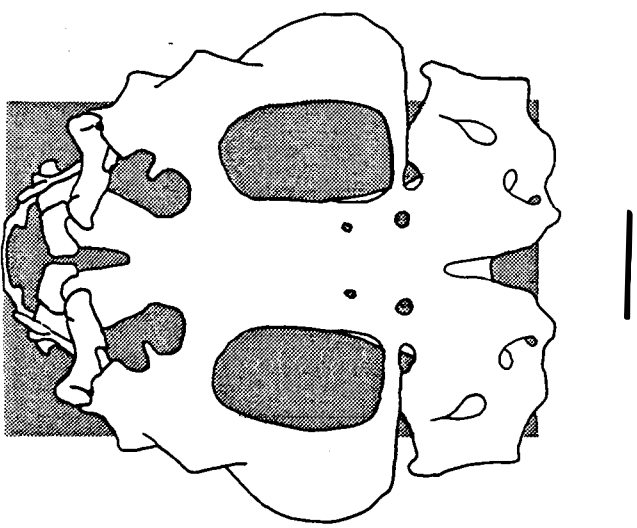
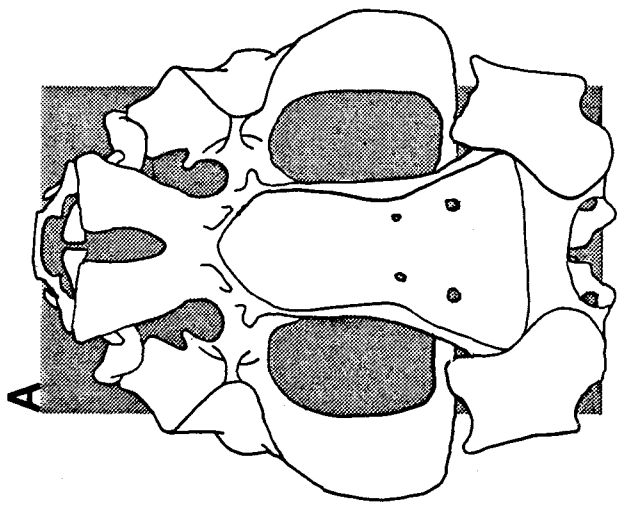
orbitonasalis, and a foramen trochleare. The taeniae tecti marginales are continuous with the capsulae auditivae.

In the floor of the braincase, the foramina craniopalatina and foramina carotica primaria are present in *Pleurodema brachyops* and *P. brachyops*<sup>2</sup>, however the former are indistinguishable in *P. tucumana* (Fig. 9). There is a large frontoparietal fontanelle. In *P. tucumana*, the tectum synoticum bears a rounded posterior protrusion and a reduced taenia tectum medialis. In *P. brachyops*<sup>2</sup>, the frontoparietal fontanelle is subdivided by the taenia tectum transversalis and taenia tectum medialis.

Each capsula auditiva is approximately 25% of the total chondrocranial length and approximately 27% of the total width of the chondrocranium. Laterally on the capsula auditiva, the crista parotica bears a processus anterolateralis that is most distinct in *P. tucumana*. A processus posterolateralis of the crista parotica is also present. Ventral to the crista parotica is a large fenestra ovalis, which is partially occluded by a cartilaginous operculum (Fig. 10). The cartilaginous operculum is lacking in *Pleurodema brachyops*. *Pleurodema* lacks a larval processus oticus.

Fig. 9. Dorsal and ventral view of chondrocranium. A.  
*Pleurodema brachyops* at stage 35. B. *P. brachyops*2 at stage 37. C.  
*P. tucumana* at stage 35. Bar = 1.0 mm



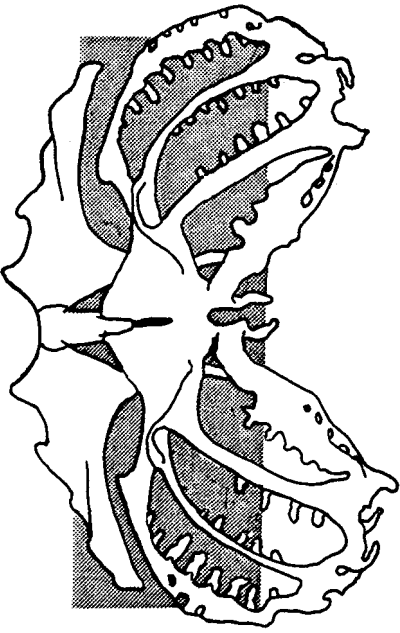
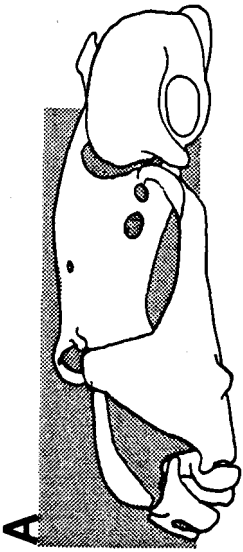
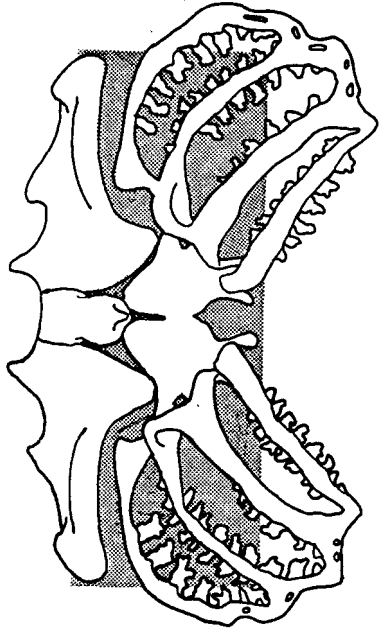
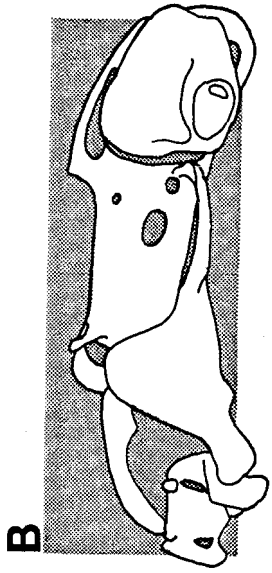
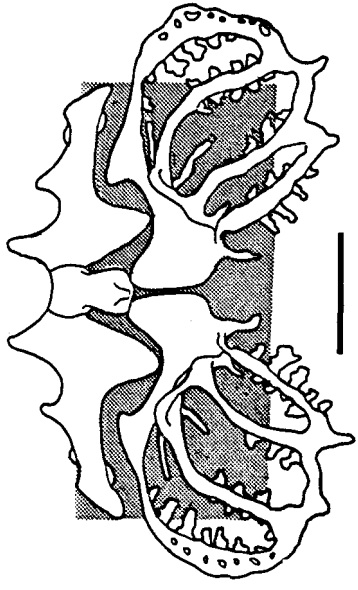
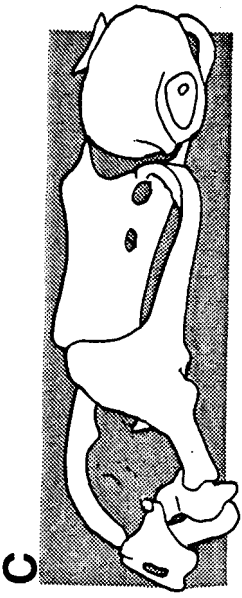


C

B

A

Fig. 10. Lateral view of chondrocranium and ventral view of  
hyobranchial apparatus. A. *Pleurodema brachyops* at stage 35. B. *P.*  
*brachyops2* at stage 37. C. *P. tucumana* at stage35. Bar = 1.0 mm



The processus ascendens has an intermediate attachment to the braincase (sensu Sokol, 1981). The posterior curvature of the palatoquadrate is wide, however, it does not extend past the level of attachment of the processus ascendens (Fig. 9). Due to dorsal curving of the posterior and lateral margins of the palatoquadrate, a slight pocket-like depression exists in *Pleurodema tucumana* at the level of the processus ascendens. The lateral margin of the palatoquadrate bears a facies hyoidis and a processus muscularis quadrati. A commissura quadratoorbitalis is present. The processus pseudopterygoideus is present in *P. tucumana*. The pars articularis quadrati articulates broadly with the horizontal region of cartilago Meckeli.

Cartilago Meckeli is sigmoid in shape. The medial region of cartilago Meckeli is more elongate and curves less anteriorly in *Pleurodema brachyops* (Fig. 9). A well-developed medial protrusion exists on the posteroventral margin of cartilago Meckeli in *P. brachyops*. The cartilagine infrarostrales articulate posteriorly with cartilago Meckeli. In ventral view, the posterior margin of each cartilago infrarostralis in *P. brachyops* and *P. brachyops2* is

concave. Furthermore, the posterior margin of the cartilagineae infrarostrales is overall broadly V-shaped ventrally.

The pars reuniens is poorly chondrified. A processus anterior hyalis, a smaller processus anterolateralis hyalis, and a processus posterior hyalis are present on the ceratohyal. Copula I is absent. Copula II is continuous with the pars reuniens. Copula II bears a processus urobranchialis, a rounded posteroventral protrusion best-developed in *Pleurodema brachyops*. Copula II articulates posteriorly with the plana hypobranchiales, and in *P. brachyops*, these are continuous. The plana hypobranchiales are not fused medially in *P. tucumana*, however, in both *P. brachyops* and *P. brachyops2*, the plana hypobranchiales are fused posteriorly.

Each planum hypobranchiale is associated with four dorsally concave ceratobranchials and four dorsal spiculae. In *Pleurodema brachyops* and *P. brachyops2*, spiculae I and II are indistinguishable. All of the ceratobranchials are continuous posteriorly with commissurae terminales; commissurae terminales II and III each bear a posteroventral process. A network of poorly chondrified cartilage exists among the ceratobranchials. This cartilaginous

network is lacking on the medial margin of ceratobranchial III. In *P. brachyops*, this network is also lacking on the lateral margin of ceratobranchial II. Proximally, ceratobranchial I bears a well-developed medially concave processus anterior branchialis. Ceratobranchial I is perforated. In *P. brachyops*, ceratobranchial IV is also perforated. *Pleurodema brachyops*2 lacks perforations on ceratobranchials I and IV, but the commissurae terminales are fenestrated. A closed processus branchialis is present between ceratobranchial II and III.

## INTERNAL ORAL ANATOMY

### *LIMNOMEDUSA MACROGLOSSA*

The buccal floor is shaped like a tear-drop, wider than long (Fig. 11). Four infralabial papillae are transversely oriented; the medial pair are attenuate with pustulate anterior margins while the lateral pair are broader with seven to ten pustulations on their tips. Four lingual papillae lie in a cluster at the midline. The most anterior is palmate and the other three are bifurcated at least once. The buccal floor arena is U-shaped and contains about 50-60

papillae per side among about half as many pustulations. The buccal floor arena papillae are unbifurcated and, for the most part, are directed medially or anteriorly. Prepocket papillae are indistinguishable. The ventral velum is smooth, and its margin hangs free and bears a marginal projection over each filter cavity. Four blunt papillae are on either side of the median notch. The buccal roof of *Limnomedusa* is pear-shaped, and tooth-like projections extend from the lateral portions of the upper lip (Fig. 12). Posterior to the keratinized upper beak, hundreds of pustulations cover the prenarial arena. A wide transversely compressed papilla extends medially into the prenarial arena from each side. A semicircular pustulated ridge lies anterior to the prenarial valves. Two prenarial papillae exist on each side. The postnarial arena has two rows of anteriorly serrated papillae on either side of the midline increasing in size posteriorly. Postnarial papillae have a very broad continuous base, and some of these papillae extend posteriorly past the median ridge. The median ridge contains a total of seven papillae that decrease in size laterally.

Fig. 11. Scanning electron micrograph of the buccal floor of *Limnomedusa macroglossa* at stage 37. (15Kv, 30x, Bar = 1.0 mm). The anterior of the specimen is toward the top of the page.





Fig. 12. Scanning electron micrograph of the buccal roof of *Limnomedusa macroglossa* at stage 37. (15Kv, 30x, Bar = 1.0 mm). The anterior of the specimen is toward the top of the page.



The buccal roof arena has two papillae just posterior to the median ridge among about 50 pustulations, and two more papillae posterior to these so they appear as four corners of a square. The buccal roof arena papillae are well-developed and are arranged in two rows among scattered pustulations. A few lateral roof papillae exist anterior to a smooth semicircular region surrounding the buccal roof arena. The glandular zone is well defined and secretory pits are visible. The dorsal velum bears many pustulations, however, it is discontinuous at the midline where it bears six to eight papillae.

#### *PHYSALAEEMUS GRACILIS*

The buccal floor is triangular (Fig. 13). Two pairs of infralabial papillae are present, the anteromedial pair is smaller, while the posterolateral pair is larger and more rugose. The four lingual papillae are all equal size bearing pustulate tips; the medial pair abut each other. The buccal floor arena is defined by two posteromedial rows of large papillae, some of which bifurcate. Between these papillae are about 30 pustulations. The buccal

pockets are angled about 25° off the transverse plane. The ventral velum is textured, but lacks any distinguishable glandular zone or secretory pits. A distinct free lip, lacking any marginal protrusions is discontinuous at the median notch.

The upper lip bears six papillae laterally, exterior to the keratinized beak (Fig. 14). The prenarial arena contains many pustulations anteriorly, but posteriorly the surface is smooth. However, a ridge exists posteriorly bearing four peaks; each peak exhibits three to five pustulations. Prenarial papillae appear to be lacking in *Physalaemus gracilis*. Nares are approximately one-third of the way back into the oral cavity. The postnarial arena is broadly triangular. Two moderate sized pustulations are medial to two large papillae with serrated apices. On each side of the buccal floor, the pair of lateral ridge papillae share a common base and both have jagged tips. The median ridge is semicircular and free anteriorly.

The buccal roof arena is circular and is delimited by about ten papillae having pustulate tips. Between the papillae are 35-40 pustulations. A semicircular row of pustulations lies anterior to the

Fig. 13. Scanning electron micrograph of the buccal floor of *Physalaemus gracilis* at stage 37. (15Kv, 30x, Bar = 1.0 mm). The anterior of the specimen is toward the top of the page.

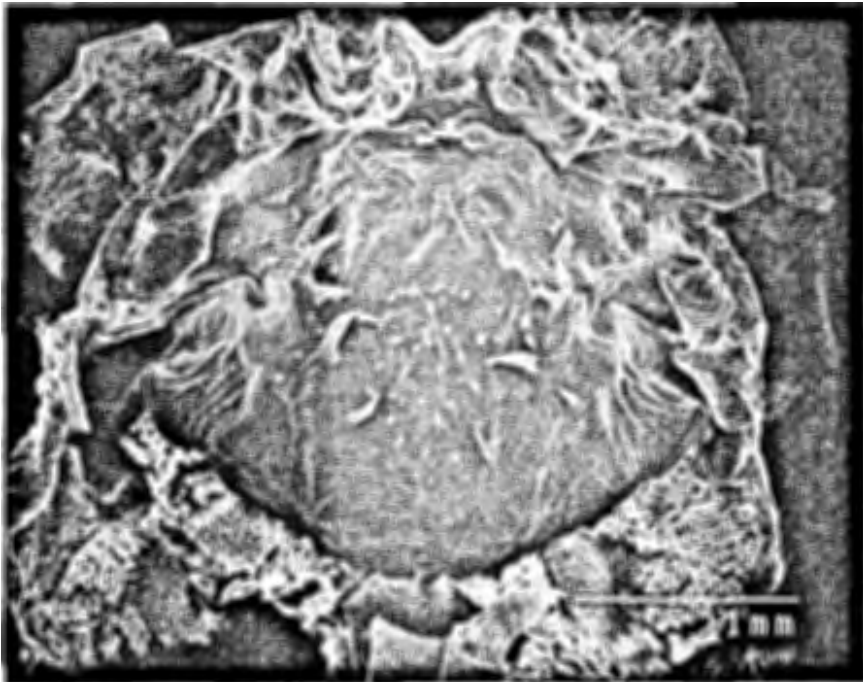


Fig. 14. Scanning electron micrograph of the buccal roof of *Physalaemus gracilis* at stage 37. (15Kv, 30x, Bar = 1.0 mm). The anterior of the specimen is toward the top of the page.





glandular zone, which is full of secretory pits. The anterior margin of the glandular zone is wavy laterally, and medially, the zone itself is thinner. The dorsal velum is interrupted medially.

*PHYSALAEMUS HENSELII*

The buccal floor produces two large polyfurcated infralabial papillae, both angled medially (Fig. 15). The two attenuate lingual papillae are adjacent to each other on the midline. The buccal floor arena is demarcated by ten bifurcating papillae. Three longitudinal rows of pustulations extend posteriorly toward the ventral velum. The buccal pockets located 60% of the posterior distance of the buccal floor, and these are angled 30° off the transverse plane. The ventral velum bears a distinct wavy lip bearing a few random marginal projections. No median notch is evident.

The prenarial arena of the buccal roof is covered with many small antler-like papillae near the beak (Fig. 16). These papillae are graded posteriorly into pustulations. Posteriorly in the prenarial arena a multi-peaked ridge exists bearing 15-20 pustulations. Prenarial papillae are indistinguishable. The nares are 25% of the

distance back into the oral cavity. The postnarial arena bears two well- developed papillae each containing many small branches. The lateral ridge papillae are rugose, broad based, and bear five to six pustulations on their tip. The median ridge bears 10-15 distinct pustulations along its anterior margin. The buccal floor is rugose. The buccal roof arena is demarcated by six well-developed bifurcating papillae between which are approximately 10 pustulations. About 30 pustulations form a semicircle around the buccal roof arena anterior to the glandular zone. The anterior margin of the glandular zone is wavy.

Fig. 15. Scanning electron micrograph of the buccal floor of *Physalaemus henselii* at stage 31. (15Kv, 40x, Bar = 1.0 mm). The anterior of the specimen is toward the top of the page.

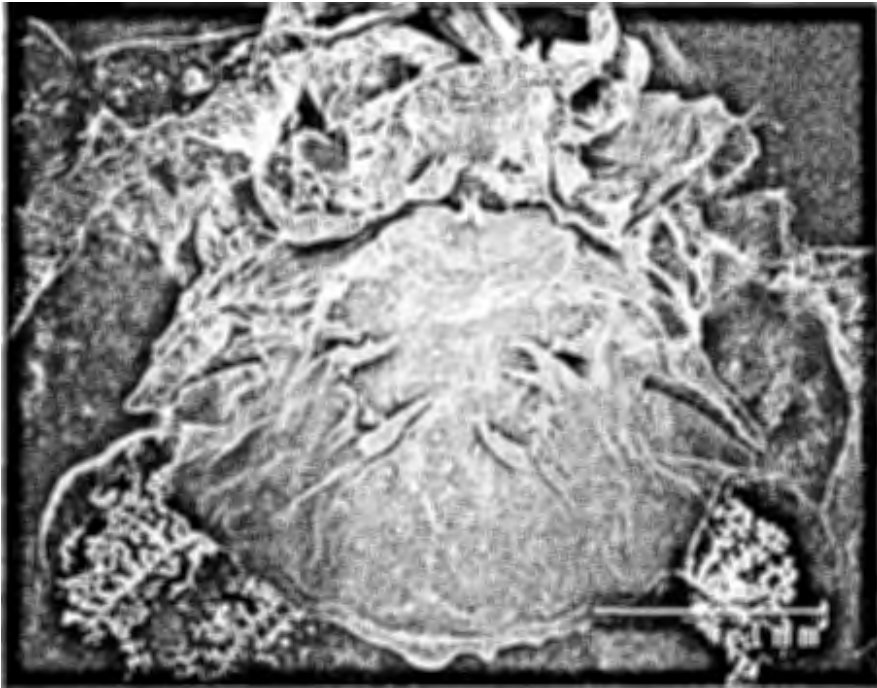


Fig. 16. Scanning electron micrograph of the buccal roof of *Physalaemus henselii* at stage 31. (15Kv, 40x, Bar = 1.0 mm). The anterior of the specimen is toward the top of the page.



## LARVAL CHARACTERS FOR PHYLOGENETIC ANALYSIS

The present study, combined with previous chondrocranial descriptions and character matrices (Lavilla, 1992; Lavilla and Fabrezi, 1992; Larson and de Sá, 1998), identified the following 28 characters:

- A. Ventromedial fusion of suprarostrals. Corpora are independent in the subfamily Hylodinae, fused in Ceratophryinae and *Edalorhina perezii*, and both conditions exist present in the Telmatobiinae. 0 = unfused, 1 = fused.
- B. Dorsal fusion of the suprarostrals and ala. The corpora and ala are independent in Hylodinae, fused in Ceratophryinae, and both conditions are present in the other subfamilies. 0 = unfused, 1 = fused.
- C. Ventral fusion of the suprarostrals and ala. The suprarostrals are ventrally fused in Ceratophryinae, however, this fusion is variably present in all other subfamilies. 0 = unfused, 1 = fused.
- D. Cornua trabeculae length relative to total length of the chondrocranium. The cornua trabeculae of Hylodinae are greater



than 25% of the length of the chondrocranium. The cornua trabeculae of the members of *Leptodactylus*, *Limnomedusa*, *Alsodes*, *Odontophrynus*, and *Telmatobius* are 20-25% the length of the chondrocranium. *Physalaemus* and *Edalorhina* have shorter cornua trabeculae, between 15-20% of the total chondrocranial length. *Ceratophrys*, *Adenomera*, and *Cycloramphus* have very short cornua trabeculae, less than 15% of the length of the chondrocranium. This character was variable among the remaining genera. 0 = >25%, 1 = 20-24%, 2 = 15-19%, 3 = <15%.

E. The length of the capsulae auditivae relative to total chondrocranial length. Except for *Cycloramphus stejnegeri*, *Telmatobiinae*, *Hylodinae*, and *Ceratophryinae* have capsulae auditivae that are less than 30% of the length of the chondrocranium. This character is variable within *Leptodactylinae*. 0 = less than 30%, 1 = greater than 30%.

F. Processus anterolateralis of the crista parotica. It is lacking in the subfamily *Ceratophryinae* and present in all others. 0 = present, 1 = absent.

- G. Larval processus oticus. This character is only present in *Ceratophrys* and *Alsodes barrioi*. 0 = absent, 1 = present.
- H. Projection of posterior curvature of palatoquadrate. This character is only present in two leptodactylines, *Edalorhina perezii* and *Leptodactylus chaquensis*. 0 = absent, 1 = present.
- I. Processus posterolateralis of the crista parotica.<sup>‡</sup> This character is absent in Ceratophryinae, present in Hylodinae, and variably present in the other subfamilies. 0 = absent, 1 = present.
- J. Posterolateral extension of the palatoquadrate. The posterior curvature of the palatoquadrate is anterior to the attachment of the processus ascendens in Hylodinae. It is past the level of the processus ascendens in Ceratophryinae. This character is variable among the remaining subfamilies. 0 = anterior to the processus ascendens, 1 = at the level of the processus ascendens, 2 = posterior to the processus ascendens.
- K. Attachment of the processus ascendens. The processus ascendens of Leptodactylinae has an intermediate attachment to the braincase with the exception of *Leptodactylus petersii*, which has a low attachment. The processus ascendens of Hylodinae and

*Ceratophrys* also has a low attachment. This character is variable in all other genera. 0 = low, 1 = intermediate, 2 = high.

L. Processus pseudopterygoideus. This character is variably present in Telmatobiinae and Leptodactylinae; it is absent in Ceratophryinae and Hylodinae. 0 = absent, 1 = present.

M. Fusion of the processus pseudopterygoideus to the braincase. It is fused in *Alsodes barrioi* and *Telmatobius pisanoi*. 0 = unfused, 1 = fused.

N. Pars articularis quadrati. The pars articularis quadrati is distinct from the processus muscularis in Hylodinae, Telmatobiinae, and Leptodactylinae, except for *Leptodactylus petersii* and *L. chaquensis*. the condition is variable in Ceratophryinae. 0 = distinct from the processus muscularis quadrati, 1 = not distinct.

O. Processus muscularis quadrati. *Cycloramphus stejnegeri*, *Adenomera marmorata*, *Crossodactylus gaudichaudii*, and *Lepidobatrachus* have a reduced processus muscularis quadrati. All other taxa have a well-developed processus muscularis quadrati. 0 = well-developed, 1 = reduced.

P. Commissura quadratoorbitalis. This connection is absent in Ceratophryinae and Hylodinae; it is variable in other subfamilies. 0 = absent, 1 = present.

Q. Processus anterolateralis hyalis. This process is present in Leptodactylinae and Telmatobiinae, except *Telmatobius bolivianus*. It is variable in Hylodinae and absent in Ceratophryinae. 0 = absent, 1 = present.

R. Processus branchialis. A processus branchialis is absent in Telmatobiinae and Hylodinae. It is variable in other subfamilies. 0 = open, 1 = closed.

S. Processus lateralis of the cornua trabeculae. Except for *Cycloramphus stejnegeri*, this process is present in Telmatobiinae and Hylodinae. It is variable in other subfamilies. 0 = present, 1 = absent.

T. Frontoparietal fontanelle. The frontoparietal fontanelle may be divided by the taenia tectum medialis and taenia tectum transversalis. It is variable in all subfamilies. 0 = divided, 1 = undivided.

U. Taeniae tecti marginales in relation to the capsula auditiva.

They are not continuous in *Physalaemus* and *Pleurodema borellii*.

0 = continuous, 1 = not continuous.

V. Foramen trochleare. This foramen is variable present in all subfamilies. 0 =distinguishable, 1 = indistinguishable.

W. Ventral protrusion of the posteromedial margin of cartilago Meckeli. This protrusion is variable within Leptodactylinae. It is not present in the other subfamilies. 0 = absent, 1 = distinct.

X. Copula I. This cartilage is present in *Telmatobius bolivianus*, *Limnomedusa macroglossa*, and *Ceratophrys cornuta*. 0 = absent, 1 = present.

Y. Processus quadratoethmoidalis. This character was not found in *Lepidobatrachus* or *Cycloramphus stejnegeri*; it is present in the rest of the Telmatobiinae, Hylodinae, and Leptodactylinae, and is variable in *Ceratophrys*. 0 = present, 1 = absent.

Z. Plana hypobranchiales. The fusion of these cartilages is variably present in each of the subfamilies. 0 = not fused, 1 = fused posteromedially, 2 = completely fused.

Aa. Processus urobranchialis. This process is lacking in *Cycloramphus stejnegeri*, however, it is present in Telmatobiinae, Hyloinae, and Leptodactylinae, and is variable in Ceratophryinae.

0 = present, 1 = extremely reduced or absent.

Ab. Cartilagine infrarostrales. The cartilagine infrarostrales of *Cycloramphus stejnegeri* and Ceratophryinae are fused. 0 = unfused, 1 = fused.

The data matrix for these character states can be found in Table 1.

**TABLE 1:** Data matrix for phylogenetic analysis.

|                                    | ABC                         | DEF                      | GHI | JKL        | MNO | PQR | STU | VWX | YZA | aAb |  |
|------------------------------------|-----------------------------|--------------------------|-----|------------|-----|-----|-----|-----|-----|-----|--|
| <i>Hyla lanciformis</i>            | 110                         | 11000000000000           | 001 | 1000100000 | 0   |     |     |     |     |     |  |
| <i>Alsodes barrioi</i>             | 000                         | 101101201100110010000000 | 0   |            |     |     |     |     |     |     |  |
| <i>Cycloramphus stejnegeri</i>     | 101311000220001010110100121 | 1                        |     |            |     |     |     |     |     |     |  |
| <i>Odontophrynus lavillai</i>      | 1101000011N1000110010NN0000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Odontophrynus americanus</i>    | 0101000001N1000110010NN0000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Telmatobius bolivianus</i>      | 100100000210000000010N01010 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Telmatobius ceiorum</i>         | 1001000012010000100000NQ000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Telmatobius pisanoi</i>         | 0001000012111000100000N0000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Ceratophrys cornuta</i>         | 111301100200000001000101101 | 1                        |     |            |     |     |     |     |     |     |  |
| <i>Ceratophrys cranwelli</i>       | 111301100200010000100N00000 | 1                        |     |            |     |     |     |     |     |     |  |
| <i>Lepidobatrachus laevis</i>      | 1112010002N0011000110N00121 | 1                        |     |            |     |     |     |     |     |     |  |
| <i>Lepidobatrachus llanensis</i>   | 111101000220011000000N00121 | 1                        |     |            |     |     |     |     |     |     |  |
| <i>Crossodactylus gaudichaudii</i> | 000001001000001010010100020 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Hylodes nasus</i>               | 000000001000000000000100000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Adenomera marmorata</i>         | 110310001210001010100010000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Edalorhina perezii</i>          | 010200011111000010000000010 | N                        |     |            |     |     |     |     |     |     |  |
| <i>Leptodactylus chaquensis</i>    | 110110011210010111000010010 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Leptodactylus gracilis</i>      | 110110001110000110110110020 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Leptodactylus petersi</i>       | 110111000200010111110000020 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Leptodactylus rhodomystax</i>   | 110110001210000110000010010 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Limnomedusa macroglossa</i>     | 100100000111000111000011000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Physalaemus biligonigerus</i>   | 1102000000N0000110011NN0000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Physalaemus cuqui</i>           | 1002010001N0000110011NN0000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Physalaemus gracilis</i>        | 110200000111000010001000000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Physalaemus henselii</i>        | 110211000210000010011000000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Physalaemus pustulosus</i>      | 110210000111000110001100000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Pleurodema borellii</i>         | 1112000002N1000111011NN0000 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Pleurodema brachyops</i>        | 110200001110000111110010010 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Pleurodema brachyops2</i>       | 111100001110000111000000020 | 0                        |     |            |     |     |     |     |     |     |  |
| <i>Pleurodema tucumana</i>         | 111100001111000111010100000 | 0                        |     |            |     |     |     |     |     |     |  |

## DISCUSSION

### CHONDROCRANIAL MORPHOLOGY AND SKELETOGENESIS

Chondrocranial synapomorphies were identified at the generic and subfamilial level. Ceratophryinae is united by the following synapomorphies: 1) fused infrarostrals, 2) fused suprarostrals, 3) posterior curvature of the palatoquadrate extending past the level of attachment of the processus ascendens, 4) processus anterolateralis hyalis absent, 5) commissura quadratoorbitalis absent, and 6) processus pseudopterygoideus absent. Other characters vary within the subfamily and within genera of the subfamily.

Sokol (1981) defined three conditions for the attachment of the processus ascendens to the braincase: high, intermediate, and low. A “high” attachment, which is considered the primitive condition for anurans (Sokol, 1981) corresponds to the fusion of the processus ascendens to the braincase above the foramen oculomotorium. An attachment behind, and at the level of, the foramen oculomotorium corresponds to Sokol’s “intermediate” condition. The most derived condition, a “low” attachment,



corresponds to the fusion of the processus ascendens below the foramen oculomotorium. *Lepidobatrachus* has a high attachment, while *Ceratophrys* has a low attachment (sensu Sokol, 1981). The size of the processus muscularis quadrati (reduced in *Lepidobatrachus*) and the degree of fusion of the plana hypobranchiales (fused in *Lepidobatrachus*) also varies between these two genera. The processus lateralis trabeculae is variably present in *Ceratophrys* and *Lepidobatrachus*. The frontoparietal fontanelle is open in *Lepidobatrachus laevis*, a derived condition (sensu Sokol, 1981). *Ceratophrys cranwelli* has a commissura quadratoethmoidalis on the commissura quadratocranialis anterior and a processus urobranchialis on copula II, while no other species in the subfamily have these elements. *Ceratophrys cornuta* is the only ceratophryine reported to have a closed processus branchialis (Wild, 1997).

The loss and fusion of chondrocranial components in Ceratophryinae are adaptations associated with a carnivorous diet (Cei, 1968; Heyer, 1979; Ruibal and Thomas, 1988; Wassersug and Heyer, 1988, Larson and de Sá, 1998). Another character associated

with carnivory is the shortening of the cornua trabeculae (de Sá, 1994). The cornua trabeculae of *Ceratophrys* are less than 15% of the total length of the chondrocranium. The length of the cornua trabeculae is variable in Telmatobiinae and Leptodactylinae.

*Cycloramphus stejnegeri* and *Adenomera marmorata* have cornua trabeculae that represent less than 15% of their total chondrocranial length. However, these are not carnivorous taxa. Lavilla (1991) and De la Riva (1995) reported that these taxa have non-feeding larvae, surviving solely off of yolk reserves. Therefore, the shortening of the cornua trabeculae may be associated with chondrocranial modifications associated with their non-feeding larval ecology.

The majority of known leptodactylids have cornua trabeculae that are 20-25% of the total chondrocranial length. This is slightly shorter than the reported average length of cornua trabeculae, 33% of the chondrocranial length, for free-swimming pond-type larvae (Sokol, 1981; de Sá, 1988). *Physalaemus*, *Edalorhina*, and some species of *Pleurodema* have slightly shorter cornua trabeculae, representing 15-20% of the chondrocranial length. Hylodinae have

cornua trabeculae that are greater than 25% of the chondrocranial length.

The two species studied from Hylodinae share several chondrocranial characteristics. However, *Crossodactylus gaudichaudii* exhibits the following derived character states as defined by Sokol (1981): 1) processus anterolateralis of the crista parotica absent, 2) taenia tecti medialis and taenia tecti transversalis absent, and 3) processus muscularis quadrati reduced. *Hylodes nasus* has unfused plana hypobranchiales and lacks a processus anterolateralis hyalis.

The chondrocrania of Telmatobiinae are greatly diverse, but they share the following synapomorphies: 1) larval processus oticus present, 2) open processus branchialis, 3) a well-developed processus muscularis quadrati, 4) processus anterolateralis hyalis present, and 5) processus lateralis trabeculae present.

The fusion of the suprarrostral corpora and alae varies in Telmatobiinae, both inter- and intragenerically. The corpora of *Cycloramphus stejnegeri* are ventromedially fused and in turn, they are fused with the alae dorsolaterally. *Alsodes barrioi* and

*Telmatobius pisanoi* have four independent suprarostrals components, while *T. bolivianus* and *T. ceiorum* only have the suprarostrals corpora fused ventromedially. The attachment of the processus ascendens to the braincase is also variable.

*Cycloramphus stejnegeri* has a high attachment, *T. bolivianus* and *T. pisanoi* have an intermediate attachment, and *A. barrioi* and *T. ceiorum* have a low attachment (sensu Sokol, 1981). The posterior curvature of the palatoquadrate in *Odontophrynus* extends to the level of the attachment of the processus ascendens; however, in other known telmatobiines, it extends beyond this point.

Considerable chondrocranial variation exists in the Leptodactylinae; however, the subfamily is characterized by suprarostrals corpora that are fused ventromedially and an intermediate attachment of the processus ascendens. In addition, they possess a processus anterolateralis hyalis, a well-developed processus muscularis quadrati, a processus quadratoethmoidalis, and lack a larval processus oticus. *Limnomedusa macroglossa* is unique in having a pronounced finger-like processus anterolateralis of the crista parotica and a copula I. *Adenomera marmorata* has a

reduced processus muscularis quadrati and a noticeably narrow commissura quadratocranialis anterior. *Physalaemus* tadpoles are characterized by an open processus branchialis and the lack of continuity between the orbital cartilages and the capsulae auditivae.

*Pleurodema brachyops* specimens showed clear differences in chondrocranial morphology. The specimens described as *Pleurodema brachyops* differed from *P. brachyops*2 specimens by possessing the following character states: 1) ventral fusion of suprarostral corpora and alae absent, 2) taenia tectum medialis and taenia tectum transversalis absent, and 3) ventral protrusion on the posteromedial margin of cartilago Meckeli distinct, 4) processus lateralis trabeculae absent, and 5) cornua trabeculae that represent less than 20% of the total chondrocranial length. The cornua trabeculae of *P. brachyops* were noticeably broader than those of *P. brachyops*2.

Skeletogenesis has been reported for four species of Leptodactylidae, *Ceratophrys cornuta* (Wild, 1997), *Eleutherodactylus nubicola* (Lynn, 1942), *E. guentheri* (Lynn and Lutz, 1946), and *E. coqui* (Hanken et al., 1992). *Eleutherodactylus*

exhibits direct development, consequently, deviations in its pattern of skeletogenesis from other leptodactylids are probably related to the lack of a free-swimming tadpole.

Among free-swimming larvae, ossification begins later for *Physalaemus* than other reported anurans including dendrobatids (Henle, 1992; Haas, 1995; de Sá and Hill, 1998), microhylids (de Sá and Trueb, 1991), *Hyla* and *Pseudacris* (Hylidae) (Gaudin, 1973; de Sá, 1988), and other leptodactylids (Wild, 1997), however, skeletogenesis in *Physalaemus* occurs earlier than that reported for Myobatrachidae (Davies, 1989) and *Osteopilus* (Trueb, 1966) occurs later in development than *Physalaemus*.

Cranial ossification in *Physalaemus pustulosus* begins before *P. gracilis* (Table 2). In general, the first three cranial elements to ossify in anurans are the frontoparietals, parasphenoid, and exoccipitals (Hanken and Hall, 1988). Current data for *Physalaemus gracilis* agrees with this pattern. However, in *P. pustulosus* the premaxillae appear before the exoccipitals. The premaxillae and squamosals appear after the onset of metamorphosis (about stage

**TABLE 2:** Sequence of skeletal ossification in *Physalaemus gracilis* and *Physalaemus pustulosus*. Endochondral bones are in bold type. The dashed line indicates the end of metamorphosis.

| Gosner Stage | <i>Physalaemus gracilis</i> |                             | <i>Physalaemus pustulosus</i> |                             |
|--------------|-----------------------------|-----------------------------|-------------------------------|-----------------------------|
|              | <u>CRANIAL</u>              | <u>POST-CRANIAL</u>         | <u>CRANIAL</u>                | <u>POST-CRANIAL</u>         |
| 36           |                             |                             | Frontoparietals               |                             |
| 37           | Frontoparietals             |                             |                               | <b>Femurs</b>               |
| 38           | Parasphenoid                | <b>Neural Arches</b>        | Parasphenoid                  | <b>Clavicles</b>            |
|              |                             | <b>Transverse processes</b> |                               | <b>Tibiofibulae</b>         |
| 39           |                             | Clavicles                   | Premaxillae                   | <b>Vertebral centra</b>     |
|              |                             | <b>Femurs</b>               |                               |                             |
|              |                             | <b>Humeri</b>               |                               |                             |
| 40           | Premaxillae                 | Cleithra                    | Squamosals                    | <b>Tibiales</b>             |
|              | Exoccipitals                | <b>Tibiofibulae</b>         | Exoccipitals                  | <b>Fibulares</b>            |
|              |                             | <b>Tibiales</b>             |                               | <b>Humeri</b>               |
|              |                             | <b>Fibulares</b>            |                               | <b>Radii</b>                |
|              |                             | <b>Metacarpals</b>          |                               | <b>Ulnae</b>                |
|              |                             | <b>Metatarsals</b>          |                               | <b>Scapulae</b>             |
|              |                             | <b>Radii</b>                |                               | <b>Ilia</b>                 |
|              |                             | <b>Ulnae</b>                |                               | <b>Neural Arches</b>        |
|              |                             | <b>Coracoids</b>            |                               |                             |
|              |                             | <b>Scapulae</b>             |                               |                             |
|              |                             | <b>Ilia</b>                 |                               |                             |
|              |                             | <b>Vertebral centra</b>     |                               |                             |
| 41           | Squamosals                  | <b>Carpals</b>              | Angulosplenials               | Cleithra                    |
|              | <b>Prootics</b>             | <b>Tarsals</b>              | Nasals                        | <b>Ischia</b>               |
|              |                             | <b>Ischia</b>               | Septomaxillae                 | <b>Transverse processes</b> |
|              |                             | <b>Urostyle</b>             | <b>Prootics</b>               | <b>Coracoids</b>            |
|              |                             |                             |                               | <b>Metacarpals</b>          |
|              |                             |                             |                               | <b>Carpals</b>              |
|              |                             |                             |                               | <b>Metatarsals</b>          |
|              |                             |                             |                               | <b>Tarsals</b>              |
|              |                             |                             |                               | <b>Urostyle</b>             |
| 42           | Angulosplenials             |                             | Maxillae                      |                             |
|              | Nasals                      |                             |                               |                             |
|              | Maxillae                    |                             |                               |                             |
|              | Dentaries                   |                             |                               |                             |
| 43           | Pterygoids                  |                             | Pterygoids                    |                             |
|              | Septomaxillae               |                             | Dentaries                     |                             |
| 44           |                             |                             |                               |                             |
| 45           |                             |                             | Palatines                     |                             |
|              |                             |                             | <b>Mentomeckelians</b>        |                             |
|              |                             |                             |                               |                             |
|              | Palatines                   |                             | Vomers                        |                             |
|              | <b>Mentomeckelians</b>      |                             | Quadratojugals                |                             |
|              | Vomers                      |                             | <b>Columellae</b>             |                             |
|              | Quadratojugals              |                             | <b>Sphenethmoids</b>          |                             |
|              | <b>Columellae</b>           |                             | <b>Opercula</b>               |                             |
|              | <b>Sphenethmoids</b>        |                             |                               |                             |
|              | <b>Opercula</b>             |                             |                               |                             |

42) in most anurans including Hylidae (Gaudin, 1973; de Sá, 1988; de Sá and Lavilla, 1996), *Hamptophryne* (de Sá and Trueb, 1991), *Dendrobates* (Haas, 1995; de Sá and Hill, 1998), *Bombina* (Maglia and Púgener, 1998), and *Ceratophrys* (Wild, 1997). These elements were observed earlier in *Physalaemus*, between stages 39 - 41. Furthermore, the prootics usually are present by stage 38 in Dendrobatidae (Haas, 1995; de Sá and Hill, 1998), *Hyla* and *Pseudacris* (Gaudin, 1973; de Sá, 1988; de Sá and Lavilla, 1996), *Ceratophrys* (Wild, 1997), and *Hamptophryne* (de Sá and Trueb, 1991), however, in *Physalaemus* the prootics appear during stage 40. The septomaxillae are observable as early as stage 38 in *Dendrobates* (de Sá and Hill, 1998) and *Phyllomedusa* (de Sá and Lavilla, 1996) or after the completion of metamorphosis in *Epipedobates* (de Sá and Hill, 1998) and *Pseudophryne* (Davies, 1989). The variation in developmental pattern of this bone is also seen in *Physalaemus*, appearing in stage 41 of *P. pustulosus* and stage 43 in *P. gracilis*. Ossification of the mentomeckelians and the palatines occurs post-metamorphically in most anurans (Trueb, 1985; Davies, 1989; de Sá and Trueb, 1991; de Sá and Lavilla, 1996;



de Sá and Hill, 1998), and the present data for *Physalaemus gracilis* agrees with this tenet, however, in *P. pustulosus*, these bones appear in stage 45.

The post-cranial ossification sequence is less reported for anurans. Generally, the pectoral girdle does not ossify before the pelvic girdle and the ischium is the last post-cranial bone to form pre-metamorphically; *Physalaemus* demonstrates these patterns. Additionally, the carpals and tarsals ossify post-metamorphically in most frogs, however, these elements form at stage 41 in *Physalaemus*. Overall, the patterns of post-cranial skeletogenesis among the two species of *Physalaemus* observed is similar throughout development with the exceptions of the neural arches and transverse processes. These elements appear at stage 38 in *P. gracilis* and at stages 40 and 41, respectively, in *P. pustulosus*. The developmental differences between *Physalaemus* and other taxa seem to be in the pattern of specific bones, not regions of ossification.

## INTERNAL ORAL ANATOMY

The examination of the internal oral anatomy of Leptodactylidae provided some clues on the evolution the group. The internal oral anatomy of leptodactylid larvae correlates with their ecology (Wassersug and Heyer, 1988). Members of Telmatobiinae and Hylodinae have more buccal floor arena papillae and buccal roof arena papillae than either Ceratophryinae or Leptodactylinae. The ceratophryine species whose internal oral anatomy has been described previously have macrophagous tadpoles, and the loss of papillae has been postulated an adaptation to their feeding mode (Cei, 1968; Ruibal and Thomas, 1988). Additionally, several leptodactylid larvae develop in a foam nest feeding on yolk reserves. The observed reduction in the number of papillae in Leptodactylinae correlates with the amount of time spent as a free-swimming tadpole. Foam nesting is not observed in *Limnomedusa macroglossa* (Gudynas and Gehrau, 1981), and *Limnomedusa* has more than 30 papillae on their buccal floor and about 20 papillae on their buccal roof. Furthermore, *Physalaemus* larvae initially develop inside a foam nest, but later larvae escape

the nest and complete their development as a free-swimming tadpole. *Physalaemus* has less than ten papillae on their buccal roof and floor. *Adenomera* larvae complete their development in the foam nest, and they lack papillae on their buccal roof and floor (Wassersug and Heyer, 1988).

*Physalaemus henselii* differs from other members of the genus by having only two infralabial papillae and two lingual papillae. A characteristic of leptodactylid larvae is the presence of four infralabial papillae (Wassersug and Heyer, 1988).

#### PHYLOGENETIC ANALYSIS

The 28 characters identified here (Table 1) were used in phylogenetic analyses with *Hyla lanciformis* (Hylidae) as the outgroup. A heuristic search resulted in four equally parsimonious trees, (114 steps long, C.I. .289, Fig. 17). A strict consensus tree is given in Figure 18.

This analysis identifies two major clades within Leptodactylidae: A) Telmatobiinae, Ceratophryinae, and Hylodinae (clade I) and B) Leptodactylinae and *Odontophrynus* (clade II) (Figs.

17, 18). Clade I can be further sub-divided into two monophyletic groups; the first consists of Hylodinae, *Alsodes*, *Telmatobius pisanoi*, and *T. ceiorum*, and the second consists of Ceratophryinae and *Cycloramphus*.

The four trees differ in the relationships of two taxa:

*Telmatobius bolivianus* and *Pleurodema borellii*. <sup>‡</sup>*Telmatobius bolivianus* alternates as the sister taxa to the Hylodinae-*Alsodes*-*Telmatobius* clade or to the Ceratophryinae-*Cycloramphus* clade. The strict consensus tree shows an unresolved trichotomy among these two clades and *T. bolivianus* (Fig. 18).

*Pleurodema borellii* alternatively clusters as the sister group to a monophyletic assemblage of three *Physalaemus* or *Pleurodema borellii* forms an unresolved trichotomy with *Physalaemus* and *Edalorhina*.

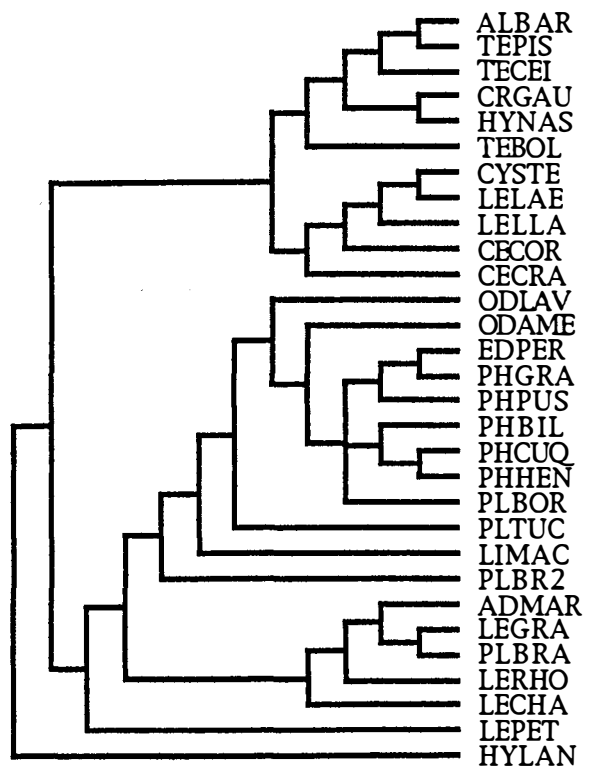
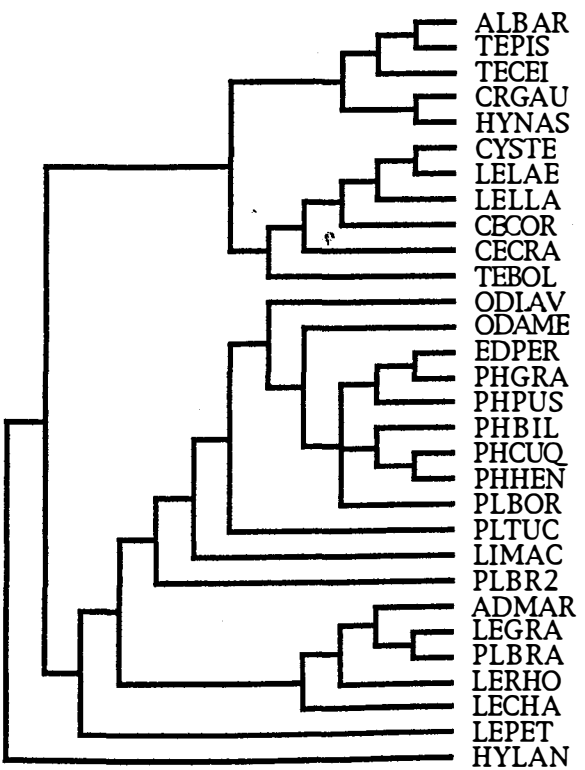
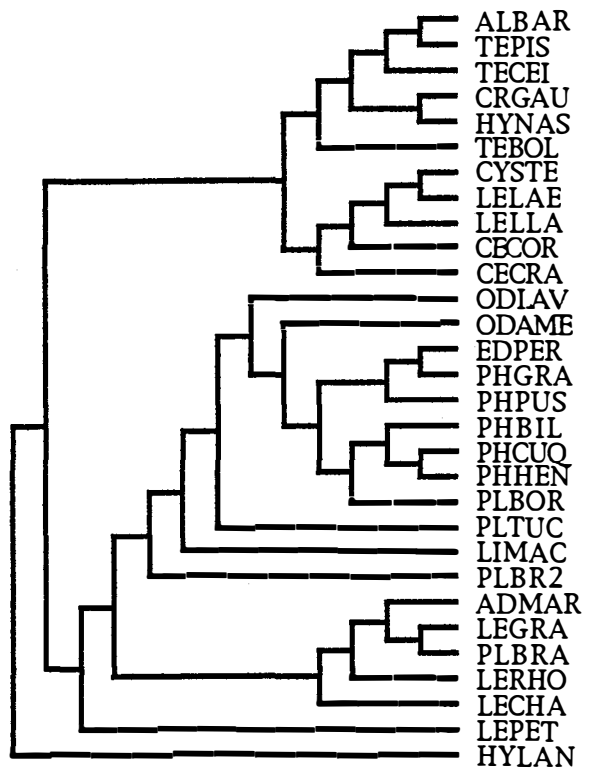
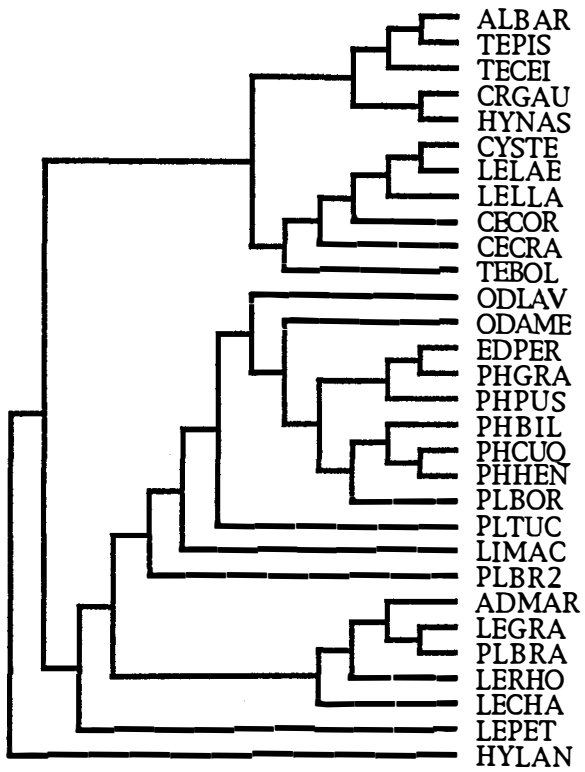
Within Leptodactylidae, clade I is supported by having capsulae auditivae that are less than 30% of the total chondrocranial length ( $E_0$ ), an open processus branchialis ( $R_0$ ), and processus anterolateralis hyalis absent ( $Q_0$ ). However, the capsulae auditivae of *Cycloramphus stejnegeri* are greater than 30% of the

total chondrocranial length. Furthermore, *Ceratophrys cornuta* has a closed processus branchialis. An equally parsimonious interpretation of the evolution of the processus anterolateralis hyalis is for it to be present in the ancestor and to have been lost independently in several lineages.

Within clade I, a group consists of Ceratophryinae and *Cycloramphus*. This group is supported by suprarostrals corpora and alae that are ventrally fused ( $C_1$ ), cornua trabeculae that are less 15% of the chondrocranial length ( $D_3$ ), and a processus anterolateralis of the crista parotica absent ( $F_1$ ), larval processus oticus present ( $G_1$ ), pars articularis quadrati that is not distinct from the processus muscularis in lateral view ( $N_1$ ), and fused infrarostrals ( $Ab_1$ ). A reversion to cornua trabeculae that are greater than 15% of the chondrocranial length occurs in *Lepidobatrachus*. Shortening of the cornua trabeculae has been previously associated with a carnivorous diet (de Sá, 1994). *Lepidobatrachus* is carnivorous, but has longer cornua trabeculae than expected. This can be explained if we consider that *Lepidobatrachus* larvae are carnivorous, but macrophagous, swallowing prey whole through suction feeding (Cei,

Fig. 17. Four equally parsimonious trees produced from the data matrix. C.I. = .289, Tree length = 114 steps. Species are as follows:

Outgroup = HYLAN - *Hyla lanciformis* ♂  
 Ceratophryinae = CECOR - *Ceratophrys cornuta*  
                   CECRA - *Ceratophrys cranwelli*  
                   LELAE - *Lepidobatrachus laevis*  
                   LELLA - *Lepidobatrachus llanensis*  
 Hylodinae = CRGAU - *Crossodactylus gaudichaudii*  
                   HYNAS - *Hylodes nasus*  
 Leptodactylinae = ADMAR - *Adenomera marmorata*  
                       EDPER - *Edalorhina perezii*  
                       LECHA - *Leptodactylus chaquensis*  
                       LEGRA - *Leptodactylus gracilis*  
                       LEPET - *Leptodactylus petersii*  
                       LERHO - *Leptodactylus rhodomystax*  
                       LIMAC - *Limnomedusa macroglossa*  
                       PHBIL - *Physalaemus biligonigerus*  
                       PHCUQ - *Physalaemus cuqui*  
                       PHGRA - *Physalaemus gracilis*  
                       PHHEN - *Physalaemus henselii*  
                       PHPUS - *Physalaemus pustulosus*  
                       PLBOR - *Pleurodema borellii*  
                       PLBRA - *Pleurodema brachyops*  
                       PLBR2 - *Pleurodema brachyops2*  
                       PLTUC - *Pleurodema tucumana*  
 Telmatobiinae = ALBAR - *Alsodes barrioi*  
                       CYSTE - *Cycloramphus stejnegeri*  
                       ODAME - *Odontophrynus americanus*  
                       ODLAV - *Odontophrynus lavillai*  
                       TEBOL - *Telmatobius bolivianus*  
                       TECEI - *Telmatobius ceiorum*  
                       TEPIS - *Telmatobius pisanoi*



1968; Ruibal and Thomas, 1988). The *Lepidobatrachus* and *Cycloramphus* clade loses the larval processus oticus. The pars articularis quadrati in *Ceratophrys cornuta* and *Cycloramphus* are distinct. Previous analyses have not associated *Cycloramphus* with Ceratophryinae (Lynch, 1971; Heyer, 1975). The chondrocranial characteristics that currently support this clade may result from larval ecological adaptations.

Within clade I, Hylodinae clusters with *Alsodes*, *Telmatobius pisanoi*, and *T. ceiorum*. This clade is supported by having independent suprarostrals ( $A_0$ ), processus posterolateralis of the crista parotica ( $I_1$ ), and processus anterolateralis hyalis present ( $Q_1$ ). However, the suprarostrals of *Telmatobius ceiorum* become fused ventromedially, and a processus anterolateralis hyalis is present in *Hylodes*. Hylodinae forms a monophyletic group and the sister-group to the other three species in the clade. The monophyly of Hylodinae concurs with previous phylogenetic analyses (Heyer, 1975; Larson and de Sá, 1998) (Fig.17). However, this cluster suggests a paraphyletic *Telmatobius* with respect to *Alsodes*. Furthermore, the alternative placement of *T. bolivianus* would make

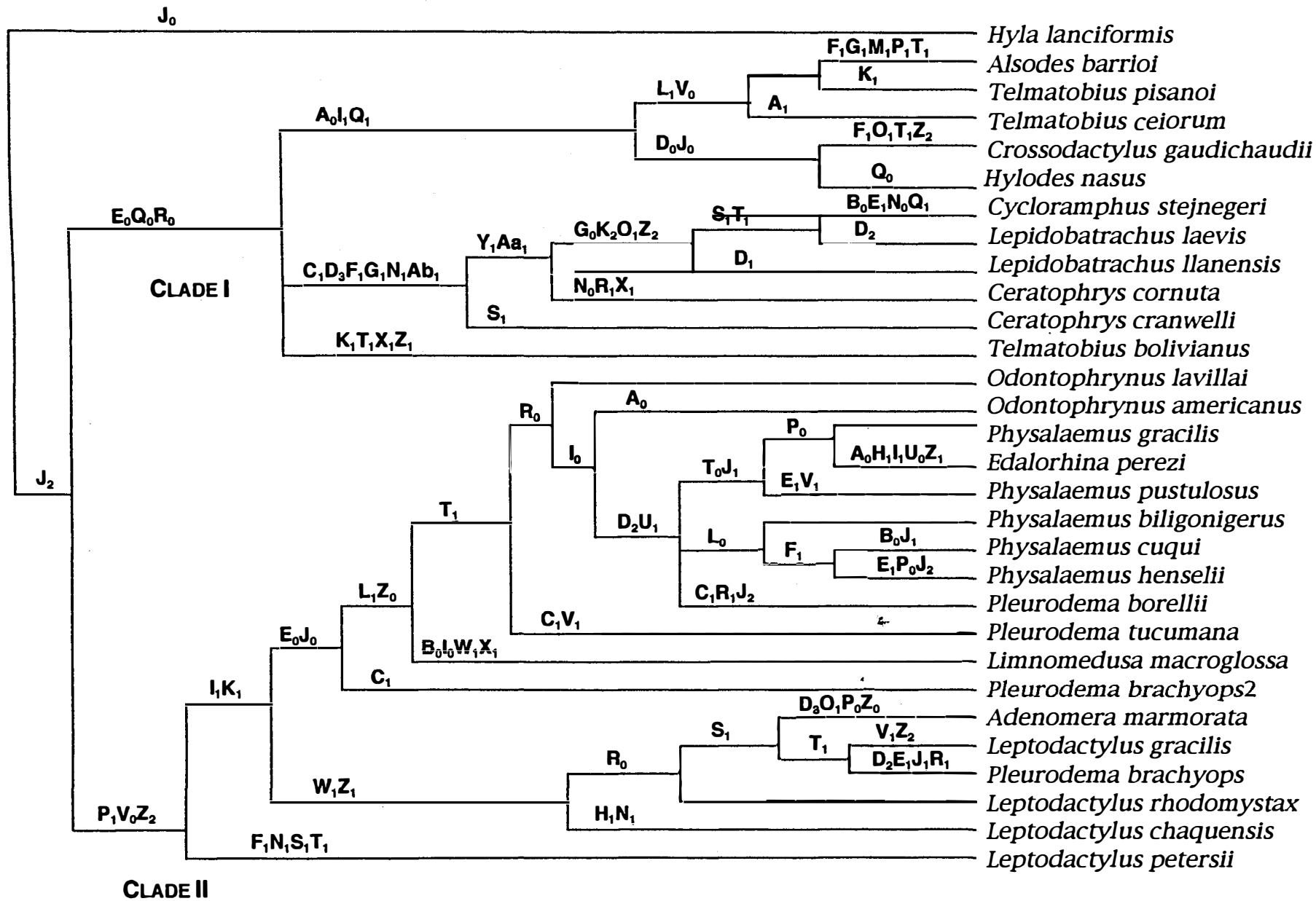


*Telmatobius* polyphyletic. The present arrangement for Telmatobiinae is polyphyletic; *Cycloramphus* clusters with Ceratophryinae while *Odontophrynus* clusters with Leptodactylinae. Lynch (1971) suggests that Leptodactylinae derived from a telmatobiine ancestor, however, the current phylogeny suggests that Leptodactylinae-*Odontophrynus* clade is the sister group of the other leptodactylids.

Clade II is supported by the following characters: commissura quadratoorbitalis present ( $P_1$ ), foramen trochleare distinguishable ( $V_0$ ), and plana hypobranchiales that are completely fused ( $Z_2$ ). *Leptodactylus petersii* is the sister group to the rest of this clade, making *Leptodactylus* paraphyletic, and the remaining members of the clade are supported by a processus posterolateralis of the crista parotica ( $I_1$ ) and an intermediate attachment of the processus ascendens ( $K_1$ ). The commissura quadratoorbitalis is lost in *Adenomera marmorata*, *Physalaemus henselii*, *P. gracilis*, and *Edalorhina perezii*. Additionally, the foramen trochleare is

Fig. 18. Strict consensus tree. Characters are as follows:

- A. Ventromedial fusion of suprarostral corpora. (0) unfused, (1) fused.
- B. Dorsal fusion of the suprarostral corpus and ala. (0) unfused, (1) fused.
- C. Ventral fusion of the suprarostral corpus and ala. (0) unfused, (1) fused.
- D. Cornua trabeculae length relative to total length of the chondrocranium. (0) >25%, (1) 20-25%, (2) 15-20%, (3) <15%.
- E. Length of the capsulae auditivae relative to total chondrocranial length. (0) <30%, (1) >30%.
- F. Processus anterolateralis of the crista parotica. (0) present, (1) absent.
- G. Larval processus oticus. (0) absent, (1) present.
- H. Projection of the posterior curvature of the palatoquadrate. (0) absent, (1) present.
- I. Processus posterolateralis of the crista parotica. (0) absent, (1) present.
- J. Posterolateral extension of the palatoquadrate. (0) anterior to the processus ascendens, (1) at the level of the processus ascendens, (2) posterior to the level of the processus ascendens.
- K. Attachment of the processus ascendens. (0) low, (1) intermediate, (2) high.
- L. Processus pseudopterygoideus. (0) absent, (1) present.
- M. Fusion of the processus pseudopterygoideus to the braincase. (0) unfused, (1) fused.
- N. Pars articularis quadrati. (0) distinct from the processus muscularis quadrati, (1) not distinct.
- O. Processus muscularis quadrati. (0) well-developed, (1) reduced.
- P. Commissura quadratoorbitalis. (0) absent, (1) present.
- Q. Processus anterolateralis hyalis. (0) absent, (1) present.
- R. Processus branchialis. (0) open, (1) closed.
- S. Processus lateralis trabeculae. (0) present, (1) absent.
- T. Frontoparietal fontanelle. (0) undivided, (1) divided by taenia tectum medialis and taenia tectum transversalis.
- U. Taeniae tecti marginales in relation to the capsulae auditivae. (0) continuous, (1) not continuous.
- V. Foramen trochleare. (0) distinguishable, (1) indistinguishable.
- W. Ventral protrusion of the posteromedial margin of cartilago Meckeli. (0) absent, (1) present.
- X. Copula I. (0) absent, (1) present.
- Y. Processus quadratoethmoidalis. (0) present, (1) absent.
- Z. Plana hypobranchiales. (0) not fused, (1) fused posteromedially, (2) completely fused.
- Aa. Processus urobranchialis. (0) present, (1) extremely reduced or absent.
- Ab. Cartilagine infrarostrales: (0) not fused, (1) fused.



indistinguishable in *Leptodactylus gracilis*, *Pleurodema tucumana*, and *Physalaemus pustulosus*. The evolution of the fusion of the plana hypobranchiales can have several equally parsimonious routes; the ancestor for the Leptodactylinae-*Odontophrynus* clade could have exhibited any of the three character states.

Heyer (1975) pointed out that *Pleurodema* presented confusing relationships with other leptodactylines. Wassersug and Heyer (1988) showed that interspecific differences in *Pleurodema* larvae were greater than most other leptodactylid genera. This analysis results in a grossly polyphyletic *Pleurodema*. The relationships of this genus are not resolved through chondrocranial data. *Pleurodema* is considered to be a primitive leptodactyline (Duellman and Veloso, 1977), but *P. brachyops* clusters within *Leptodactylus* in the *Adenomera-Leptodactylus* clade, both of which are considered to be advanced leptodactylines and have been closely related in other arrangements (Heyer, 1974, 1975; De la Riva, 1995). Moreover, *Physalaemus* is paraphyletic with respect to *Pleurodema borellii* and *Edalorhina*.

*Limnomedusa macroglossa* is nested within the Leptodactylinae-*Odontophrynus* clade. This arrangement agrees with Heyer (1975), Frost (1985), and Duellman (1993). It is interesting to note that the foramen oculomotorium of *Limnomedusa* is divided by a cartilaginous bar, and this condition has also been reported for *Pleurodema bibroni*, *Caudiverbera caudiverbera*, and *Heleophryne* (Reinbach, 1939; Sokol, 1981).

*Odontophrynus* groups within Leptodactylinae in this arrangement and does not form a monophyletic genus. Previous studies have not allied *Odontophrynus* with Leptodactylinae (Lynch, 1971). Heyer (1975) suggested a close relationship between *Odontophrynus* and both *Ceratophrys* and *Lepidobatrachus*, however, this assertion is not supported by chondrocranial data.

This study suggests that we must be careful when using larval characters in the phylogenetic analysis of Leptodactylidae at the familial level. Tadpoles are subjected to selective pressures throughout their development, and these pressures may lead to larval adaptation, or caenogenesis, which in turn can lead to homoplasy (Haeckel, 1866; de Beer, 1958; Smith, 1997; Hall and

Wake, 1998). Convergences in larval morphologies are common, especially when larvae occupy similar ecological niches or have a similar life history (Wassersug and Heyer, 1988; Smith, 1997; Hall and Wake, 1998). Developmental patterns are plastic, and resulting caenogenesis can misrepresent relationships in phylogenetic analyses (Smith, 1997). In future studies, chondrocranial anatomy should be combined with non-larval characteristics in order to understand the role of caenogenesis in resulting phylogenies. However, chondrocranial anatomy is probably more useful to understand the evolution of closely related taxa (e.g. intrageneric comparisons).

## LITERATURE CITED

- Barrio, A. 1964. Especies crípticas del género *Pleurodema* que conviven en una misma área, identificadas por el canto nupcial (Anura: Leptodactylidae). *Physis* 24: 471-489.
- Barrio, A. 1971. Sobre la coespecificidad de *Limnomedusa misionis* Schmidt y *Limnomedusa macroglossa* (Dumeril et Bibron) (Anura, Leptodactylidae). *Physis* 30: 667-672.
- Barrio, A. and P. Rinaldi de Chieri. 1970. Estudios citogeneticos sobre el género *Pleurodema* y sus consecuencias evolutivas (Amphibia, Anura, Leptodactylidae). *Physis* 30: 309-319.
- Barrio, A. and P. Rinaldi de Chieri. 1971. Contribucion al esclarecimiento de la posicion taxofiletica de algunos batracios patagonicos de la familia Leptodactylidae mediante el analisis cariotipico. *Physis* 30: 673-685.
- Bogart, J. P. 1970. Systematic problems in the amphibian family Leptodactylidae (Anura) as indicated by karyotypic analysis. *Cytogenetics* 9: 369-383.

- 
- Bogart, J. P. 1973. Evolution of anuran karyotypes. *In*: Vial, J. L. (ed.), Evolutionary biology of the anurans: contemporary research on major problems. University of Missouri Press, Columbia. 337-349 pp.
- Bogart, J. P. 1974. A karyosystematic study of frogs in the genus *Leptodactylus* (Anura: Leptodactylidae). *Copeia* 3: 728-737.
- Boulenger, G. A. 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collections of the British Museum. 2<sup>nd</sup> Ed. London, xvi + 503 pp.
- Brooks, D. R. and D. A. Mclennan. 1991. Phylogeny, ecology, and behavior. The Univeresity of Chicago Press, Chicago. 434 pp.
- Cannatella, D. C., D. M. Hillis, P. T. Chippindale, L. Weigt, A. S. Rand, and M. J. Ryan. 1998. Phylogeny of frogs of the *Physalaemus pustulosus* species group, with an examination of data incongruence. *Syst. Biol.* 47(2): 311-335.
- Cannatella, D. C. and W. E. Duellman. 1984. Leptodactylid frogs of the *Physalaemus pustulosus* group. *Copeia* 4: 902-921.



- Cardoso, A. J. and W. R. Heyer. 1995. Advertisement, aggressive, and possible seismic signals of the frog *Leptodactylus sypfax* (Amphibia, Leptodactylidae). *Alytes* 13(2): 67-76.
- Cei, J. M. 1968. Notes on the tadpoles and breeding ecology of *Lepidobatrachus* (Amphibia: Ceratophryidae). *Herpetology* 24: 141-146.
- Cope, E. D. 1865. Sketch of the primary groups of Batrachia Salientia. *Nat. Hist. Rev.* 5: 97-120.
- Cope, E. D. 1889. The Batrachia of North America. *Bull. U.S. Natl. Mus.* 34: 1-525.
- Davies, M. 1989. Ontogeny of bone and the role of heterochrony in the myobatrachine genera *Uperoleia*, *Crinia*, and *Pseudophryne* (Anura: Leptodactylidae: Myobatrachinae). *J. Morphol.* 200: 269-300.
- de Beer, G. R. 1937. The development of the vertebrate skull. Oxford University Press, Oxford. 552 pp.
- de Beer, G. R. 1958. Embryos and ancestors. Oxford University Press, Oxford.

- De Jongh, H. J. 1968. Functional morphology of the jaw apparatus of larvae and metamorphosing *Rana temporaria*. L. Neth. J. Zool. 18: 1-103.
- De la Riva, I. 1995. A new reproductive mode for the genus *Adenomera* (Amphibia: Anura: Leptodactylidae): taxonomic implications for certain Bolivian and Paraguayan populations. Studies on Neotropical Fauna and Environment. 30(1):15-29.
- de Sá, R. O. 1988. Chondrocranium and ossification sequence of *Hyla lanciformis*. J. Morphol. 195: 345-355.
- de Sá, R. O. 1994. Chondrocranial structure and adaptations in anuran larvae. J. Morphol. 220: 341.
- de Sá, R. O. and S. Hill. 1998. Chondrocranial anatomy and skeletogenesis in *Dendrobates auratus*. J. Herpetol. 32(2): 205-210.
- de Sá, R. O. and D. M. Hillis. 1990. Phylogenetic relationships of the pipid frogs *Xenopus* and *Silurana*: an integration of ribosomal DNA and morphology. Mol. Biol. Evol. 7(4): 365-376.

- de Sá, R. O. and E. O. Lavilla. 1996. Características de la osificación craneal en *Phyllomedusa boliviana* (Anura: Hylidae). Cuad. Herp. 9(2): 69-73.
- de Sá, R. O. and E. O. Lavilla. 1997. The tadpole of *Pseudis minuta* (Anura: Pseudidae), an apparent case of heterochrony. Amphibia-Reptilia 18: 229-240.
- de Sá, R. O. and L. Trueb. 1991. Osteology, skeletal development, and chondrocranial structure of *Hamptophryne boliviana* (Anura: Microhylidae). J. Morphol. 209: 311-330.
- Dingerkus, G. and L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain. Tech. 52: 229-232.
- Duellman, W. E. 1973. Frogs of the *Hyla geographica* group. Copeia 3: 515-533.
- Duellman, W. E. 1975. On the classification of frogs. Occ. Pap. Mus. Nat. Hist. Univ. Kansas. 42: 1-15.
- Duellman, W. E. 1993. Amphibian species of the world: additions and corrections. Univ. Kansas Mus. Nat. Hist. Special Publ. 21: 1-372.

- Duellman, W. E. and L. Trueb. 1994. *Biology of Amphibians*. The Johns Hopkins University Press, Baltimore. 670 pp.
- Duellman, W. E. and A. Veloso M. 1977. Phylogeny of *Pleurodema* (Anura: Leptodactylidae): a biogeographic model. *Occ. Pap. Mus. Nat. Hist. Univ. Kansas* 64: 1-46.
- Fabrezi, M. and E. O. Lavilla. 1993. Anatomía del condrocráneo en larvas de tres especies de *Telmatobius* del grupo meridional (Anura: Leptodactylidae). *Physis* 48(114-115): 39-46.
- Fabrezi, M. and R. Vera. 1997. Caracterización morfológica de larvas de anuros del noroeste argentino. *Cuad. Herp.* 11(1-2): 37-49.
- Ford, L. S. 1989. The phylogenetic position of poison-dart frogs (Dendrobatidae): reassessment of the neobatrachian phylogeny with commentary on complex character systems. Ph.D. Dissertation, The University of Kansas, Lawrence, Kansas.
- Ford, L. S. and D. C. Cannatella. 1993. The major clades of frogs. *Herpetological Monographs* 7: 94-117.
- Formas, J. R. 1975. Las larvas de las especies chilenas pertenecientes al género *Eupsophus* grupo *nodosus* (Anura: Leptodactylidae). *Bol. Soc. Biol. Concepcion* 49: 231-237.

- Formas, J. R. 1976. Descriptions of *Batrachyla* tadpoles. J. Herpetol. 10: 221-225.
- Frost, D. R. (ed.), 1985. Amphibian species of the world. Lawrence, Allen Press & Ass. Syst. Coll. 732 pp.
- Gaudin, A. J. 1973. The development of the skull in the Pacific tree frog, *Hyla regilla*. Herpetologica 29(3): 205-218.
- Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16: 183-190.
- Gould, S. J. 1977. Ontogeny and Phylogeny. Harvard University Press, Cambridge. 501 pp.
- Green, D. M. and S. K. Sessions. 1991. Amphibian cytogenetics and evolution. Academic Press, New York. 456 pp.
- Greer, B. J. and K. D. Wells. 1980. Territorial and reproductive behavior of the tropical american frog *Centrolenella fleischmanni*. Herpetologica 36(4): 318-326.
- Gudynas, E. and A. Gehrau. 1981. Notas sobre la distribución y ecología de *Limnomedusa macroglossa* (Duméril and Bibron,

- 1841) en Uruguay (Anura, Leptodactylidae). Iheringia, Ser. Zool., Porto Alegre 60: 81-99.
- Haas, A. 1995. Cranial features of dendrobatid larvae (Amphibia: Anura: Dendrobatidae). J. Morphol. 224: 241-264.
- Haas, A. 1996. Das larvale Cranium von *Gastrotheca riobambae* und seine Metamorphose (Amphibia, Anura, Hylidae). Verh. Naturwiss. Ver. Hamburg 36: 33-162.
- Haas, A. 1996b. Non-feeding and feeding tadpoles in hemiphractine frogs: larval head morphology, heterochrony, and systematics of *Flectonus goeldii* (Amphibia: Anura: Hylidae). J. Zoo. Syst. Evol. Research 34: 163-171.
- Haas, A. 1997. The larval hyobranchial apparatus of discoglossoid frogs: its structure and bearing on the systematics of the anura (Amphibia: Anura). J. Zool. Syst. Evol. Research 35: 179-197.
- Haeckel, E. 1866. Generelle Morphologie der Organismen: allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch Begründet durch die von Charles Darwin reformierte Descendenz-Theorie. 2 vols. Georg Reimer, Berlin.

Hall, B. K. and M. H. Wake. 1999. Introduction: larval development, evolution, and ecology. *In* Hall, B. K. and M. H. Wake (eds.), *The origin and evolution of larval forms*. Academic Press, New York. 1-19 pp.

Hanken, J. and B. K. Hall. Skull development during anuran metamorphosis: I. Early development of the first three bones to form the exoccipital, the parasphenoid, and the frontoparietal. *J. Morphol.* 195: 247-256.

Hanken, J., M. W. Klymkowsky, C. H. Summers, D. W. Seufert, and N. Ingebrigtsen. 1992. Cranial ontogeny in the direct-developing frog, *Eleutherodactylus coqui* (Anura: Leptodactylidae), analyzed using whole-mount immunohistochemistry. *J. Morphol.* 211: 95-118.

Hay, J. M., I. Ruvinsky, S. B. Hedges, and L. R. Maxson. 1995. Phylogenetic relationships of amphibian families inferred from DNA sequences of mitochondrial 12S and 16S ribosomal RNA genes. *Mol. Biol. Evol.* 12: 928-937.

- Henle, K. 1992. Zur Amphibienfauna Perus nebst Beschreibung eines neuen *Eleutherodactylus* (Leptodactylidae). Bonn. Zool. Beitr. 43: 79-129.
- Heyer, W. R. 1969a. Studies on the genus *Leptodactylus* (Amphibia, Leptodactylidae) III. a redefinition of the genus *Leptodactylus* and a description of a new genus of leptodactylid frogs. Contributions in Science 155: 1-14.
- Heyer, W. R. 1969b. The adaptive ecology of the species groups of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). Evolution 23: 421-428.
- Heyer, W. R. 1970. Studies on the frogs of the genus *Leptodactylus* (Amphibia: Leptodactylidae). VI. Biosystematics of the *melanonotus* group. Contributions in Science 191: 1-48.
- Heyer, W. R. 1973. Systematics of the *marmoratus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). Contributions in Science 251: 1-50.
- Heyer, W. R. 1974. Relationships of the *marmoratus* species group (Amphibia, Leptodactylidae) within the subfamily Leptodactylinae. Contributions in Science 253: 1-46.



- Heyer, W. R. 1975. A preliminary analysis of the intergeneric relationships of the frog family Leptodactylidae. *Smithsonian Contr. Zool.* 199: 1-55.
- Heyer, W. R. 1977. A discriminant function analysis of the frogs of the genus *Adenomera* (Amphibia: Leptodactylidae). *Proc. Biol. Soc. Wash.* 89(51): 581-592.
- Heyer, W. R. 1978. Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Natural History Museum of Los Angeles County Science Bulletin.* 29: 1-85.
- Heyer, W. R. 1979. Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smithsonian Contr. Zool.* 301: 1-43.
- Heyer, W. R. 1984. The systematic status of *Adenomera griseigularis* Henle, with comments on systematic problems in the genus *Adenomera* (Amphibia: Leptodactylidae). *Amphibia-Reptilia* 5: 97-100.
- Heyer, W. R. 1994. Variation within the *Leptodactylus-wagneri* complex of frogs (Amphibia: Leptodactylidae). *Smithsonian Contr. Zool.* 546: 1-124.

- Heyer, W. R. and L. R. Maxson. 1982. Distributions, relationships, and zoogeography of lowland frogs. The *Leptodactylus* complex in South America, with special reference to Amazonia. In Prance, G. T. (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. 375-388 pp.
- Hillis, D. M., L. K. Ammerman, M. T. Dixon, and R. O. de Sá. 1993. Ribosomal DNA and the phylogeny of frogs. Herpetol. Monogr. 7: 118-131.
- Hillis, D. M. and S. K. Davis. 1987. Evolution of the 28S ribosomal RNA gene in anurans: Regions of variability and their phylogenetic implications. Mol. Biol. Evol. 4: 117-125.
- Howard, A. K., J. D. Forester, J. M. Ruder, and R. Powell. 1997. Diets of two syntopic frogs: *Eleutherodactylus abbotti* and *E. armstrongi* (Leptodactylidae) from the Sierra de Baoruco, Hispaniola. Herp. Nat. Hist. 5(1): 66-72.
- King, M. 1990. Amphibia. In Bernard, J. and C. Gwent (eds.), Animal Cytogenetics. Gerbruder Borntraeger, Stuttgart. 241 pp.

- Kluge, J. J. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Syst. Zool* 38: 7-25.
- Kovács, T. and J. Török. 1997. Determination of minimum sample size to estimate diet diversity in Anuran species. *Herpetological Journal* 7: 43-47.
- Langone, J. A. and C. M. Prigioni. 1985. Observaciones sobre una puesta de *Limnomedusa macroglossa* (Duméril and Bibron, 1841) (Anura: Leptodactylidae). *Act. Jor. Zool. Uruguay* 83-86 pp.
- Larson, P. M. and R. O. de Sá. 1998. Chondrocranial morphology of *Leptodactylus* larvae (Leptodactylidae: Leptodactylinae): its utility in phylogenetic reconstruction. *J. Morphol.* 238: 287-305.
- Laurent, R. F. 1979. Esquisse d'une phylogenese des anoures. *Bull. Soc. Zool. France* 104: 397-422.
- Laurent, R. F. 1986. Sous classe des lissamphibiens. Systematique. *In* Grassé, P.-P. and M. Delsol (eds.), *Traité de Zoologie*, Tome 14, 1B. Masson, Paris.

- Lavilla, E. O. 1983. Sistemática de larvas de Telmatobiinae (Anura: Leptodactylidae). Ph.D. Dissertation. Fac. Cs. Nat. Univ. Nac. Tucuman, Argentina. v + 354 pp.
- Lavilla, E. O. 1985. Diagnósis generica y agrupación de las especies de *Telmatobius* (Anura: Leptodactylidae) en base a caracteres larvales. *Physis* 43(105): 63-67.
- Lavilla, E. O. 1988. Lower Telmatobiinae (Anura: Leptodactylidae): generic diagnoses based on larval characters. *Occ. Pap. Mus. Nat. Hist. Univ. Kansas* 124: 1-19.
- Lavilla, E. O. 1991. Condrocáneo y esqueleto visceral en larvas de *Cycloramphus stejnegeri* (Leptodactylidae). *Amphibia-Reptilia* 12: 33-38.
- Lavilla, E. O. 1992. Estructura del condrocáneo y esqueleto visceral de larvas de *Alsodes barrioi* (Anura: Leptodactylidae). *Acta Zool. Lill.* XLII, 1: 13-18.
- Lavilla, E. O. and I. De la Riva. 1993. La larva de *Telmatobius bolivianus* (Anura, Leptodactylidae). *Alytes* 11(2): 37-46.

- Lavilla, E. O. and M. Fabrezi. 1992. Anatomia craneal de larvas de *Lepidobatrachus llanensis* y *Ceratophrys cranwelli* (Anura: Leptodactylidae). *Acta Zool. Lill.* XLII, 1: 5-11.
- Lavilla, E. O. and G. J. Scrocchi. 1986. Morfometria larval de los generos de Telmatobiinae (Anura: Leptodactylidae) de Argentina y Chile. *Physis* 44: 39-43.
- Lobo, F. 1995. Analisis filogenético del género *Pseudopaludicola* (Anura: Leptodactylidae). *Cuad. Herp.* 9(1): 21-43.
- Lynch, J. D. 1969. Taxonomic notes on Ecuadorian frogs (Leptodactylidae: *Eleutherodactylus*). *Herpetologica* 25: 262-274.
- Lynch, J. D. 1970. Systematic status of the American leptodactylid frog genera *Engystomops*, *Eupemphix*, and *Physalaemus*. *Copeia* 4: 488-496.
- Lynch, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Misc. Publ. Mus. Nat. Hist. Univ. Kans.* 53:1-238.

- Lynch, J. D. 1973. The systematic status of the Colombian leptodactylid frog, *Leptodactylus mantipus* Boulenger. *Herpetologica* 29(3): 232-235.
- Lynch, J. D. 1978. A re-assessment of the telmatobiine leptodactylid frogs of Patagónia. *Occ. Pap. Mus. Nat. Hist. Univ. Kansas* 72:1-57.
- Lynn, W. G. 1942. The embryology of *Eleutherodactylus nubicola*, an anuran which has no tadpole stage. *Contrib. Embryol. Carnegie Inst. Wash. Publ.* 541: 27-62.
- Lynn, W. G. and B. Lutz. 1946. The development of *Eleutherodactylus guentheri* Stdnr. 1864. *Bol. Mus. Nac. Zool.* 71: 1-46.
- Maglia, A. M. and L. A. Pugéner. 1998. Skeletal development and adult osteology of *Bombina orientalis* (Anura: Bombinatoridae). *Herpetologica* 54(3): 344-363.
- Martin St. Ange, J. G. 1831. Recherches anatomiques et physiologiques sur les organes transitoires et la métamorphose des batraciens. *Annls. Sci. nat.* 25: 366-434.

- Martins, M. 1989. Deimatic behavior in *Pleurodema brachyops*. J. Herpetol. 23(3): 305-307.
- Maxson, L. R. and W. R. Heyer. 1988. Molecular systematics of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). Fieldiana 41: 1-13.
- Noble, G. K. 1922. The phylogeny of the Salientia: I. The osteology and the thigh musculature; their bearing on classification and phylogeny. Bull. Amer. Mus. Nat. Hist. 46: 1-87.
- Noble, G. K. 1931. The Biology of the Amphibia. New York: McGraw-Hill Book Co.
- Orton, G. L. 1953. The systematics of vertebrate larvae. Syst. Zool. 2:63-75.
- Orton, G. L. 1957. The bearing of larval evolution on some problems in frog classification. Syst. Zool. 6: 79-86.
- Parker, H. W. 1927. A revision of the frogs of the genera *Pseudopaludicola*, *Physalaemus*, and *Pleurodema*. Ann. Mag. Nat. Hist. 9(20): 450-478.
- Parsons, T. S. and E. E. Williams. 1963. The relationships of the modern Amphibia: a re-examination. Q. Rev. Biol. 38: 26-53.

- Premo, D. B. and A. H. Atmowidjojo. 1987. Dietary pattern of the “crab eating frog”, *Rana cancrivora* in West Java. *Herpetologica* 43(1): 1-6.
- Reig, O. A. 1958. Propositiones para una nueva macrosistemática de los anuros. Nota preliminar. *Physis* 21: 109-118.
- Reinbach, W. 1939. Untersuchungen über die entwicklung des kopfskeletts von *Calyptocephalus gayi*. *Jenaische Zeitschrift Für Naturwissenschaft.* 72: 15-362.
- Richardson, M. K. 1995. Heterochrony and the phylotypic period. *Dev. Biol.* 172: 412-421.
- Ruibal, R. and E. Thomas. 1988. The obligate carnivorous larvae of the frog, *Lepidobatrachus laevis* (Leptodactylidae). *Copeia* 3: 591-604.
- Ruvinsky, I. and L. R. Maxson. 1996. Phylogenetic relationships among Bufonoid frogs (Anura: Neobatrachia) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 5(3): 533-548.
- Ryan, M. J. and A. S. Rand. 1995. Remale responses to ancestral advertisement calls in túngara frogs. *Science* 269: 390-392.



- Schulze, F. E. 1870. Die Geschmacksorgane der Froschlarven. Arch. mikr. Anat. 6: 407-419.
- Schulze, F. E. 1892. Über die inneren Kiemen der Batrachierlarven. II. Mittheilung. Skelet, Musculatur, Blutgefasse, Filterapparat, respiratorische Anhänge und Athmungsbewegungen erwachsener Larven von *Pelobates fuscus*. Abhdl. der Konigl. Preuss. Akad. Wiss. Berlin, (1): 1-66.
- Smith, A. B. 1997. Echinoderm larvae and phylogeny. Annu. Rev. Syst. Evol. 28:219-241.
- Sokol, O. M. 1975. The phylogeny of anuran larvae: a new look. Copeia 1: 1-23.
- Sokol, O. M. 1977. The free swimming *Pipa* larvae, with a review of pipid larvae and pipid phylogeny (Anura: Pipidae). J. Morphol. 154: 357-426.
- Sokol, O. M. 1981. The larval chondrocranium of *Pelodytes punctatus*, with a review of tadpole chondrocrania. J. Morphol. 169: 161-183.
- Starrett, P. H. 1973. Evolutionary patterns in larval morphology. In: Vial, J. L. (ed.), Evolutionary biology of the anurans:

- contemporary research on major problems. University of Missouri Press, Columbia 252-271 pp.
- Swofford, D. L. 1993. Phylogenetic analysis using parsimony. Illinois Biodiversity Survey. Champagne, Illinois. 110 pp.
- Toft, C. A. 1995. Evolution of diet specialization in poison-dart frogs (Dendrobatidae). *Herpetologica* 51: 202-216.
- Trueb, L. 1966. Morphology and development of the skull in the frog *Hyla septentrionalis*. *Copeia* 4:562-573.
- Trueb, L. 1973. Bones, frogs, and evolution. *In*: Vial, J. L. (ed.), Evolutionary biology of the anurans: contemporary research on major problems. University of Missouri Press, Columbia 65-132 pp.
- Trueb, L. 1985. A summary of osteocranial development in anurans with notes on the sequence of cranial ossification in *Rhinophrynus dorsalis* (Anura: Pipidae: Rhinophrynidae). *South African J. Sci.* 81: 181-185.
- Trueb, L. and P. Alberch. 1985. Miniaturization and the anuran skull: a case study of heterochrony. *In* Fortschritte der

- Zoologie, Band 30, Duncker and Fleischer (eds.), Vertebrate Morphology. Gustav Fischer Verlag, New York 113-120 pp.
- Trueb, L. and J. Hanken. 1992. Skeletal development in *Xenopus laevis* (Anura: Pipidae). *J. Morphol.* 214: 1-41.
- Veloso, A., R. Galleguillos, N. Diaz. 1973. Karyotypic analysis of allopatric populations of *Pleurodema thaul*<sup>s</sup>(Lesson). *Amphibia, Leptodactylidae. Caryologia* 26: 69-76.
- Wakahara, M. 1996. Heterochrony and neotenic salamanders: possible clues for understanding the animal development and evolution. *Zool. Sci.* 13: 765-776.
- Wassersug, R. J. 1973. Aspects of social behavior in anuran larvae. *In: Vial, J. L. (ed.), Evolutionary biology of the anurans: contemporary research on major problems.* University of Missouri Press, Columbia 273-297 pp.
- Wassersug, R. J. 1976. Oral morphology of anuran larvae: terminology and general description. *Occ. Pap. Mus. Nat. Hist. Univ. Kansas* 48: 1-23.
- Wassersug, R. J. 1980. Internal oral features of larvae from eight anuran families: functional, systematic, evolutionary and

- ecological considerations. Misc. Publ. Mus. Nat. Hist. Univ. Kans. 68: 1-146.
- Wassersug, R. J. and W. R. Heyer. 1988. A survey of internal oral features of Leptodactyloid larvae (Amphibia: Anura). Smithsonian Contr. Zool. 457:1-99.
- Wassersug, R. J. and K. Hoff. 1982. Developmental changes in the orientation of the anuran jaw suspension: a preliminary exploration into the evolution of anuran metamorphosis. *In* Hecht, et al. (ed.), Evolutionary Biology, Vol. 15. Plenum Publishing Corp. 223-246 pp.
- Wells, K. D. 1977. The social behavior of anuran amphibians. *Anim. Behav.* 25: 666-693.
- Wild, E. R. 1997. Description of the adult skeleton and developmental osteology of the hyperossified horned frog, *Ceratophrys cornuta* (Anura: Leptodactylidae). *J. Morphol.* 232: 169-206.

**APPENDIX 1:** List of stages and measurements in millimeters of larvae used in this study. BL = body length, TL = total length, SEM = dissected and prepared for scanning electron microscopy of internal oral anatomy, C&S = cleared and double-stained, L = late in the stage (Gosner, 1960), E = early in the stage (Gosner, 1960).

*Adenomera marmorata* USNM 209363

| # | Stage | BL   | TL    | Status |
|---|-------|------|-------|--------|
| 1 | 36    | 6.19 | 16.79 | C&S    |
| 3 | 36    | 6.18 | 13.77 | C&S    |

*Edalorhina perezii* USNM 342752

| # | Stage | BL    | TL    | Status |
|---|-------|-------|-------|--------|
| 1 | 36    | 10.64 | 25.65 | C&S    |

*Limnomedusa macroglossa*

| #  | Stage | BL    | TL    | Status |
|----|-------|-------|-------|--------|
| 2  | 34    | 13.51 | 37.44 | C&S    |
| 4  | 40E   | 10.97 | 29.53 | C&S    |
| 6  | 31    | 10.12 | 29.32 | C&S    |
| 7  | 37    | 13.07 | 33.28 | C&S    |
| 9  | 37    | 14.16 | 37.18 | SEM    |
| 12 | 39    | 16.86 | 42.16 | C&S    |
| 13 | 41L   | 16.64 | 39.30 | C&S    |

*Pleurodema brachyops* USNM 302093

| # | Stage | BL    | TL    | Status |
|---|-------|-------|-------|--------|
| 1 | 35    | 11.30 | 25.07 | C&S    |
| 3 | 35    | 11.43 | 27.56 | C&S    |
| 4 | 36    | 11.63 | 27.23 | C&S    |
| 6 | 37    | 10.25 | 19.92 | C&S    |

*Physalaemus henselii*

| #   | Stage | BL    | TL    | Status |
|-----|-------|-------|-------|--------|
| 1   | 33    | 10.6  | 34.2  | C&S    |
| 2   | 31    | 9.2   | 31.0  | C&S    |
| 3   | 38    | 9.90  | 27.1  | C&S    |
| 4   | 40    | 9.60  | 27.78 | C&S    |
| 5   | 44    | 11.4  | 12.8  | C&S    |
| 9   | 28    | 6.6   | 17.1  | C&S    |
| 12  | 31    | 9.42  | 32.10 | SEM    |
| 16  | 41    | 10.58 | 31.02 | C&S    |
| 17  | 39    | 8.3   | 27.4  | C&S    |
| 18  | 30    | 9.3   | 24.9  | C&S    |
| 21  | yg    | 8.8   | 8.8   | C&S    |
| 23  | 41    | 10.9  | 30.7  | C&S    |
| 24  | 40E   | 10.50 | 31.7  | C&S    |
| 25  | 37    | 10.0  | 28.1  | C&S    |
| 28  | 40    | 10.2  | 25.8  | C&S    |
| 28  | 40    |       |       | C&S    |
| 29  | 45    | 10.4  | 12.4  | C&S    |
| 141 | 38    | 10.3  | 24.6  | C&S    |

*Pleurodema tucumana* USNM 3071910

| # | Stage | BL    | TL    | Status |
|---|-------|-------|-------|--------|
| 1 | 31    | 8.74  | 19.17 | C&S    |
| 2 | 34    | 9.41  | 20.83 | C&S    |
| 3 | 35E   | 9.37  | 22.51 | C&S    |
| 4 | 35    | 11.18 | 29.46 | C&S    |

Appendix 1 CONTINUED

| <i>Physalaemus gracilis</i> |       |      |       |        | <i>Physalaemus gracilis</i> continued |       |      |      |        |
|-----------------------------|-------|------|-------|--------|---------------------------------------|-------|------|------|--------|
| #                           | Stage | BL   | TL    | Status | #                                     | Stage | BL   | TL   | Status |
| 1                           | 27    | 4.5  | 10.7  | C&S    | 95                                    | 35    | 9.2  | 20.6 | C&S    |
| 3                           | 29    | 6.0  | 15.4  | C&S    | 97                                    | 40    | 9.7  | 25.4 | C&S    |
| 4                           | 32    | 6.6  | 16.6  | C&S    | 99                                    | 33    | 8.3  | 18.9 | C&S    |
| 5                           | 30    | 7.1  | 16.7  | C&S    | 100                                   | 34    | 8.3  | 19.9 | C&S    |
| 7                           | 34    | 7.7  | 18.0  | C&S    | 101                                   | 37L   | 9.0  | 22.8 | C&S    |
| 12                          | 29    | 6.7  | 16.6  | C&S    | 104                                   | 33    | 5.7  | 16.8 | C&S    |
| 13                          | 27    | 5.8  | 9.2   | C&S    | 105                                   | 41    | 9.8  | 25.4 | C&S    |
| 16                          | 31    | 5.6  | 15.8  | C&S    | 106                                   | 45    | 8.67 | 15.9 | C&S    |
| 18                          | 34    | 7.8  | 19.3  | C&S    | 108                                   | 31    | 6.5  | 10.7 | C&S    |
| 21                          | 29    | 6.4  | 16.0  | C&S    | 113                                   | 37    | 9.5  | 25.0 | C&S    |
| 22                          | 39    | 9.1  | 23.6  | C&S    | 115                                   | 40E   | 9.4  | 25.9 | C&S    |
| 24                          | 36    | 7.8  | 19.7  | C&S    | 119                                   | 44    | 9.0  | 13.0 | C&S    |
| 25                          | 37    | 9.1  | 24.77 | SEM    | 120                                   | 41    | 10.0 | 26.4 | C&S    |
| 30                          | 34L   | 8.4  | 20.9  | C&S    | 122                                   | 41    | 10.6 | 28.9 | C&S    |
| 32                          | 37    | 8.0  | 21.9  | C&S    | 126                                   | 43    | 9.3  | 17.5 | C&S    |
| 37                          | 42L   | 8.6  | 22.6  | C&S    | 128                                   | 38    | 8.6  | 24.0 | C&S    |
| 40                          | 45    | 8.1  | 10.3  | C&S    | 131                                   | 38    | 8.7  | 22.8 | C&S    |
| 43                          | 39E   | 8.3  | 22.2  | C&S    | 135                                   | yg    | 10.6 | 10.6 | C&S    |
| 49                          | 45    | 8.3  | 10.5  | C&S    | 133                                   | 44    | 8.2  | 11.5 | C&S    |
| 51                          | 44    | 9.8  | 12.9  | C&S    | 137                                   | 45    | 9.7  | 11.9 | C&S    |
| 53                          | 40    | 9.4  | 23.9  | C&S    | 138                                   | 43    | 10.9 | 15.8 | C&S    |
| 58                          | 42    | 9.0  | 22.9  | C&S    | 139                                   | 35    | 8.7  | 22.9 | C&S    |
| 59                          | 37    | 8.3  | 22.8  | C&S    | 140                                   | 42    | 8.1  | 23.3 | C&S    |
| 61                          | 41    | 9.4  | 24.7  | C&S    | 142                                   | 45    | 9.1  | 10.6 | C&S    |
| 62                          | 32    | 7.0  | 17.5  | C&S    | 144                                   | 42    | 9.1  | 10.6 | C&S    |
| 66                          | 39    | 9.1  | 22.4  | C&S    | 146                                   | 36    | 8.6  | 21.2 | C&S    |
| 68                          | 40    | 9.3  | 24.9  | C&S    | 148                                   | 41    | 9.5  | 24.8 | C&S    |
| 69                          | 42    | 9.8  | 20.9  | C&S    | 150                                   | 30    | 6.1  | 17.5 | C&S    |
| 73                          | 45    | 8.6  | 9.9   | C&S    | 151                                   | 38    | 9.0  | 23.2 | C&S    |
| 77                          | 37    | 7.88 | 20.40 | SEM    | 152                                   | 43    | 8.7  | 18.6 | C&S    |
| 78                          | 33    | 7.1  | 12.1  | C&S    | 153                                   | 42    | 9.1  | 24.0 | C&S    |
| 84                          | 28    | 6.4  | 10.3  | C&S    | 154                                   | 44    | 9.4  | 13.2 | C&S    |
| 86                          | 45    | 8.1  | 8.3   | C&S    |                                       |       |      |      |        |
| 87                          | 38    | 9.0  | 22.8  | C&S    |                                       |       |      |      |        |
| 90                          | 40    | 9.7  | 23.10 | C&S    |                                       |       |      |      |        |

APPENDIX 1 continued

| <i>Physalaemus pustulosus</i> |       |      |       |        | <i>Physalaemus pustulosus</i> continued |          |      |       |        |
|-------------------------------|-------|------|-------|--------|---|----------|------|-------|--------|
| #                             | Stage | BL   | TL    | Status | #                                       | Stage    | BL   | TL    | Status |
| 2                             | 39    | 8.8  | 27.7  | C&S    | 88                                      | 44       | 9.3  | 13.6  | C&S    |
| 5                             | 43    | 10.1 | 17.4  | C&S    | 90                                      | 45       | 8.3  | 9.6   | C&S    |
| 8                             | yg    | 9.6  | 9.6   | C&S    | 92                                      | 41       | 9.7  | 26.7  | C&S    |
| 13                            | yg    | 8.8  | 8.8   | C&S    | 93                                      | 33       | 7.2  | 19.1  | C&S    |
| 15                            | 45    | 9.8  | 11.0  | C&S    | 94                                      | 41       | 9.2  | 24.6  | C&S    |
| 18                            | 45    | 10.4 | 11.0  | C&S    | 95                                      | 37       | 5.9  | 23.0  | C&S    |
| 20                            | 43    | 8.6  | 11.9  | C&S    | 97                                      | 34       | 7.1  | 18.4  | C&S    |
| 24                            | 45    | 9.7  | 9.8   | C&S    | 100                                     | 36       | 8.5  | 22.1  | C&S    |
| 26                            | yg    | 11.3 | 11.3  | C&S    | 102                                     | yg       | 8.9  | 8.9   | C&S    |
| 30                            | 43    | 9.2  | 17.1  | C&S    | 106                                     | 45       | 6.8  | 8.4   | C&S    |
| 31                            | 38    | 9.0  | 25.3  | C&S    | 108                                     | 42       | 8.70 | 24.9  | C&S    |
| 32                            | 41    | 8.6  | 9.6   | C&S    | 112                                     | 41       | 8.4  | 26.3  | C&S    |
| 34                            | 41    | 9.7  | 27.9  | C&S    | 114                                     | 35       | 6.8  | 19.1  | C&S    |
| 37                            | yg    | 9.2  | 9.2   | C&S    | 117                                     | 33       | 7.1  | 18.0  | C&S    |
| 43                            | 43    | 8.6  | 20.2  | C&S    | 119                                     | 38       | 8.4  | 26.2  | C&S    |
| 44                            | yg    | 9.8  | 9.8   | C&S    | 123                                     | yg       | 8.4  | 8.4   | C&S    |
| 45                            | yg    | 10.3 | 10.3  | C&S    | 125                                     | 45       | 6.8  | 8.0   | C&S    |
| 47                            | 38    | 9.7  | 26.6  | C&S    | 126                                     | 43       | 8.3  | 22.9  | C&S    |
| 49                            | yg    | 9.8  | 9.8   | C&S    | 127                                     | 44       | 7.79 | 14.19 | C&S    |
| 53                            | 44    | 7.6  | 9.3   | C&S    | 128                                     | 44       | 8.11 | 14.5  | C&S    |
| 55                            | yg    | 8.6  | 8.6   | C&S    | 130                                     | 40       | 9.82 | 25.59 | C&S    |
| 57                            | yg    | 9.7  | 9.7   | C&S    | 131                                     | 36       | 8.2  | 21.9  | C&S    |
| 59                            | 42    | 9.2  | 23.5  | C&S    | 133                                     | 32       | 6.8  | 12.7  | C&S    |
| 60                            | yg    | 9.5  | 9.5   | C&S    | 134                                     | 33       | 7.8  | 21.4  | C&S    |
| 61                            | 38    | 9.1  | 24.8  | C&S    | 141                                     | 34       | 7.5  | 20.3  | C&S    |
| 63                            | 41    | 10.0 | 28.8  | C&S    | 142                                     | 41       | 8.6  | 25.1  | C&S    |
| 65                            | 31    | 5.8  | 12.2  | C&S    | 143                                     | 41       | 9.1  | 25.6  | C&S    |
| 68                            | 41    | 9.3  | 26.1  | C&S    | 144                                     | 38       | 8.5  | 23.9  | C&S    |
| 72                            | 35    | 7.1  | 11.2  | C&S    | 147                                     | 39       | 8.5  | 23.1  | C&S    |
| 75                            | 43    | 10.3 | 22.8  | C&S    | 150                                     | 32       | 7.0  | 18.0  | C&S    |
| 76                            | 40    | 9.17 | 25.95 | C&S    | 152                                     | 40       | 9.7  | 28.2  | C&S    |
| 77                            | 44    | 8.05 | 12.81 | C&S    | 157                                     | 40       | 9.9  | 28.8  | C&S    |
| 79                            | 38    | 7.7  | 23.0  | C&S    | 158                                     | 41       | 8.1  | 24.1  | C&S    |
| 81                            | 34    | 6.2  | 11.1  | C&S    | 159                                     | yg/adult |      |       | C&S    |
| 83                            | 41    | 9.3  | 24.0  | C&S    | 160                                     | adult    |      |       | C&S    |
| 85                            | 43    | 9.3  | 21.6  | C&S    |   |          |      |       |        |
| 87                            | 36    | 8.7  | 22.4  | C&S    |   |          |      |       |        |