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Chondrocranial Morphology of *Leptodactylus* Larvae (Leptodactylidae: Leptodactylinae): Its Utility in Phylogenetic Reconstruction

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ABSTRACT Chondrocranial morphology of leptodactylid frogs is scarcely known and has not been completely described for any species of *Leptodactylus*. We describe the diversity of chondrocranial morphology in the genus *Leptodactylus* based on the analysis of 22 species, representing the four species groups: the *fuscus* Group, *ocellatus* Group, *melanonotus* Group, and *pentadactylus* Group. Furthermore, 26 characters are identified and used in a phylogenetic analysis. The phylogenetic analysis using *Physalaemus*, *Crosodactylus*, and *Hylodes* as outgroups suggests two monophyletic clades within *Leptodactylus*: the *melanonotus-ocellatus* clade and the *pentadactylus-fuscus* clade. However, it does not support the monophyly of the species groups as currently recognized and it suggests a paraphyletic *Leptodactylus*. Enforcing the monophyly of the ingroup, i.e., *Leptodactylus*, results in the same major two clades of *Leptodactylus*. *Leptodactylus riveroi*, a taxon previously unassigned to any species group, appears most closely related to the *melanonotus-ocellatus* clade based on chondrocranial characteristics. *J. Morphol.* 238:287–305, 1998. © 1998 Wiley-Liss, Inc.

KEY WORDS: Chondrocrania; anatomy; larvae; *Leptodactylus*; variation; phylogeny

Most studies of cranial morphology in anurans have focused on variation and characteristics of the ossified adult skull. Whereas characters derived from the study of adult osteology have played an important role in anuran systematics, few authors have studied characters of the larval chondrocranium in an evolutionary context. In part, this can be attributed to a lack of available comparative baseline data needed to understand character diversity and chondrocranial evolution (de Sá and Trueb, '91). Recently, a number of papers have contributed to expand our understanding of tadpole chondrocrania (e.g., Wiens, '89; Lavilla and Fabrezi, '92; Lavilla and De la Riva, '93; Púgener and Maglia, '97; Wild, '97). A few studies have used chondrocranial characters in a phylogenetic context (Sokol '77, '81; de Sá and Trueb, '91; Haas, '95, '96, '97); however, those papers compared chondrocrania among distantly related taxa. No study has attempted a comparative morphological analysis of a large number of congeneric species. Understanding the variation of chondrocranial characters among closely related species rep-

resents the other end of the phylogenetic spectrum. Furthermore, it is important if we are going to use chondrocranial characters in phylogenetic studies. This study is the first to examine phylogenetic variation in the chondrocrania of 22 closely related species.

Leptodactylus currently consists of approximately 61 recognized species, which are clustered into four species groups: the *fuscus* Group, the *ocellatus* Group, the *melanonotus* Group, and the *pentadactylus* Group (Heyer, '69). The current clustering of species of *Leptodactylus* into these four "species groups" points to the presence of morphological variation in the genus; at least enough variation to recognize "species groups" within the genus. Consequently, *Leptodactylus* is an ideal candidate to examine phylogenetic

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variation of chondrocranial morphology among closely related species and its possible correlation to currently recognized species groups.

Whereas there is some available information on adult osteology (Lynch, '71, '73), there is no complete description of the chondrocranium of any species of *Leptodactylus*. Brief references to individual chondrocranial structures are available for *Leptodactylus chaquensis* (Sokol, '81), *L. pentadactylus*, and *L. ocellatus* (Haas, '95). Analysis of chondrocranial variation within *Leptodactylus* may provide additional characters to support or refute the monophyly of the species groups; furthermore, it may help to resolve relationships among the species groups. Additionally, such analysis may help to determine whether chondrocranial anatomy provides useful diagnostic characters to differentiate closely related species.

Herein, we analyze chondrocranial morphology for approximately one third of the currently recognized species of *Leptodactylus*. The chondrocrania of 22 species within the genus *Leptodactylus* are analyzed with the following goals: 1) to describe and analyze chondrocranial anatomy in the genus *Leptodactylus*; 2) to identify characters that may help to further define the species groups and their evolutionary relationships; and 3) to contribute baseline chondrocranial data that can be used for comparative purposes within the Leptodactylidae and Neobatrachia as a whole.

MATERIALS AND METHODS

Chondrocranial descriptions are based on a total of 151 tadpoles and juveniles representing 22 species and four species groups within the genus *Leptodactylus*. Species included in this study are *Leptodactylus albibras*, *L. bufonius*, *L. fuscus*, *L. gracilis*, *L. labialis*, *L. labrosus*, *L. latinasus*, *L. longirostris*, and *L. mystacinus* of the *fuscus* Group; *L. chaquensis*, *L. insularum*, and *L. ocellatus* of the *ocellatus* Group; *L. melanonotus*, *L. petersii*, *L. podicipinus*, and *L. validus* of the *melanonotus* Group; and *L. knudseni*, *L. labyrinthicus*, *L. pentadactylus*, and *L. rhodomystax* of the *pentadactylus* Group. In addition, *L. silvanimbus*, which has recently been associated with the *melanonotus* Group (Heyer et al., '96), and one unassigned species, *L. riveroi*, were examined. Specimens of *L. melanonotus* that come from localities in Belize and Costa Rica show clear differences in chondrocranial morphology. We refer to

them as *L. melanonotus* CR (Costa Rica sample) and *L. melanonotus* B (Belize sample) and describe them separately. Specimens are deposited in the United States National Museum of Natural History (USNM), Smithsonian Institution. Specimens examined, developmental stages available, collection data, and catalogue numbers are listed in Appendix A.

All specimens were wild-caught, preserved in 4% formalin, and staged using the table of Gosner ('60). Tadpoles were cleared and double-stained for bone and cartilage by using a modified version of the technique of Dingerkus and Uhler ('77). Chondrocranial terminology follows de Sá ('88), de Sá and Trueb ('91), and Haas ('95). Illustrations of chondrocrania and branchial baskets were made using a Wild MC3 stereomicroscope with a camera-lucida attachment. Specimens were illustrated at comparable developmental stages (stages 30–37) whenever possible; however, all available stages were examined for chondrocranial descriptions.

Phylogenetic analysis was done using PAUP program version 3.1 (Swofford, '93). Multistate characters were run unordered to avoid a priori assumptions of the evolutionary path of the transformation series. Out-group comparison was used to polarize all characters. Relationships within the Leptodactylidae, and within the leptodactylid subfamilies, are unresolved (Maxon and Heyer, '88; Ford and Cannatella, '93; Ruvinsky and Maxson, '96). Lynch ('71) considered both the Hylodinae and the Leptodactylinae to be derived from the Telmatobinae. Herein, we take a conservative approach and use representatives from these two subfamilies as outgroups. Outgroups included are *Physalaemus pustulosus* (Leptodactylinae), *Hylodes nasus*, and *Crossodactylus gaudichaudii* (Hylodinae). *Hylodes* and *Crossodactylus* must be considered more distantly related outgroups to *Leptodactylus*, whereas *Physalaemus* represents a more closely related outgroup.

RESULTS

The chondrocranial description presented here is representative for all species; individual divergences from the general description, as well as ontogenetic changes in chondrocranial morphology, are noted when applicable. If information for a given species is not presented, it is because the character state for that species could not be determined based on the limited specimens available.

The typical chondrocranium of *Leptodactylus* is slightly longer than it is wide, until about stage 41 when major metamorphic rearrangements of the chondrocranium begin. The chondrocranial width is approximately 85–90% of the total length (Fig. 1); exceptions are *L. bufonius*, in which the chondrocranium is slightly narrower (about 82% of chondrocranial length) and *L. knudseni*, *L. insularum*, and *L. validus*, in which

chondrocranial width is approximately equal to the length. Chondrocranial height is about 20–25% of its total length and approximately 30% of its total width.

Neurocranium

Ethmoidal region

The paired suprarostal cartilages support the upper horny break; each suprarostal consists of a central corpus and a lateral

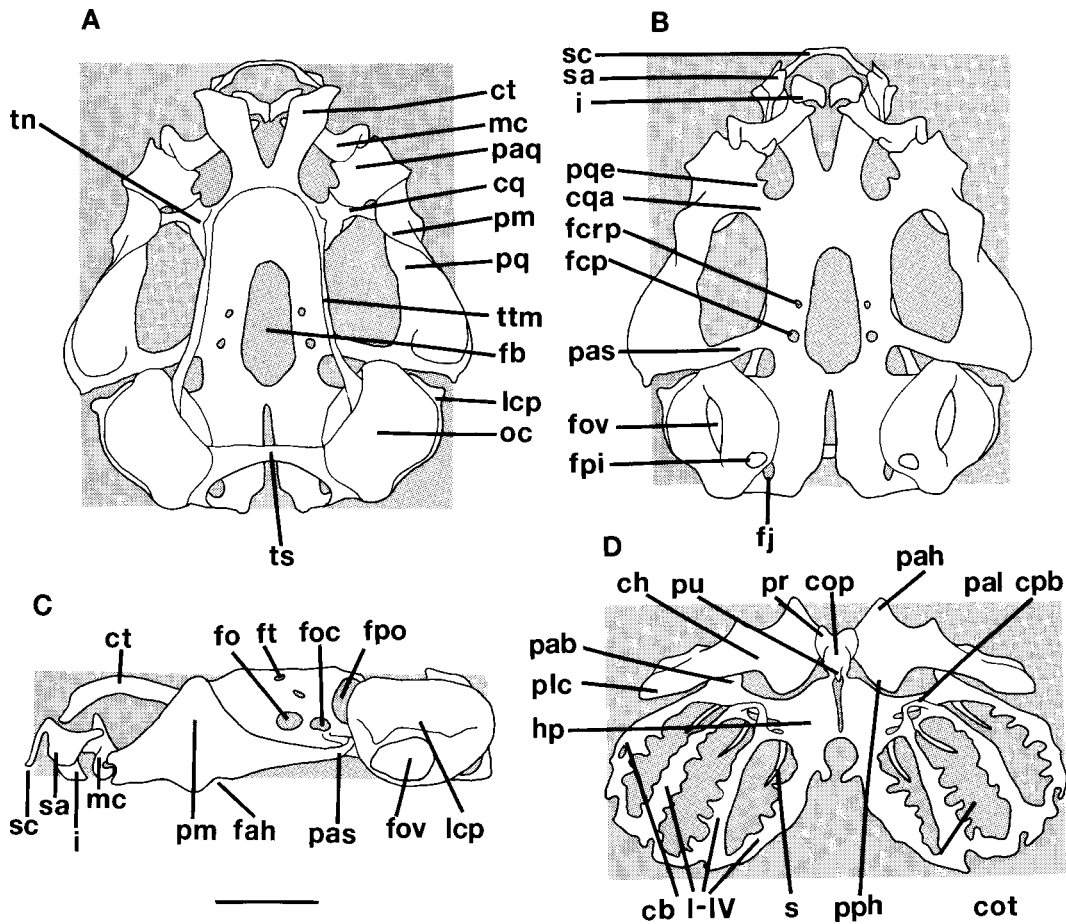


Fig. 1. Chondrocranium of *Leptodactylus melanonotus* B larva (*melanonotus* Group), stage 33 (USNM #519940). (A) dorsal, (B) ventral, and (C) lateral views; (D) ventral view of hyobranchial apparatus. cb I-IV, ceratobranchials I-IV; cbp, closed processus branchialis; ch, ceratohyal; cop, copula posterior; cot, commissura terminalis; cq, commissura quadratoorbitalis; cqa, commissura quadratoorbitalis anterior; ct, cornua trabeculae; fah, facies articularis hyalis; fb, fenestra basicranialis; fcp, foramen caroticum primarium; fcrp, foramen craniopalatinum; fj, foramen jugulare; foc, foramen oculomotorium; fpi, foramen perilymphaticum inferior; fo,

foramen opticum; fov, fenestra ovalis; fp, foramen prooticum; ft, foramen trochleare; hp, hypobranchial plate; i, infraostal cartilage; lcp, larval crista parotica; mc, Meckel's cartilage; oc, otic capsule; pah, processus anterior hyalis; pal, processus anterolateralis hyalis; pph, processus posterior hyalis; pas, processus ascendens; paq, pars articularis quadrati; pm, processus muscularis quadrati; pq, palatoquadrata; pqe, processus quadratoethmoidalis; pr, pars reuniens; pu, processus urobranchialis; s, spicule; sa, suprarostal ala; sc, suprarostal corpus; tn, tectum nasi; ts, tectum synoticum; ttm, tania tecti marginalis. Bar = 1.0 mm.

ala (Fig. 2). The central corpora lie between the cornua trabeculae at the anterior end of the chondrocranium. The two corpora are fused ventromedially, forming a continuous, horizontal bar of cartilage between the corpora. In all species, the corpora are continuous dorsolaterally with the alae through a relatively narrow strip of cartilage. The lateral alae are flat, wide sheets of cartilage that are rounded ventrally; each ala curves posteriorly from its point of fusion with the corpora. A small, rounded enlargement near the dorsomedial margin of the ala serves as the point of articulation of the cornua trabeculae to the suprarostal. The posterodorsal margin of each ala possesses a well developed processus posterior dorsalis. An adrostral tissue mass is present near the tip of the processus posterior dorsalis.

The suprarostals of members of the *fuscus* Group and *Leptodactylus rhodomystax* have wide and, in frontal view, U-shaped corpora (Fig. 2a). In *L. rhodomystax* and *L. mystacinus* the ventral margins of the corpora have lateral projections facing similar projections from the lateral alae; however, these are not fused with each other (Fig. 2a). In *L. albilabris*, *L. bufonius*, and *L. longirostris* these projections are fused, forming a narrow, poorly chondrified ventral connection between the corpora and the alae. The ventromedial connection between the corpora of *L. pentadactylus*, *L. knudseni*, and *L. labyrinthicus* is very thin (Fig. 2b). Furthermore, in these species the medial separation between the corpora is narrow, forming a deep U, and there is an extensive ventral connection between the corpora and the alae. As a result, in these taxa each suprarostal is a single element bearing a small round or

ovoid hole. The suprarostals of all species of the *ocellatus* and *melanonotus* Groups examined, *L. riveroi*, and *L. silvanimbus* have slender corpora (Fig. 2c,d). In these taxa, the corpora are fused ventromedially by a relatively long, thin connection and the space between the corpora acquires a wider U- to V-shaped appearance. No ventral connection or lateral projections between the corpora and alae are present in any members of the *ocellatus* and *melanonotus* Groups, *L. riveroi*, or *L. silvanimbus*.

In most *Leptodactylus* species, the cornua trabeculae represent about 20% of the total chondrocranial length. However, in members of the *pentadactylus* Group (except *L. rhodomystax*) they are shorter, representing between 10–15% of the chondrocranial length (Figs. 3c, 4h,i). The cornua trabeculae diverge anteriorly from the planum trabeculare anticum and are expanded distally to varying degrees. Their anterior margins are uneven in most species and flex ventrally to articulate with the suprarostal alae. The widths of the cornua trabeculae of *L. rhodomystax* (Fig. 4j) are similar to other species in the *pentadactylus* Group and they also bear a relatively straight anterior margin. However, they resemble the cornua trabeculae in some members of the *fuscus* Group, particularly *L. albilabris*, *L. latinasus*, *L. longirostris*, and *L. fuscus*, in terms of the depth and narrowness of their divergence and in having a slightly outwardly rounded lateral margin. The cornua trabeculae are of variable width in the *fuscus* Group, with those of *L. bufonius* (Fig. 4b) being slightly narrower among the species examined. The cornua trabeculae of all species of the *ocellatus* and *melanonotus* Groups examined, *L. riveroi*, and *L. silvanimbus* are narrower proximally and only slightly wider distally (Figs. 1A, 3b, 4k–r). In addition, in the *ocellatus* Group, *L. melanonotus* CR, and *L. silvanimbus* the V-shaped area between the cornua trabeculae is slightly wider than in other species. *Leptodactylus labyrinthicus*, *L. knudseni*, and *L. pentadactylus* have shorter and wider cornua trabeculae than any other species examined. Their anterior margins are almost straight and the cornua trabeculae are of almost uniform width throughout their length, except for *L. knudseni* (Fig. 4h), in which they are slightly wider distally. The divergence of the cornua trabeculae in these taxa forms a sharp and distinct V shape.

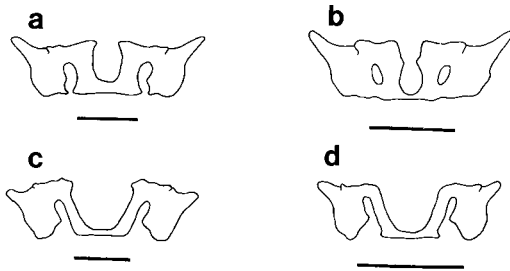


Fig. 2. Suprarostal cartilages. **a:** *Leptodactylus mystacinus*, stage 36 (USNM #519948). **b:** *L. pentadactylus*, stage 29 (USNM #519997). **c:** *L. ocellatus*, stage 36 (USNM #519962). **d:** *L. melanonotus* B, stage 33 (USNM #519940). Bar = 1.0 mm.

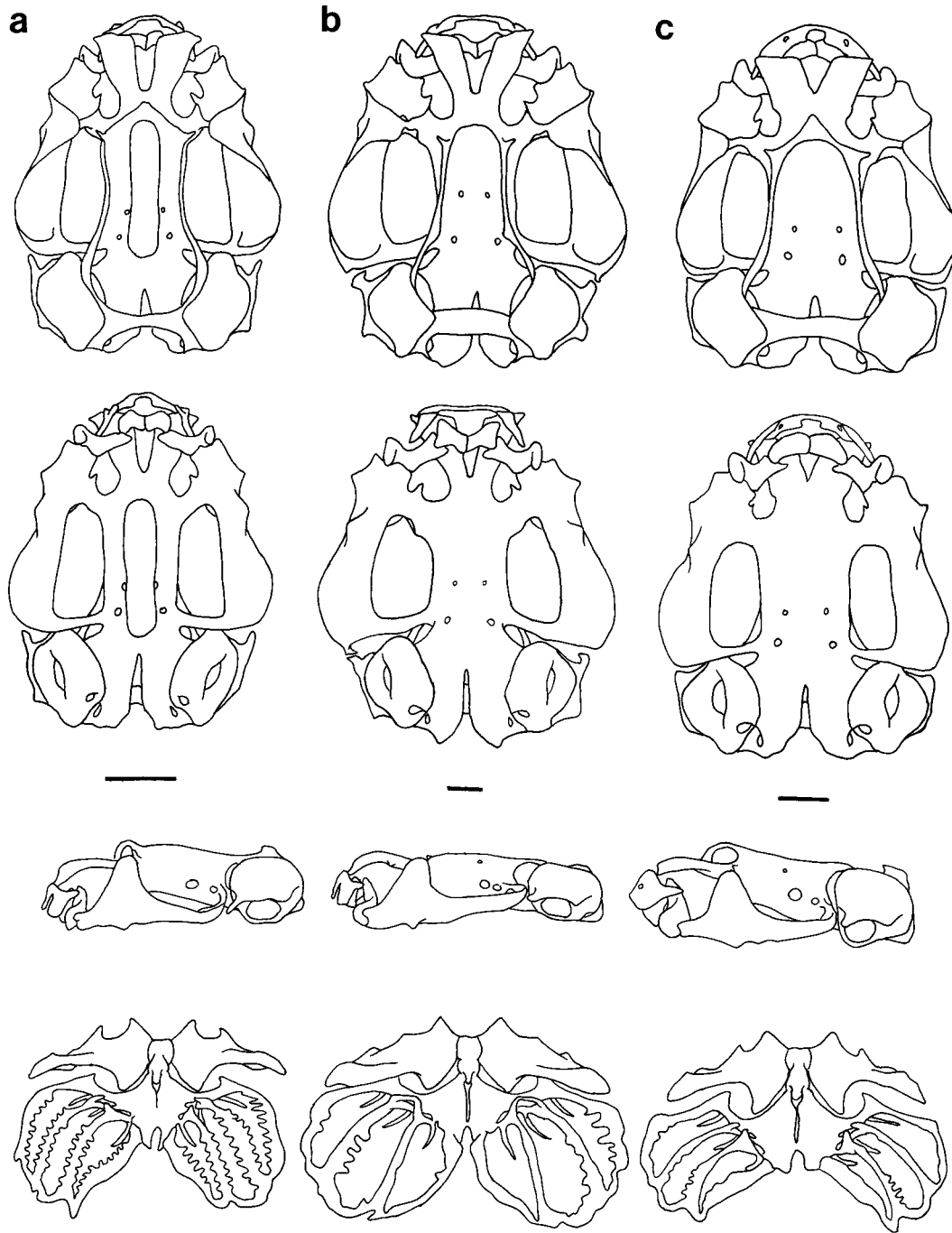


Fig. 3. Dorsal, ventral and lateral views of chondrocrania and ventral view of hyobranchial apparatus. **a:** *Leptodactylus latinasus* larva (*fuscus* Group), stage 35 (USNM #520298). **b:** *L. ocellatus* larva (*ocellatus* Group), stage 37 (USNM #519962). **c:** *L. labyrinthicus* larva (*pentadactylus* Group), stage 36 (USNM #520296). Bar = 1.0 mm.

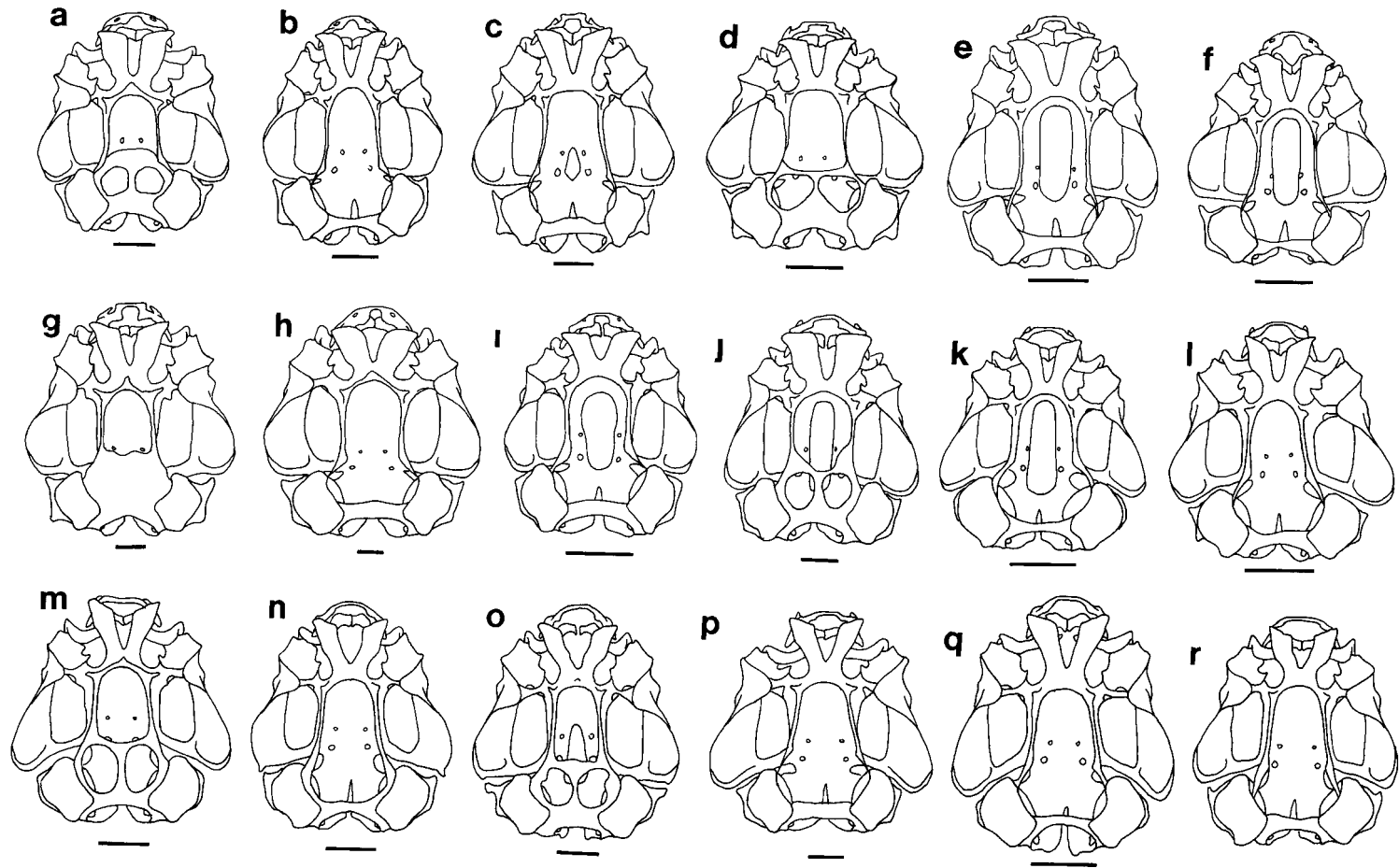


Fig. 4. Dorsal view of chondrocranium. **a:** *Leptodactylus albilabris*, stage 32 (USNM #520280). **b:** *L. bufonius*, stage 35 (USNM #520286). **c:** *L. gracilis*, stage 35 (USNM #519898). **d:** *L. labialis*, stage 37 (USNM #519928). **e:** *L. labrosus*, stage 31 (USNM #520295). **f:** *L. longirostris*, stage 33 (USNM #520299). **g:** *L. mystacinus*, stage 37 (USNM #519952). **h:** *L. knudseni*, stage 36 (USNM #520293). **i:** *L. pentadactylus*, stage 29 late/30 early (USNM #519995). **j:** *L. rhodomystax*, stage 27 (USNM #520306). **k:** *L. petersii*, stage 36 (USNM #520301). **l:** *L. podicipinus*, stage

33 (USNM #520304). **m:** *L. validus*, stage 37 (USNM #520313). **n:** *L. melanonotus* CR, stage 35 (USNM #520283). **o:** *L. chaquensis*, stage 37 (USNM #519881). **p:** *L. insularum*, stage 36 (USNM #520291). **q:** *L. riveroi*, stage 27 (USNM #520308). **r:** *L. silvanimbus*, stage 31 (USNM #520311). a–g are species in the *fuscus* Group, h–j are species in the *pentadactylus* Group, k–m are species in the *melanonotus* Group, and n–p are species in the *ocellatus* Group. Bar = 1.0 mm.

The ligamentum quadratoethmoidale extends between the commissura quadratocranialis anterior and the lateral margin of the cornua trabeculae near their point of divergence. This ligament attaches to a variably developed ventrolateral process on the cornua trabeculae, the processus lateralis trabeculae. The processus lateralis trabeculae is poorly developed in *Leptodactylus bufonius*, *L. fuscus*, *L. gracilis*, *L. knudseni*, *L. melanonotus* CR, *L. chaquensis*, *L. riveroi*, and *L. silvanimbus*. However, in *L. albilabris*, *L. labialis*, *L. mystacinus*, *L. labyrinthicus*, *L. rhodomystax*, *L. ocellatus*, *L. melanonotus* B, and *L. validus* it is a better developed and blunt process. The processus lateralis trabeculae is not distinct in *L. labrosus*, *L. latinus*, *L. longirostris*, *L. pentadactylus*, *L. insularum*, *L. petersii*, and *L. podicipinus*.

The posterior confluence of the cornua trabeculae is continuous with the planum trabeculare anticum, which, in turn, continues with the planum ethmoidale that forms the anterior wall of the braincase. In the region just posterior to this confluence, the planum trabeculare anticum is slightly longer and narrower in *Leptodactylus riveroi*, *L. silvanimbus*, and species of the *ocellatus* and *melanonotus* Groups. In most specimens illustrated (Figs. 1A, 3, 4), the tectum nasi has started to form on each side as a rounded projection located dorsal to the commissura quadratocranialis anterior (as early as stage 27 in *L. riveroi* and *L. rhodomystax*).

Orbitotemporal region

The central area of the cranial floor is closed by a thin cartilage, the planum intertrabeculare, which eventually occludes the fenestra basicranialis and contributes to the cranial floor during development. The planum intertrabeculare forms from extensions of the trabeculae cranii laterally and the planum trabeculare anticum anteriorly. The cranial floor has two sets of foramina. The anterior, smaller pair are the foramina craniopalatina, while the larger, posterior pair correspond to the foramina carotica primaria (Fig. 1A,B). In early stages, the foramina craniopalatina are particularly difficult to identify because of the large fenestra basicranialis.

The lateral walls of the braincase are formed by the orbital cartilages. The orbital cartilages attach posterodorsally to the otic capsules, although this connection may not be completely developed or clearly visible in

early stages. This connection forms the dorsal margin of the foramen prooticum, a large, elongate foramen located between the anterior edge of the otic capsule and the posterior margin of the orbital cartilage (Fig. 1C). The prootic foramen is somewhat variable in size. Two other large foramina are visible in the posteroventral portion of the orbital cartilage. The slightly larger anterior foramen is the foramen opticum, whereas the smaller posterior foramen is the foramen oculomotorium. Additionally, a small trochlear foramen is located anterodorsal to the optic foramen; this foramen is variably visible.

The frontoparietal fontanelle is large and ovoid in shape. It is bordered laterally by the taenia tecti marginales, posteriorly by the tectum synoticum, and anteriorly by the planum ethmoidale. In some species the frontoparietal fontanelle further divides during development into an anterior frontal and two posterior parietal fenestrae (Fig. 4a,d,j,m,o). This subdivision occurs by the medial growth of the taenia tecti transversales from the taenia tecti marginales and the elongation of the taenia tecti medialis anteriorly from the medial portion of the tectum synoticum. The subdivision of the frontoparietal fenestra begins at stage 34 in *Leptodactylus melanonotus* B; however, it already has begun by stage 27 in *L. rhodomystax*, stage 31 in *L. silvanimbus*, and stage 32 in *L. albilabris*. Among the available specimens of *L. chaquensis*, *L. labialis*, and *L. riveroi*, frontal and parietal fenestrae are present by stage 37 and by stage 38 in *L. podicipinus*. *Leptodactylus mystacinus* is unique among examined species in having the posterior half of the frontoparietal fenestra covered by a continuous sheet of cartilage as early as stage 35 (Fig. 4g). Formation of parietal fenestrae was not observed in this species among the specimens examined.

Otooccipital region

The otic capsules are ovoid and represent about 30% of the total chondrocranial length. In dorsal view, the otic capsule bears a laterally projecting and wide larval crista parotica in most species. Anteriorly, the crista parotica bears a well-developed processus anterolateralis; posteriorly, it is enlarged forming a distinct, triangular processus posterolateralis. The processus anterolateralis is stout and triangular in all members of the *pentadactylus* Group, *Leptodactylus silvanimbus*, *L. albilabris*, and *L. labrosus*; long and finger-like in all other members of the

fuscus Group; stout and rectangular in *L. melanonotus* CR, *L. ocellatus*, and *L. chaquensis*; a small rounded to triangular bump in *L. insularum*, *L. melanonotus* B, and *L. podicipinus*; and poorly developed and difficult to identify in *L. petersii*, *L. validus*, and *L. riveroi*. The processus anterolateralis approaches a knob-like projection of the posterolateral curvature of the palatoquadrate in *L. chaquensis*, *L. ocellatus*, *L. melanonotus* CR, and *L. melanonotus* B. However, while they are nearly in contact in *L. ocellatus* and *L. melanonotus* CR, fusion of these structures does not occur. The processus posterolateralis is reduced in *L. melanonotus* B, *L. podicipinus*, and *L. riveroi* and seems to be absent in *L. petersii* and *L. validus*. A large fenestra ovalis is visible ventrolaterally on the otic capsule, directly below the crista parotica.

The arcus occipitalis extends ventrally from the posteromedial margin of the otic capsule, fusing with the planum basale and giving rise to the occipital condyles. The planum basale and the arcus occipitalis form the ventral and medial margins of the foramen jugulare. The foramen perilymphaticum inferior is found lateral to the foramen jugulare in the ventromedial margin of the otic capsule (visible ventrally, Fig. 5).

Visceral components

Palatoquadrate

The palatoquadrate of *Leptodactylus* is narrow anteriorly and it expands continuously posteriorly, becoming outwardly rounded in all species except *L. bufonius* (Fig. 4b), in which it is not expanded posteriorly. In most species of the *fuscus* Group, the posterior curvature of the palatoquadrate is at the level of the point of attachment of the processus ascendens to the orbital cartilage. In *L. albilabris*, *L. labrosus*, *L. melanonotus* CR, all species of the pentadactylus Group, and most species of the *ocellatus* Group, the posterior curvature extends slightly past this level. In *L. melanonotus* B and *L. silvanimbus* the posterior curvature extends beyond the anterior margin of the otic capsule; however, in all other members of the *melanonotus* Group, *L. insularum*, and *L. riveroi*, this curvature extends even farther posteriorly to about one-third of the way back on the otic capsule (Fig. 4k–m,p,q). The lateral and posterior margins of the palatoquadrate also curve slightly dorsally, giving the palatoquadrate a basket-like shape in dorsal view in all species except *L. bufonius* and *L. melano-*

notus CR (Fig. 4b,n), where the palatoquadrate appears relatively flat in dorsal view.

Posteriorly, the palatoquadrate attaches to the orbital cartilage via the processus ascendens, which is a narrow, rod-like cartilage connecting the posteromedial margin of the palatoquadrate to the region of the pila antotica of the orbital cartilage (Figs. 1C, 3, 6). The processus ascendens attaches just posterior to the oculomotor foramen (see Fig. 3a,c), a condition defined as “intermediate” by Sokol ('81), in the *fuscus* Group, *pentadactylus* Group, *L. ocellatus*, and *L. chaquensis*. In the *melanonotus* Group, *L. insularum*, *L. riveroi*, and *L. silvanimbus* the processus ascendens attaches below the posteroverentral margin (see Fig. 1C) of the oculomotor foramen in a typical “low” condition (Sokol, '81).

The processus ascendens is almost perpendicular to the main axis of the chondrocranium in the *fuscus* Group, its posterior margin forming an angle of about 85–90° with the main axis of the body. This angle is about 75–80° in the *pentadactylus* Group, *Leptodactylus chaquensis*, and *L. ocellatus*, around 72° in *L. melanonotus* CR, and about 70° in *L. melanonotus* B and *L. silvanimbus*. In other species the angle is more acute, being about 65° in remaining species of the *melanonotus* Group and *L. insularum*, and about 60° in *L. riveroi*.

Anteriorly, the palatoquadrate connects to the braincase via a wide commissura quadratocranialis anterior. The commissura quadratocranialis anterior extends between the palatoquadrate, at a level just posterior to the pars articularis quadrati, and the floor of the neurocranium. The anterior margin of the commissura quadratocranialis anterior bears an overall triangular processus quadratoethmoidalis, which serves as the point of attachment for the ligamentum quadratoethmoidale. In addition, a triangular-shaped processus pseudopterygoideus is present on the posterior margin of the commissura quadratocranialis anterior in *Leptodactylus fuscus* and *L. mystacinus* (Fig. 4g). The latter process was not clearly identifiable in other *Leptodactylus*. A rod-like commissura quadratoorbitalis is present; it is formed by the fusion of the processus antorbitalis with the medial tip of the processus muscularis quadrati.

The palatoquadrate bears two distinct anterior processes, the processus muscularis

quadrati and the pars articularis quadrati. The processus muscularis quadrati is broad, flat, and extends dorsally from the lateral margin of the palatoquadrate at a level just posterior to the pars articularis quadrati. The processus muscularis quadrati is wide in the *melanonotus* Group, *ocellatus* Group, *Leptodactylus silvanimbus*, and *L. riveroi*, to the degree that, in lateral view, it is almost impossible to distinguish the pars articularis quadrati (Fig. 1C). In other *Leptodactylus* examined, the processus muscularis quadrati is narrower and the pars articularis quadrati is clearly distinguishable in lateral view (Fig. 3a,c). The dorsal edge of the processus muscularis quadrati inclines medially and attaches to the commissura quadratocranialis anterior via the commissura quadrato-orbitalis. Immediately below the processus muscularis and ventrally on the palatoquadrate, there is a notch, the facies articularis hyalis, that serves as the point of articulation of the ceratohyal to the palatoquadrate. The facies articularis hyalis is partly formed by the hyoquadrate process, a rounded, ventral enlargement of the palatoquadrate. In lateral view, the hyoquadrate process is small and triangular in most species; however, in members of the *melanonotus* Group (except *Leptodactylus melanonotus* CR), *L. riveroi*, and *L. insularum* it is enlarged and rounded in lateral view. The pars articularis quadrati corresponds to the short, wide segment of the palatoquadrate that extends anterior to the level of the processus muscularis. The pars articularis quadrati articulates almost over its entire anterior width with Meckel's cartilage.

Meckel's and infrarostral cartilages

Meckel's cartilages, together with the infrarostral cartilages, form the mandible in *Leptodactylus*. Meckel's cartilage is stout, oriented almost perpendicular to the main body axis, and is sigmoid-shaped, with its anteromedial margin being concave and its anterolateral margin convex (Fig. 1B). Laterally, Meckel's cartilage articulates broadly with the pars articularis quadrati via the processus retroarticularis. This process curves ventrally beneath the pars articularis. Medially, Meckel's cartilage articulates with the pars articularis quadrati through an enlarged, knob-like area of the ventromedial margin of Meckel's cartilage. While it is clearly present in all species, this knob tends to be more visible in some species than in others. In lateral view, the medial

portion of Meckel's cartilage expands in the vertical plane to form a dorsal processus dorsomedialis and a ventral processus ventromedialis. The posterodorsal portion of the infrarostral cartilage articulates with Meckel's cartilage in the region between these two processes.

The infrarostral cartilages provide support for the lower horny beak. Overall, the infrarostrals are wedge-shaped and their dorsolateral half is rounded, slightly thicker, and wider; they connect ventromedially, forming a V-shaped structure in anterior view. The anterior margins of the infrarostrals are outwardly curved laterally and notched medially in dorsal view. Furthermore, they are notched on their posterior margin. The posterior notch is deep in *Leptodactylus validus* (Fig. 5m). In the *pentadactylus* Group, except *L. rhodomystax* (which resembles all other species), the infrarostrals are unique in being overall rectangular, stout, wide throughout their length, and outwardly rounded over their entire anterior margin (Figs. 3c, 5h,i). The infrarostrals of *L. longirostris* are more slender than in other species (Fig. 5f).

Hyobranchial apparatus

The ceratohyalia (Figs. 1D, 3, 7) are wide, flat cartilages medially; laterally, they are twisted dorsally to articulate with the palatoquadrate at the facies articularis hyalis. The anterior margin of each ceratohyal bears two anterior processes, the processus anterior hyalis and the processus anterolateralis hyalis. Both processes are overall triangular in shape, with the processus anterior hyalis being larger and the processus anterolateralis hyalis inclining slightly medially. The processus anterior hyalis varies somewhat in shape, being pointed in the *fuscus* Group and *Leptodactylus rhodomystax* (Figs. 3, 7), wide and blunt in *L. knudseni*, *L. labyrinthicus*, and *L. pentadactylus* (Figs. 3c, 7h, i), and variably pointed to slightly rounded in the *melanonotus* Group, *ocellatus* Group, *L. riveroi*, and *L. silvanimbus* (Figs. 1D, 3, 7). The processus anterolateralis hyalis is visible only as a small bump in *L. ocellatus* and *L. melanonotus* CR (Figs. 3b, 7n). The ceratohyal also possesses a large and well-developed processus posterior hyalis. Medially, the ceratohyalia are connected by a poorly chondrified pars reuniens. The pars reuniens is attached posteriorly to a well-developed copula posterior, which bears a large processus urobranchialis. The copula

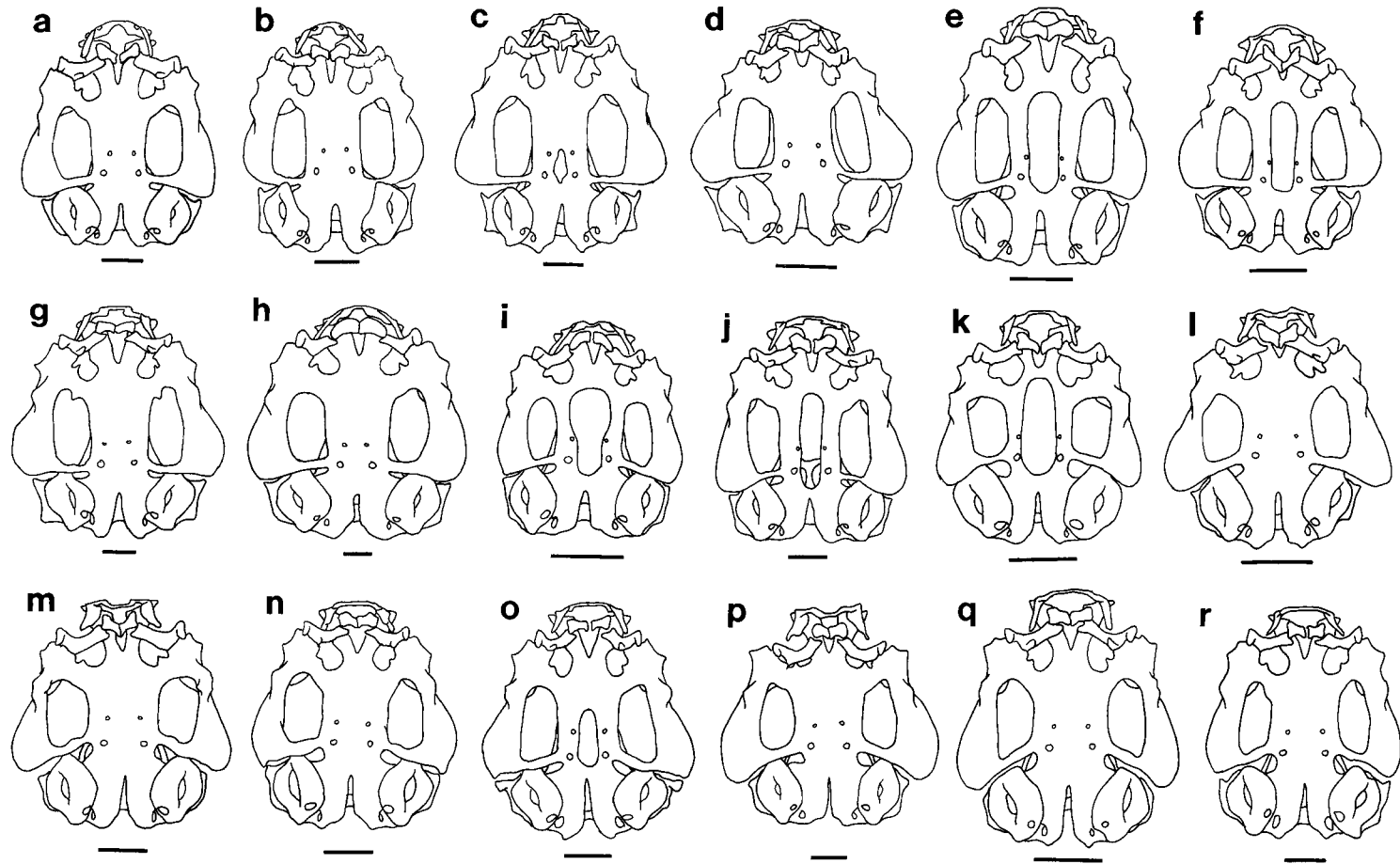


Fig. 5. Ventral view of *Leptodactylus* chondrocrania. Species as in Figure 3. Bar = 1.0 mm.

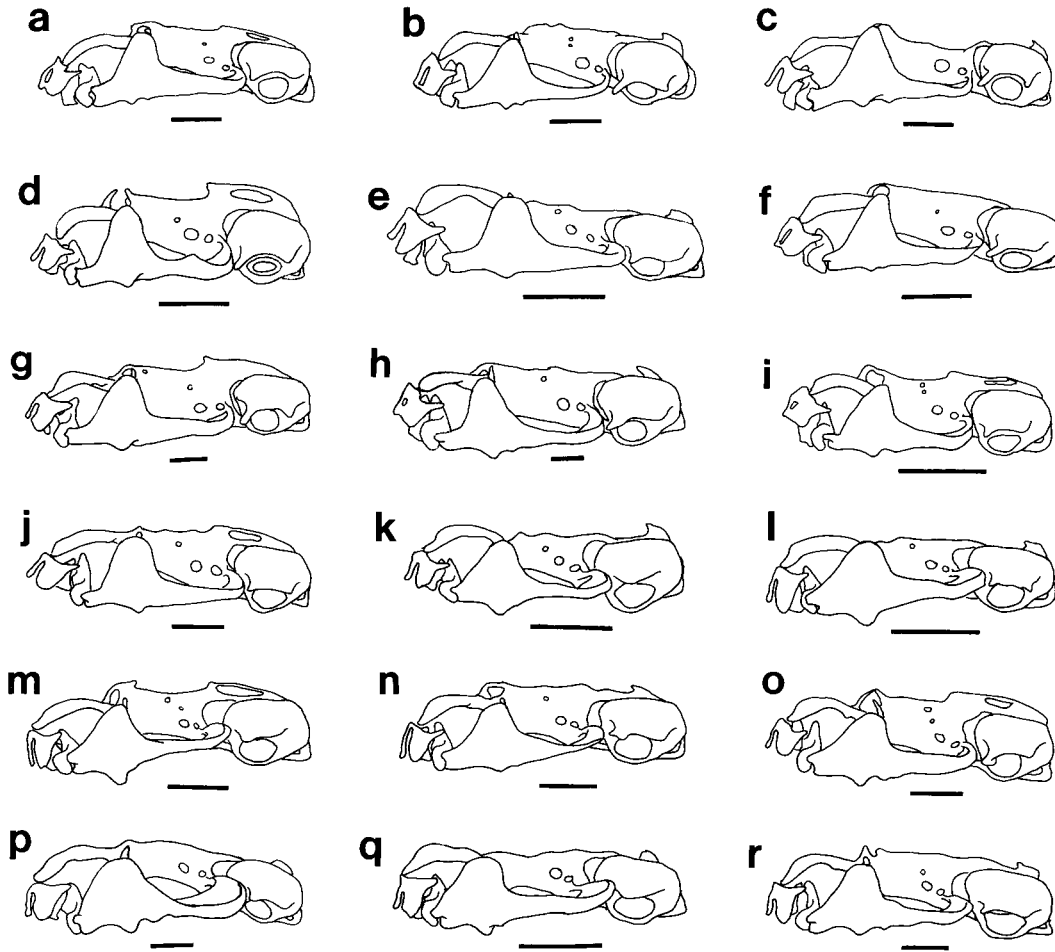


Fig. 6. Lateral view of *Leptodactylus* chondrocrania. Species as in Figure 3. Bar = 1.0 mm.

posterior connects posteriorly to the hypobranchial plates.

The hypobranchial plates are wide, flat sheets of cartilage that serve as the point of attachment for the ceratobranchials. In most species, the plates are separated medially along most of their lengths and are only distinctly fused posteriorly. However, in *Leptodactylus bufonius*, *L. fuscus*, and *L. gracilis* the hypobranchial plates are medially fused throughout their length. Similarly, in *L. labrosus*, *L. latinasus*, *L. petersii*, and *L. validus*, the plates are medially connected throughout most of their length, except for the area immediately posterior to the copula posterior. Posteriorly, the hypobranchial plates diverge, leaving an inverted U-shaped separation between their posterior edges. In

L. insularum each plate bears a small, finger-like projection on its anterior margin lateral to its point of attachment to the copula posterior (Fig. 7p).

The branchial baskets consist of four ceratobranchials that are distally continuous via commissurae terminales. Proximally, ceratobranchial I attaches to the hypobranchial plate by a wide strip of cartilage; on its anterior margin it bears a distinct, widely triangular to hook-like processus anterior branchialis that slants medially. Ceratobranchials II and IV are also fused to the hypobranchial plate, the former via a narrow bar of cartilage and the latter via a wider cartilaginous connection. Ceratobranchial III appears to be only very narrowly attached to the hypobranchial plate. Ceratobranchials I,

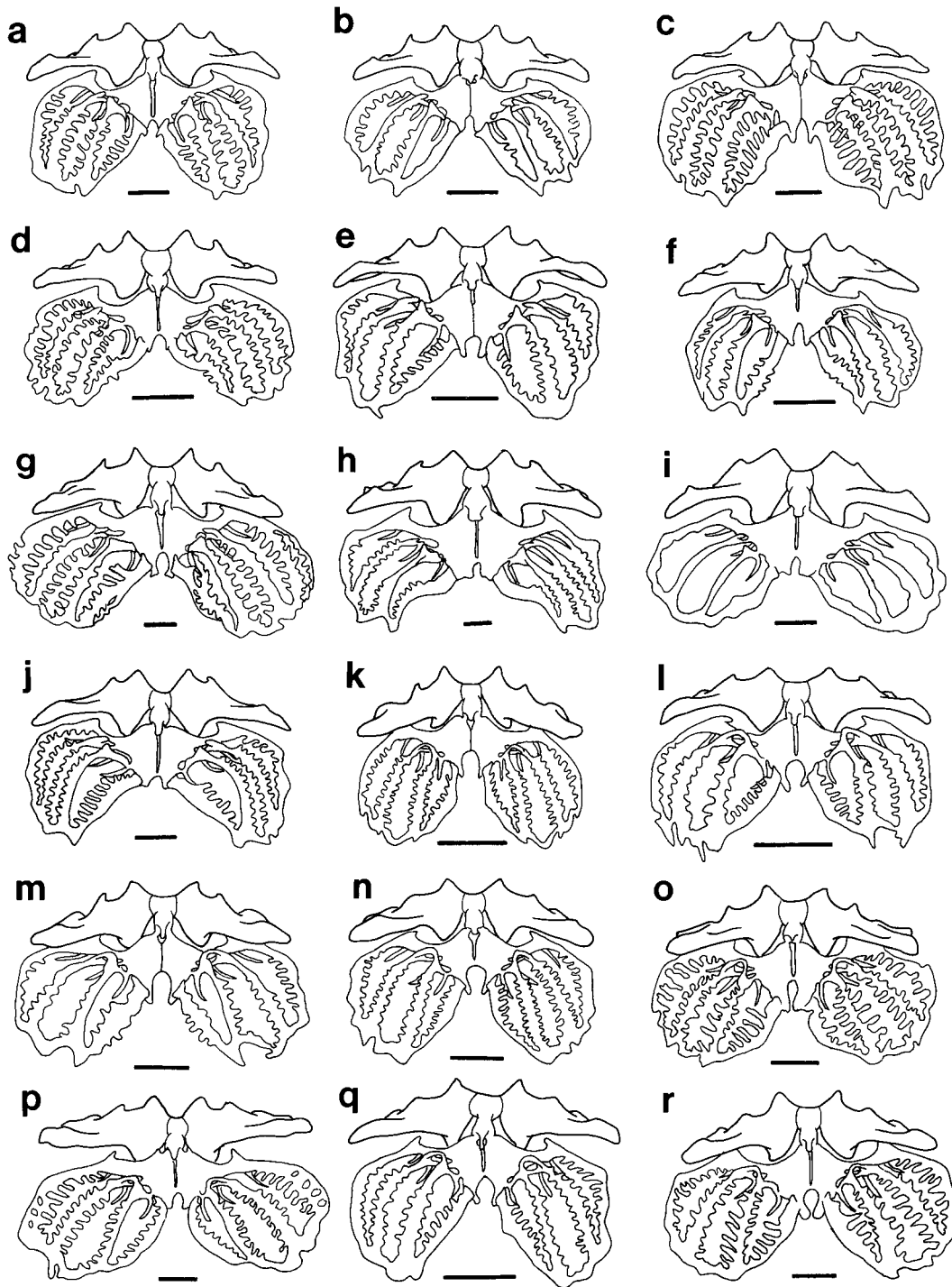


Fig. 7. Ventral view of hyobranchial apparatus of *Leptodactylus*. Species as in Figure 3, except that (i) *L. pentadactylus* corresponds to USNM #519992, stage 31. Bar = 1.0 mm.

II, and III bear a dorsally projecting spiculum near their point of attachment to the hypobranchial plate. In all members of the *ocellatus* and *melanonotus* Groups examined, *Leptodactylus riveroi*, and *L. silvanimbus*, ceratobranchials II and III are connected proximally by a closed processus branchialis (see Fig. 1D). In all examined members of the *fuscus* Group and *pentadactylus* Group, the processus branchialis is visible as two opposing, ventrally projecting cartilages extending from ceratobranchials II and III (see Fig. 3a,c). Although they appear to be connected by more lightly stained ligaments in some cases, they never fuse via a cartilaginous connection throughout development in these species.

The present study identified 26 variable chondrocranial characters in *Leptodactylus*. Description of characters is provided in Table 1; character states for each taxa included in this analysis are given in Table 2.

DISCUSSION

Chondrocranial morphology

Analysis of chondrocranial morphology in the genus *Leptodactylus* provided a number of interesting findings. Chondrocrania of the 22 species included in this study share a number of features. Overall, with the exception of three species, the chondrocranium in *Leptodactylus* tends to be slightly longer than wide. All members of the genus *Leptodactylus* studied are characterized by the following set of characters: 1) quadripartite supra-rostral cartilage with corpora fused to each other and the alae; 2) processus posterior dorsalis present on supra-rostral alae; 3) larval crista parotica present; 4) larval otic process absent; 5) commissura quadratoorbitalis present; 6) processus quadratoethmoidalis present; 7) processus dorsomedialis, processus ventromedialis, and processus retroarticularis of Meckel's cartilage present; 8) proximal ends of all ceratobranchials fused to hypobranchial plate; 9) spicules present on ceratobranchials I, II, and III; 10) processus anterior branchialis present; 11) palatoquadrate wide and outwardly rounded; and 12) otic capsules ovoid and representing approximately 30% of the length of the chondrocranium.

Also, a number of variable characters were identified. They include morphology of the supra-rostral and infra-rostral cartilages; size, shape, and degree of divergence of the cornua trabeculae; shape of the palatoquadrate; orientation and point of attachment of

TABLE 1. List of 26 chondrocranial characters used in the present study

a.	ventromedial fusion of supra-rostral corpus: (0) not fused, (1) fused.
b.	dorsal fusion of supra-rostral corpus and ala: (0) not fused, (1) fused.
c.	ventrolateral projections of supra-rostral corpus and ala: (0) absent, (1) present, (2) fused.
d.	contact between the supra-rostral corpora: (0) contact nearly along their length, (1) narrowly separated, (2) widely separated.
e.	chondrocranial width relative to chondrocranial length: (0) 80–85%, (1) 85–90%, (2) equal.
f.	length of cornua trabeculae relative to chondrocranial length: (0) 25%, (1) 20%, (2) 10–15%.
g.	planum trabeculare anticum: (0) wide, (1) narrow.
h.	frontoparietal fenestra: (0) open, (1) posterior half closed.
i.	otic capsules: (0) < than 30% of chondrocranial length, (1) 30% of chondrocranial length.
j.	processus anterolateralis of crista parotica: (0) small and triangular, (1) large and triangular, (2) long finger-like projection, (3) large and rectangular, (4) absent.
k.	projection of posterolateral curvature of palatoquadrate: (0) absent, (1) present.
l.	processus posterolateralis of crista parotica: (0) distinct, (1) reduced.
m.	posterolateral extension of the palatoquadrate: (0) does not reach the level of attachment of the processus ascendens to the braincase, (1) reaches the level of attachment of the processus ascendens to the braincase, (2) extends beyond the level of attachment of the processus ascendens to the braincase, (3) past anterior margin of otic capsules, (4) reaches 1/3 the length of the otic capsule.
n.	attachment of the processus ascendens: (0) low, (1) intermediate.
o.	angle of processus ascendens: (0) <70°, (1) 70–80°, (2) 80–90°.
p.	processus pseudopterygoideus: (0) absent, (1) present.
q.	pars articularis quadrati: (0) distinct from processus muscularis, (1) indistinct from the processus muscularis.
r.	processus muscularis: (0) large, (1) reduced.
s.	commissura quadratoorbitalis: (0) absent, (1) present.
t.	Meckel's cartilage: (0) short and stout, (1) long and narrow.
u.	infra-rostral cartilages: (0) large and notched anteriorly, (1) small and notched anteriorly, (2) small, thick, and rounded anteriorly, (3) small, slender, and notched anteriorly.
v.	processus anterolateralis hyalis: (0) absent, (1) present.
w.	anterior process of hypobranchial plate: (0) absent, (1) present.
x.	processus branchialis: (0) open, (1) closed.
y.	dorsal curving of the posterior margin of the palatoquadrate: (0) present, (1) absent.
z.	hyoquadrate process: (0) small and triangular, (1) large and rounded.

the processus ascendens; and the presence or absence of a fused processus branchialis. These characters are discussed below as examples of the extent of variation in chondrocranial morphology in *Leptodactylus*.

TABLE 2. DATA matrix showing character states of 26 variable chondrocranial characters found in *Leptodactylus* and outgroup taxa

Species	Character states																									
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t	u	v	w	x	y	z
<i>H. nasus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>C. gaudichaudii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. pustulosus</i>	1	1	0	2	1	1	0	1	1	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1
<i>L. melanonotus</i> CR	1	1	0	2	1	1	0	1	1	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1
<i>L. chaquensis</i>	1	1	0	2	1	1	0	1	1	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1
<i>L. insularum</i>	1	1	0	2	2	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>L. ocellatus</i>	1	1	0	2	1	1	0	1	1	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1
<i>L. melanonotus</i> B	1	1	0	2	1	1	0	1	1	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1
<i>L. petersii</i>	1	1	0	2	1	1	0	1	1	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1
<i>L. podicipinus</i>	1	1	0	2	1	1	0	1	1	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1
<i>L. validus</i>	1	1	0	2	2	1	1	0	1	1	0	2	0	0	1	1	1	0	0	1	0	0	1	0	0	1
<i>L. knudseni</i>	1	1	2	2	0	0	1	1	0	0	2	1	1	0	0	0	1	1	2	1	0	0	0	0	0	0
<i>L. labyrinthicus</i>	1	1	2	2	0	0	1	1	0	0	2	1	1	0	0	0	1	1	2	1	0	0	0	0	0	0
<i>L. pentadactylus</i>	1	1	2	2	0	0	1	1	0	0	2	1	1	0	0	0	1	1	2	1	0	0	0	0	0	0
<i>L. rhodomystax</i>	1	1	1	1	1	0	0	1	1	0	0	2	1	1	0	0	0	1	1	1	1	0	0	0	0	0
<i>L. albilabris</i>	1	1	2	1	1	0	0	1	1	0	2	1	2	0	0	0	1	1	1	1	0	0	0	0	0	0
<i>L. bufonius</i>	1	1	2	1	0	1	0	0	1	2	0	0	1	2	0	0	0	1	1	1	0	0	1	0	0	0
<i>L. fuscus</i>	1	1	0	1	1	0	0	1	2	0	0	1	1	2	1	0	0	1	1	1	0	0	0	0	0	0
<i>L. gracilis</i>	1	1	0	1	1	0	0	1	2	0	0	1	1	2	0	0	0	1	1	1	0	0	0	0	0	0
<i>L. labialis</i>	1	1	0	1	1	0	0	1	2	0	0	1	1	2	0	0	0	1	1	1	0	0	0	0	0	0
<i>L. labrosus</i>	1	1	0	1	1	0	0	1	2	0	0	1	1	2	0	0	0	1	1	1	0	0	0	0	0	0
<i>L. latinasus</i>	1	1	0	1	1	0	0	1	2	0	0	1	1	2	0	0	0	1	1	1	0	0	0	0	0	0
<i>L. longirostris</i>	1	1	2	1	1	0	0	1	2	0	0	1	2	0	0	0	1	1	3	1	0	0	0	0	0	0
<i>L. mystacinus</i>	1	1	1	1	0	1	2	0	0	1	2	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0
<i>L. riveroi</i>	1	1	0	2	1	1	0	1	1	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0
<i>L. silvanimbus</i>	1	1	0	2	1	1	0	1	1	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0

Specimens of *Leptodactylus melanonotus* from Belize (B) and Costa Rica (CR) show clear differences in chondrocranial structures. These include the processes of the crista parotica of the otic capsule, the posterior curvature of the palatoquadrate, and the dorsolateral margin of the palatoquadrate. These differences could represent intra-specific variation or could suggest that one of these samples represents an undescribed taxon. No information has been reported on the amount of geographic variation in chondrocranial characteristics. However, samples of *L. validus* and *L. mystacinus* used herein are also from two disjunct localities each and show no significant variation.

Species of *Leptodactylus* possess a quadripartite cartilago suprarostralis with a processus posterior dorsalis extending from the posterior margin of the alae (Fig. 2a–d). However, the characteristics of the central corpus and its attachment to the alae are variable among *Leptodactylus*. Haas (95) discussed different states of distal connection between the pars corporis and pars alaris in dendrobatid larvae. Among species examined, *L. knudseni*, *L. labyrinthicus*, and *L. pentadactylus* are unique in having an extensive distal connection between these

components of the suprarostrals (Fig. 2b). As a result, these species have a small, overall circular hole perforating their suprarostrals.

The overall shape of the infrarostrals is less variable than that of the suprarostrals. Overall, the infrarostrals are wide and rectangular in *Leptodactylus*. However, the infrarostrals of *L. longirostris* (Fig. 5f) are slightly more slender and in *L. validus* (Fig. 5m) their posterior indentation is more pronounced than in most *Leptodactylus* species. Furthermore, in *L. knudseni*, *L. labyrinthicus*, and *L. pentadactylus* the infrarostrals differ in being very stout, wide, and outwardly rounded on their anterior margin (Figs. 3c, 5h,i). The more robust infrarostrals, along with the extensive distal fusion of the suprarostrial elements, may relate to the carnivorous diet previously reported for these tadpoles (Heyer, '79).

Another character that has also been previously considered a modification correlated with a carnivorous diet is the presence of short cornua trabeculae (de Sá, '94). *Leptodactylus knudseni*, *L. labyrinthicus*, and *L. pentadactylus* have cornua trabeculae that are uniquely short and uniformly wide throughout their length (Figs. 3c, 4h,i). The cornua trabeculae are narrow in the *melanonotus* and *ocellatus* Groups, as well as in *L. silvanimbus* and *L. riveroi* (Figs. 1A, 3b, 4k–r). Additionally, the divergence between the cornua trabeculae is wider and more triangular in shape in members of the *ocellatus* Group, *L. melanonotus* CR, and *L. silvanimbus*. In *L. rhodomystax* (Fig. 4j) and species in the *fuscus* Group (Figs. 3a, 4a–g) the cornua trabeculae are wider and their divergence is less marked.

The palatoquadrate of *Leptodactylus* possesses a wide and rounded posterior curvature; however, the posterior extent of this curvature varies within the genus. Furthermore, this character is highly variable among species within the traditionally recognized "species groups."

Sokol ('81) defined three possible conditions of attachment: low, intermediate, and high—between the processus ascendens and the braincase, although Haas (95) indicated that varying degrees of these conditions are likely to be found. Overall, two conditions were present in *Leptodactylus*. In the *pentadactylus* and *fuscus* Groups, *L. chaquensis*, and *L. ocellatus* the processus ascendens attaches behind and at the same level as the

foramen oculomotorium, corresponding to Sokol's (81) "intermediate" condition (e.g., Fig. 3a,c). In the *melanonotus* Group, *L. insularum*, *L. silvanimbus*, and *L. riveroi*, the processus ascendens attaches below (e.g., Fig. 1C) the posteroventral margin of the foramen oculomotorium (Sokol's "low" condition). The angle between the posterior margin of the processus ascendens and the main axis of the body is also variable. The most acute angles are present in the *melanonotus* Group, *L. insularum*, *L. silvanimbus*, and *L. riveroi* (Figs. 1B, 5k-m,p-r).

The processus branchialis of the visceral skeleton possess two distinct states: closed (a distinct cartilaginous bridge between ceratobranchials II and III) or open (no cartilaginous bridge between ceratobranchials II and III). Among the species examined, this character points to a major evolutionary dichotomy within *Leptodactylus*. Species traditionally placed in the *pentadactylus* and *fuscus* Groups have an open processus branchialis (see Fig. 3a,c), whereas all other species of *Leptodactylus* possess a closed processus branchialis (e.g., Fig. 1D).

Phylogenetic analysis

The 26 chondrocranial characters identified here (Table 1) were used in phylogenetic analyses enforcing and not enforcing a monophyletic *Leptodactylus*, with *Physalaemus pustulosus* (Leptodactylidae: Leptodactylinae), *Hylodes nasus*, and *Crossodactylus gaudichaudii* (Leptodactylidae: Hylodinae) as outgroups.

The analysis that did not enforce a monophyletic *Leptodactylus* resulted in 17 equally parsimonious trees, (51 steps long, C.I. 0.69) with *Leptodactylus* being paraphyletic relative to *Physalaemus*. The consensus tree (50% majority-rule) for these trees is given in Figure 9a. A second analysis, with a monophyletic constrained *Leptodactylus*, resulted in 66 equally parsimonious trees, (52 steps long, C.I. 0.67); the consensus tree (50% majority-rule) for these trees is given in Figure 9b.

The present analyses identify two major clades within *Leptodactylus*, the *melanonotus-ocellatus* clade and the *pentadactylus-fuscus* clade. The *ocellatus-melanonotus* clade is supported by the following synapomorphies: presence of a closed processus branchialis, narrow suprarostrals, narrow supraorbital corpora that are widely separated and not attached distally to the alae, narrow and widely divergent cornua trabeculae, narrow planum tra-

beculare anticum posterior to the confluence of the cornua trabeculae, and a pars articularis quadrati that is indistinct from the processus muscularis in lateral view. The *fuscus-pentadactylus* clade is supported by having an open processus branchialis, pars articularis quadrati distinct from the processus muscularis in lateral view, wide and narrowly separated suprarostrals, intermediate attachment of the processus ascendens to the braincase, and a wide planum trabeculare anticum posterior to the confluence of the cornua trabeculae.

In these trees (Fig. 9a,b), *Leptodactylus melanonotus* CR, *L. chaquensis*, and *L. ocellatus* grouped together. However, *L. insularum* clustered with most species examined of the *melanonotus* Group plus *L. riveroi*. *Leptodactylus riveroi* has not been previously associated with any of the species groups. The present analyses suggest a closer relationship of this taxon to the *melanonotus-ocellatus* clade, particularly to *L. petersii* and *L. validus* (Fig. 9a). *Leptodactylus insularum* (traditionally placed in the *ocellatus* Group) and *L. riveroi* share the following characteristics with the *melanonotus* Group: posterior curvature of the palatoquadrate reaching well beyond the anterior margin of the otic capsule, an acute angle between the posterior margin of the processus ascendens and the braincase, and a "low" attachment of the processus ascendens to the braincase.

Based on external larval morphology (McCranie et al., '86) and call characteristics (Heyer et al., '96), *Leptodactylus silvanimbus* has been associated with the *melanonotus* Group. In the present analyses, *L. silvanimbus* always clustered with the *ocellatus-melanonotus* clade. Surprisingly, the two samples of *L. melanonotus* did not group together. In the analyses, *L. melanonotus* B grouped with other species of the traditional *melanonotus* Group, whereas *L. melanonotus* CR represents the sister group to the *ocellatus-chaquensis* clade.

The four species of the traditional *pentadactylus* Group, *Leptodactylus knudseni*, *L. labyrinthicus*, *L. pentadactylus*, and *L. rhodomystax*, clustered together, with a closer relationship among the former three taxa. The strong relationship among these three taxa is supported by the unique characteristics of their suprarostrals, infrarostrals, and cornua trabeculae. Their association with *L. rhodomystax* is based on characteristics of the palatoquadrate and crista parotica.

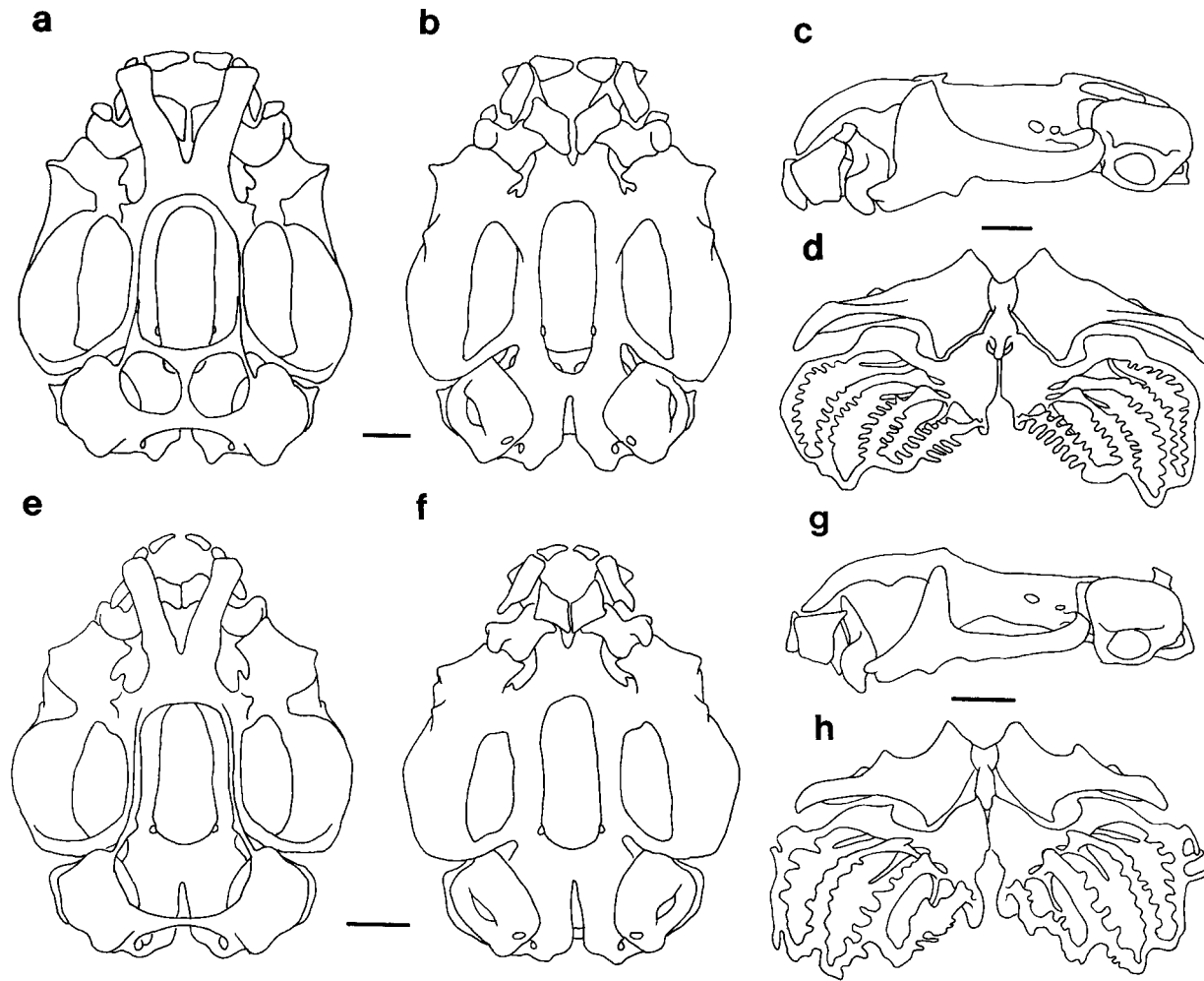


Fig. 8. Dorsal (a) and (e), ventral (b) and (f) and lateral (c) and (g) views of chondrocrania, and ventral (d) and (h) view of hyobranchial apparatus of a-d, *Hylodes nasus*, stage 25 and e-h, *Crossodactylus gaudichaudii*, stage 31. Bar = 1.0 mm.

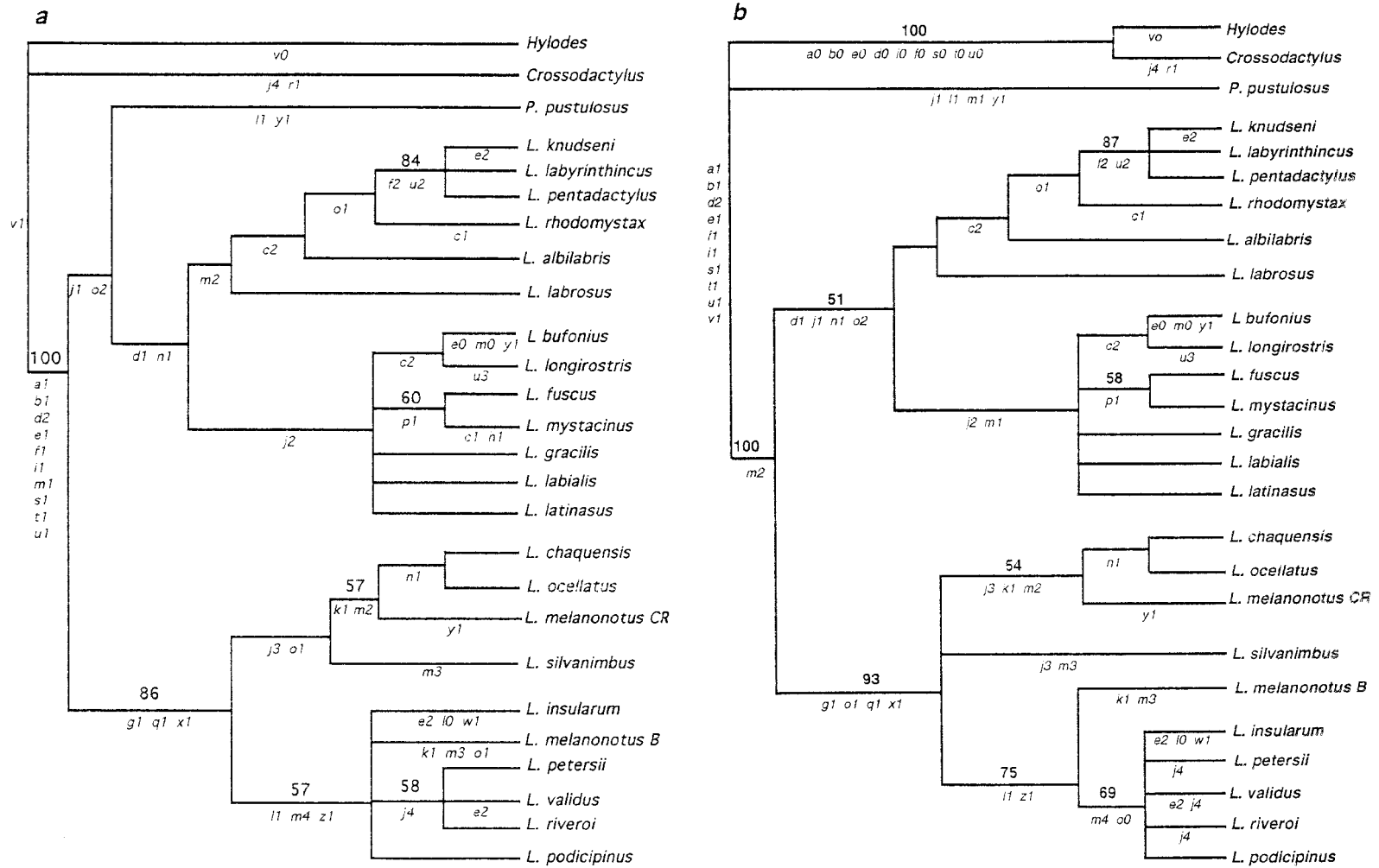


Fig. 9. 50% majority-rule consensus trees. **a**: Analysis of data without topological constraints. **b**: Analysis with a monophyletic constrained *Leptodactylus*. Both analyses used *Physalaemus pustulosus*, *Hylodes nasus*, and *Crossodactylus gaudi-*

chaudii as outgroups. Numbers above branches correspond to bootstrap values (values below 50% are not shown), letters and numbers below branches correspond to character states.

Among the traditionally recognized species groups, the *pentadactylus* Group would represent a paraphyletic assemblage because *L. albilabris* and *L. labrosus* (Fig. 9a,b) appear more closely related to species in the *pentadactylus* Group than to any other *Leptodactylus* examined.

All members of the traditional *fuscus* Group clustered together in the present analysis, except for *Leptodactylus albilabris* and *L. labrosus*. Within this strict *fuscus* clade, *L. mystacinus*-*L. fuscus* and *L. bufonius*-*L. longirostris* appear as sister taxa, whereas other relationships are unresolved.

Overall, relationships among species of *Leptodactylus* are strikingly similar (Fig. 9a,b) in both analyses (i.e., when *Leptodactylus* is constrained or not constrained to be monophyletic). However, the analysis that does not constrain a monophyletic ingroup results in a paraphyletic *Leptodactylus* by placing *Physalaemus* as the sister group to the *fuscus*-*pentadactylus* clade (Fig. 9a). Despite the present results, *Physalaemus* and *Leptodactylus* are supported as distinct genera by characteristics derived from the external morphology of adults and larvae (Lynch, '71). Consequently, herein we do not favor a systematic re-arrangement until chondrocranial data for more species of both genera become available and these data are analyzed together with data from adult and larval external morphology.

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APPENDIX A. Specimens examined and collection data.¹

Species	Number of specimens	Gosner stages	Locality	USNM number
<i>L. albilabris</i>	3	32, 34, 37	Tortola, Virgin Islands	520280-282
<i>L. bufonius</i>	3	33, 35, 37	Salta, Argentina	520285-287
<i>L. chaquensis</i>	3	37, 38, 40	Salta, Argentina	519879-881
<i>L. fuscus</i>	3	28, 34, 36	Roraima, Brazil	520288-290
<i>L. gracilis</i>	39	29-42	Dept. Canelones, Uruguay	519881-920
<i>L. insularum</i>	1	36	Isla San Andres	520291
<i>L. knudseni</i>	2	34, 36	Manaus, Amazonas, Brazil	529292-293
<i>L. labialis</i>	10	37-44	Cayo District, Belize	519928-937
<i>L. labrosus</i>	2	31, 36	Pichincha, Ecuador	520294-295
<i>L. labyrinthicus</i>	1	36	Amambay, Paraguay	520296
<i>L. latinasus</i>	2	35, 37	Salta, Argentina	520297-298
<i>L. longirostris</i>	2	33, 34	Para, Brazil	520299-300
<i>L. melanonotus B</i>	4	31-34	Cayo District, Belize	519938-941
<i>L. melanonotus CR</i>	2	35, 38	Guanacaste, Costa Rica	520283-284
<i>L. mystacinus</i>	4	31, 33, 35, 40	Montevideo, Uruguay	519942-945
<i>L. mystacinus</i>	9	35-38, 45	Misiones, Argentina	519946-954
<i>L. ocellatus</i>	18	40-46, 7 juv.	Dept. Canelones, Uruguay	519882-920
<i>L. ocellatus</i>	16	31, 34-39	San Jose, Uruguay	519955-970
<i>L. pentadactylus</i>	11	27-31, 33, 35-36, 39	Puntarenas, Costa Rica	519989-999
<i>L. petersii</i>	1	36	Madre de Dios, Peru	520301-302
<i>L. podicipinus</i>	2	33, 38	Alto Parana, Paraguay	520303-304
<i>L. rhodomystax</i>	2	27, 31	Manaus, Amazonas, Brazil	520305-306
<i>L. riveroi</i>	2	27, 37	Manaus, Amazonas, Brazil	520307-308
<i>L. silvanimbus</i>	3	27, 31, 35	Ocotepeque, Honduras	520309-312
<i>L. validus</i>	1	37	St. Paul, Tobago	520313
<i>L. validus</i>	2	31, 35	St. George, St. Vincent	520314-315

¹USNM United States National Museum of Natural History, Smithsonian Institution.