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The Chondrocranium of the Mexican Burrowing Toad, *Rhinophrynus dorsalis*

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ABSTRACT.—The chondrocranium of *Rhinophrynus dorsalis* is described and illustrated. Autapomorphies of *R. dorsalis* are the presence of the symplectic cartilage and a cartilaginous process on the ascending process of the palatoquadrate. Synapomorphies of *Rhinophrynus* shared with the Pipidae are: (1) early formation of the lower jaw and (2) presence of a suprarostral plate. Alternative developmental pathways for the formation of the suprarostral plate are considered. Histological data indicates that the suprarostral plate forms from: (1) the early fusion of the cornua trabeculae with the suprarostral cartilages, (2) an anterior growth of the ethmoid plate, and (3) subsequent fusion of the cornua trabeculae and the anterior process of the ethmoid plate. The larval crista parotica of *R. dorsalis* resembles the one described for microhylid taxa.

Taylor (1942) described pipid-like anuran larvae from a sample of tadpoles collected in Guerrero, Mexico. However, these larvae remained unidentified until the tadpole of *Rhinophrynus dorsalis* was described by Orton (1943). Orton's description included a few chondrocranial characteristics, particularly focusing on the jaw apparatus. She noted the early formation of the lower jaw and suggested that this early development may be correlated with a macrophagous diet.

Subsequently, Sokol (1977, 1981) made references to the chondrocranial anatomy for *Rhinophrynus dorsalis* larvae while evaluating the use of larval characteristics in systematics. The sequence of cranial ossification for *Rhinophrynus* larvae was described by Trueb, 1985. Description of adult osteology has been previously described (Trueb, 1973; Trueb and Cannatella, 1982).

Hay et al. (1995) placed *Rhinophrynus* as the sister group to Pipidae based on 12S and 16S rRNA sequence data. Previous morphological studies suggested the following synapomorphies for the Pipoidea: absence of mentomeckelian bones, lack of parasphenoid alae, presence of a single frontoparietal, greatly enlarged otic capsules, and larvae with paired spiracles and lacking cornified beaks and denticles (Ford and Cannatella, 1993). Of the approximately 28 species of the Pipoidea, the chondrocranium has been described thoroughly for *Xenopus laevis* (Trueb and Hanken, 1992) and partially for *Rhinophrynus dorsalis*, *Pipa carvalhoi*, and *Xenopus tropicalis* (Sokol, 1975). Herein we provide a complete description and illustration of the chondrocranium of *Rhinophrynus dorsalis*.

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MATERIALS AND METHODS

Thirty tadpoles of the Mexican Burrowing Toad, *Rhinophrynus dorsalis*, representing Neiuwkoop and Faber (1956) stages 48–62 were cleared and double-stained for bone and cartilage using standard procedures. Drawings were obtained with the help of a Wild M3C stereomicroscope with camera lucida attachment. Collection localities of specimens used in this study are: Guanacaste, Costa Rica (USNM 515945–515958); and Aguacate Lagoon, Cayo District, Belize (USNM 515959–515974). Collection numbers, measurements, and stages of material examined are given in Table 1.

Nieuwkoop and Faber's (1956) staging table for *Xenopus* was used to stage *Rhinophrynus* tadpoles. The similarity of external morphology of *Xenopus* and *Rhinophrynus* during development makes this table preferable to the Gosner's (1960) staging table. Chondrocranial terminology follows De Jongh (1968), Haas (1995), and Trueb and Hanken (1992).

RESULTS

To facilitate comparisons with the available data for *Xenopus laevis*, the chondrocranium of *Rhinophrynus dorsalis* is illustrated at developmental stage 53. The parasphenoid and frontoparietals have begun ossification and are clearly visible at stage 53.

The most anterior region of the chondrocranium, the area roofing the buccal cavity, is highly modified when compared to other free swimming anuran larvae. The cornua trabeculae, suprarostral, and ethmoid plate are fused into a single, broad, and flat element of approximately the same width as the braincase (Fig. 1). On the lateral margin of the suprarostral plate, a short and blunt lateral trabecular process occurs. This is the anterior point of attachment for the liga-

TABLE 1. Specimens of *Rhinophrynus dorsalis*. Measurements are in mm.

Specimen	Stage	Body length	Total length
USNM 515961	45	5.58	13.67
USNM 515972	45	5.23	11.04
USNM 515974	45	4.95	10.02
USNM 515968	48	6.47	14.5
USNM 515973	49	6.40	14.15
USNM 515966	50	10.14	21.21
USNM 515967	50	10.21	18.19
USNM 515960	51	12.37	26.17
USNM 515962	51	9.46	20.07
USNM 515963	51	10.17	17.98
USNM 515964	51	11.36	19.74
USNM 515969	51	10.42	19.07
USNM 515970	51	10.13	21.43
USNM 515971	51	10.05	20.21
USNM 515952	52	14.79	34.60
USNM 515953	52	13.58	33.64
USNM 515965	52	11.09	20.33
USNM 515954	53	14.73	36.54
USNM 515955	53	14.28	36.03
USNM 515956	53	15.05	35.40
USNM 515958	53	15.16	36.54
USNM 515957	Late 53	15.35	37.72
USNM 515946	54	22.20	49.54
USNM 515947	54	18.57	44.43
USNM 515959	54	16.55	36.39
USNM 515945	Late 54	19.63	37.04
USNM 515948	Late 54	19.44	46.30
USNM 515949	Late 54	19.61	48.53
USNM 515951	Late 54	19.05	46.14
USNM 515950	55	19.43	49.20

mentum quadratoethmoidale, which runs posteriorly to the processus quadratoethmoidale on the commissura quadratocranialis anterior. A processus antorbitalis is present as a prominent ridge in the area of attachment of the commissura quadratocranialis anterior to the braincase. The lateral tips of the suprarostrals are attached to the most antero-lateral edge of the pars articularis quadrati and to the commissura quadratocranialis anterior via a membranous sheet of connective tissue. This sheet of connective tissue covers the anterior area of attachment of the levator mandibulae muscle to Meckel's cartilage.

A functional lower jaw is already formed at this stage. It is composed of the fused Meckel's and infrarostral cartilages. The three points of fusion among these elements is clearly visible. The Meckel's cartilages have their greatest diameter midway between the fusion with the infrarostrals and their articulation with the processus articularis. The mid-point of the fused infrarostrals forms a triangular ventral projection.

The palatoquadrate is firmly attached to the braincase anteriorly by a broad and sturdy commissura quadratocranialis anterior and, posteriorly, by an equally sturdy processus ascendens and by a well developed otic process. A fourth attachment of the palatoquadrate is accomplished via a thin, extensive, and convoluted larval crista parotica which fuses to the lateral process of the palatoquadrate. The ascending process is wide and from its anterior margin a rounded and cylindrical process projects into the sub-ocular space. On either side and below the ascending process, the optic and oculomotor foramina are found in the lateral wall of the braincase. The prootic foramen is large and anterior to the otic capsules. The ascending process has a high attachment to the braincase. The muscular process is small and placed at a 45° angle with the sagittal plane of the body. Ventral and posterior to the muscular process, a rounded hyoquadrate process serves as the point of articulation between the palatoquadrate and the ceratohyal via the symplectic cartilage. The sympletic cartilage is small and biconcave. It remained unmodified in the more advanced stages available for this study (stage 62); consequently we could not determine its developmental outcome after metamorphosis. At the level of the ascending process, the processus ventrolateralis is present and fused with the larval crista parotica.

The larval crista parotica is well developed, thin, convoluted, and variable in size. It attaches to the otic capsule above and anterior to the fenestra ovalis. It curves forward, slightly upward and attaches anteriorly to the ventrolateral process of the palatoquadrate.

The otic capsules are large, representing one fourth the chondrocranial length. The muscular process of the otic capsule forms a sharp posterolateral corner on the otic capsule. Posteriorly, the otic capsules have two foramina, the foramen jugulare and the foramen perilymphaticum inferior. The otic capsules have a large fenestra ovalis. The operculum is not yet formed (Fig. 2).

The hyobranchial apparatus consists of a copula I, copula II, ceratohyalia, a chondrified pars reuniens, a long thin urobranchial process, hypobranchial plates, and paired ceratobranchials I–IV. The ceratobranchials and the copula II are continuous with the hypobranchial plate (Fig. 2). Ceratobranchial II has a small process close to its anterior end that projects toward ceratobranchial III, but does not contact ceratobranchial III. No spicules are present.

DISCUSSION

Chondrocranial data are scarce for anurans (de Sá, 1988). Among pipoids, chondrocranial data are represented by incomplete descriptions of *Rhinophrynus* (Sokol, 1975), *Pipa carvalhoi, Xenopus tropicalis* (Sokol, 1977), and a detailed description of *Xenopus laevis* (Trueb and
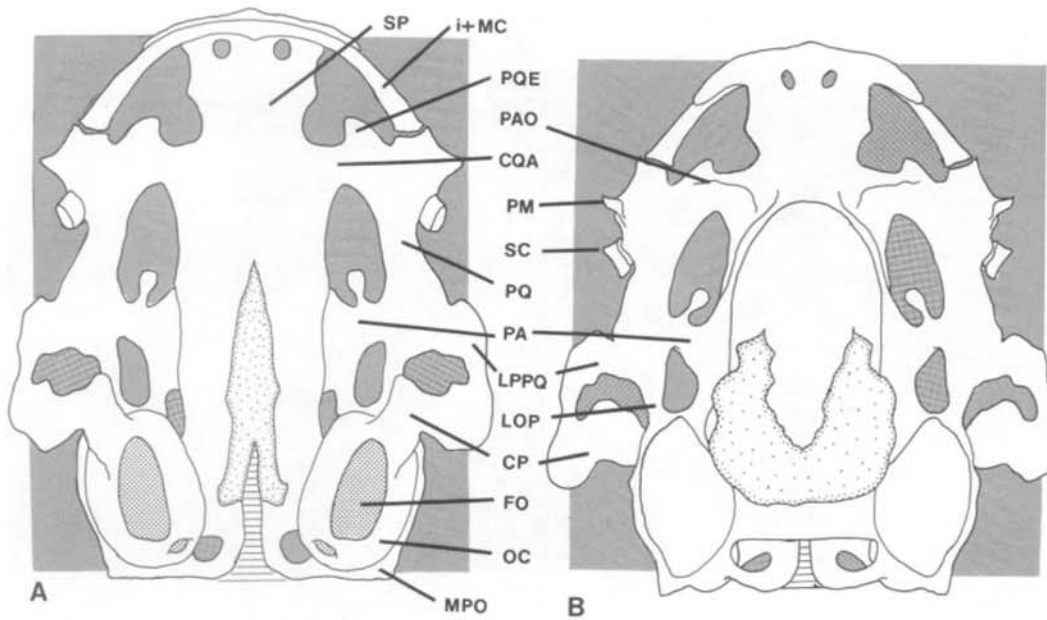
FIG. 1. Chondrocranium of *Rhinophrynus dorsalis* (USNM 515957, stage 53). A. Ventral view. B. Dorsal view. Stippling indicates bone and horizontal lines indicates notochord. CQA = commisura quadrato-cranialis anterior, i + MC = fused infrarostrals and Meckels' cartilages, FO = fenestra ovalis, LPPQ = ventrolateral process of the palatoquadrate, LOP = larval otic process, CP = larval crista parotica, OC = otic capsule, MPOC = muscular process of the otic capsule, PQE = processus quadratoethmoidale, PAO = processus antorbitalis, PM = processus muscularis, PQ = palatoquadrate, PA = processus ascendens, SC = symplectic cartilage, SP = suprarostral plate.

Hanken, 1992). The present study provides additional data on the chondrocranial anatomy of *Rhinophrynus dorsalis* and allows us to make some comparisons among pipoid chondrocrania.

The lower jaw, composed of Meckel's and angulosplenial cartilages, has been previously described from cross-sections (Orton, 1943). It is very similar to the lower jaw of *Xenopus laevis* except that the angulosplenial ossifies from a single center of ossification in *Rhinophrynus* as seen in a stage 62 specimen used in this study, unlike the dual centers reported for *Xenopus* (Trueb and Hanken, 1992).

The unique condition in which the cornua trabeculae, suprarostrals, and ethmoid plate are fused into a single unit is shared with *Xenopus laevis* (Trueb and Hanken, 1992), *X. tropicalis*, and *Pipa carvalhoi* (Sokol, 1977); however no data are available for other pipoids. The element resulting from this fusion has been named the suprarostral plate and has been considered to be homologous to the suprarostral cartilage of other anurans (Trueb and Hanken, 1992).

We agree with these authors that part of the suprarostral plate in pipoids is homologous to the suprarostral cartilage of other anurans; however, the homology of other components of the suprarostral plate is more difficult to determine. Four possibilities can be considered: (1) fusion of the cornua trabeculae along their midline, (2) posterior expansion of the suprarostrals with fusion to the ethmoid plate, (3) anterior expansion of the ethmoid plate with fusion to the suprarostrals, or (4) posterior expansion of the suprarostrals and anterior expansion of the ethmoid plate.

We examined *Rhinophrynus* tadpoles in early stages (stages 45–51) to determine the development of the suprarostral plate. Whole-mounted cleared and stained early tadpoles, stages 45–50, showed two separate cornua trabeculae that are anteriorly fused to the suprarostral cartilages. Between these stages, an anterior process of the ethmoid plate, dorsally triangular and subcylindrical in cross section (Fig. 3), extends anteriorly from the ethmoid plate between the cornua trabeculae. This process is clearly visible in some whole-mount stage 51 tadpoles and grows anteriorly to fuse with the suprarostral cartilag-
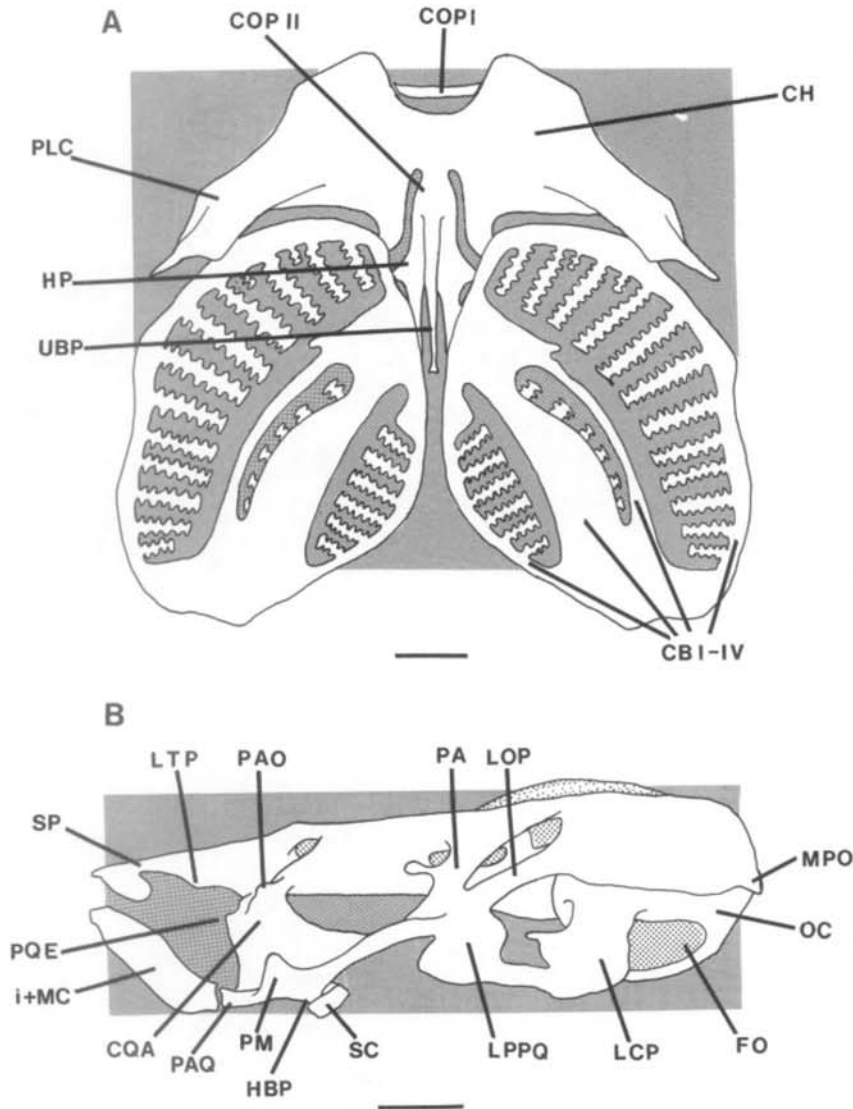
FIG. 2. Chondrocranium of *Rhinophrynus dorsalis*. A. Hyobranchial apparatus (USNM 515958, stage 53). B. Lateral view (USNM 515957, stage 53). Stippling indicates bone. COP I = copula one, COP II = copula two, CH = ceratohyale, CBI–IV = ceratobranchial one–four, HP = hyobranchial plate, PLC = processus lateralis of the ceratohyal, UBP = urobranchial process. Other labels as in Fig. 1.

es. During development the space left between the anterior process of the ethmoid plate and the cornua trabeculae "fills in" with cartilage, leaving two small anterior holes (behind what would correspond to the posterior edge of the suprarostrals). The cartilaginous occlusion of the intertrabecular space forms a continuous plate with the anterior process of the ethmoid plate, the cornua trabeculae, and the suprarostrals. In cross sections, the suprarostral plate is thicker medially and laterally in the areas cor-responding to the anterior process of the eth-moid plate and the cornua trabeculae. Between these three thick areas, the suprarostral plate is seen as a thin sheet of cartilage (Fig. 3b).

The taeniae tectorum marginali are not yet fused to the otic capsule early in stage 51 (six of nine specimens examined) leaving the foramen prooticum open dorsally. Three of the nine spec-imens have the lateral trabecular processes form-ing at this stage. The processus antorbitalis is present in two of the nine specimens at this stage.
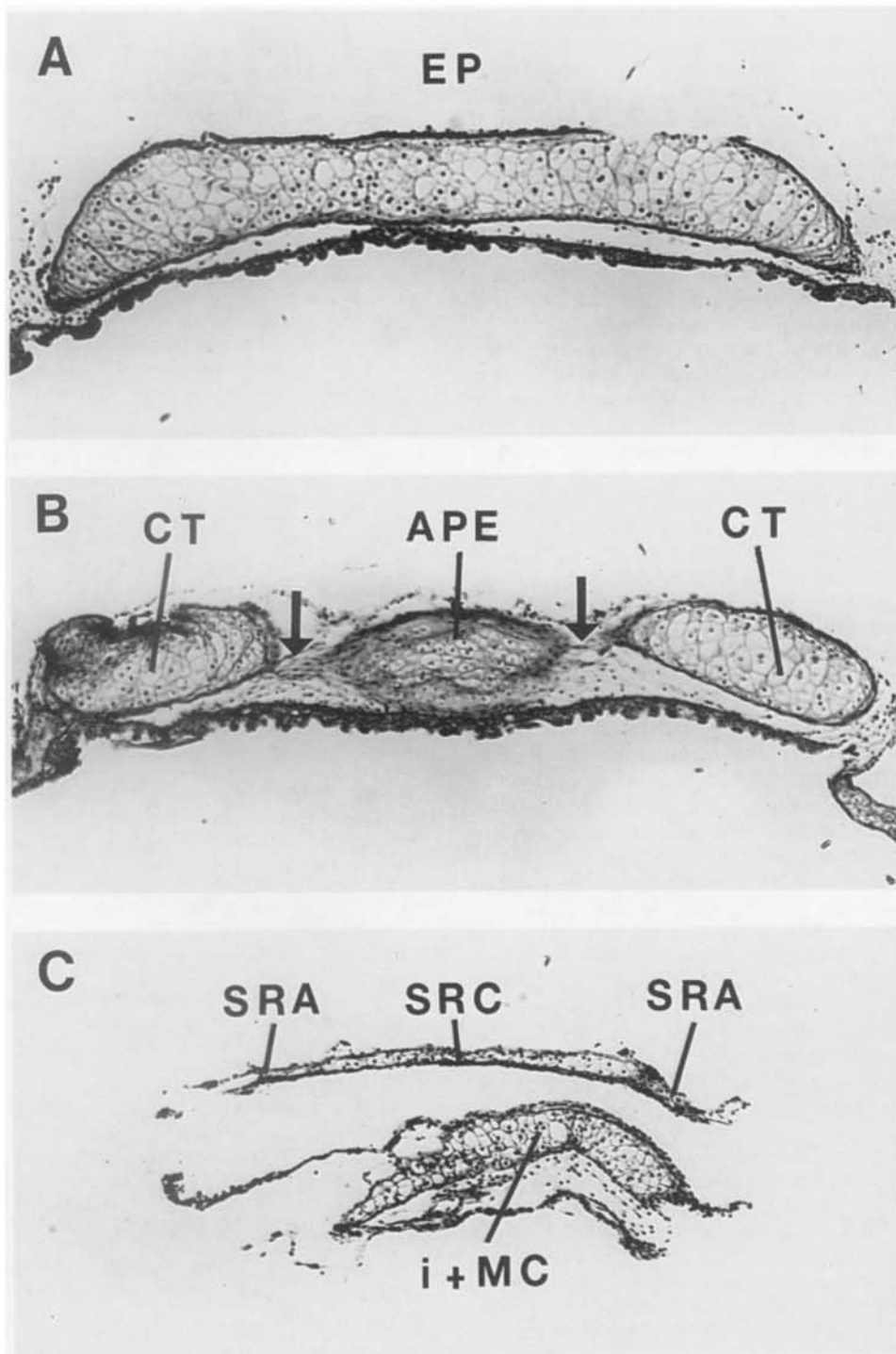
FIG. 3. Cross-sections through the suprarostral plate of *Rhinophrynus dorsalis*, stage 51. A. Posterior section through the ethmoid plate region. B. Medial section of the suprarostral plate. C. Anterior section through the suprarostral area. EP = ethmoid plate, CT = cornua trabeculae, APE = anterior process of the ethmoid plate, SRA = suprarostral alae, SRC = suprarostral corpus, i + MC = fused infrarostral and Meckel's cartilages, arrows indicate thin cartilage connecting cornua trabeculae and the anterior process of the ethmoid plate.

Chondrocranial autapomorphies for *Rhino-phrynus* are: (1) presence of a symplectic carti-lage and (2) cartilaginous extension of the pro-cessus ascendens into the sub-ocular space. Syn-apomorphies for pipoids based on larval chon-drocrania are: (1) presence of a suprarostral plate, (2) early formation of a functional lower jaw, and (3) presence of the muscular process of the otic capsule.

One characteristic that was difficult to inter-pret was the thin and convoluted larval crista parotica. In living larvae it overlays the bran-chial basket intimately and serves as the origin for the branchial pouch musculature. Staining of the larval crista parotica was irregular which may have been caused by the attachment of this musculature. The shape and attachment of the larval crista parotica to the palatoquadrate re-sembles that of some microhylids (*Hamptophryne boliviana*, de Sá and Trueb, 1991; *Dermatonotus muelleri*, Lavilla, 1992).

Although the type I larvae of the pipoids is specialized for filter feeding, early formation of the lower jaw allows for a macrophagous feed-ing style. Several wild-caught specimens exam-ined for this study had conspecific larvae in their intestines. These specimens were pre-served as they were collected; consequently this carnivory is not an artifact of collection. How-ever, it could be an effect of density since tad-poles were present at high density in a pond about 10 m × 20 m wide and 0.5 m deep.

Stage 53 was the first stage available for study with ossification of the cranium occurring. Of four specimens examined at this stage three had ossification of parasphenoid and frontoparietal present while the fourth had only ossification of the parasphenoid. Further description of ossifi-cation in *Rhinophrynus* is available in Trueb (1985) and Trueb and Cannatella (1982).

The unique chondrocranial characters de-scribed here for *Rhinophrynus* support its rela-tionship with the Pipidae. The overall shape of the larval crista parotica is convergent with that of some microhylid taxa (de Sá and Trueb, 1991).

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