MORPHOLOGY AND POSTNATAL DEVELOPMENT OF THE SKULL OF *BOLITOGLOSSA NICEFORI* (CAUDATA: PLETHODONTIDAE)

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RESUMEN

TITULO: MORFOLOGÍA Y DESARROLLO POSTNATAL DEL CRÁNEO DE *Bolitoglossa nicefori* (CAUDATA: PLETHODONTIDAE).[1]

AUTOR: Claudia Juliana Dulcey Cala[2]

PALABRAS CLAVES: desarrollo craneal; desarrollo directo; heterocronía; Plethodontidae.

DESCRIPCIÓN: La morfología craneal de la salamandra con desarrollo directo *B. nicefori* y su desarrollo postnatal son descritos y comparados con otros urodelos. Las descripciones son basadas en una serie de tamaño utilizando preparaciones esqueléticas secas y especimenes clareados y doblemente coloreados. Cuatro estados de desarrollo craneal son definidos sobre la base de eventos conspicuos que ocurrieron durante la ontogenia postnatal craneal. La morfología del cráneo adulto de *B. nicefori* es similar a aquella de otros pletodóntidos, sin embargo, algunas regiones muestran variación interespecífica. La ontogenia postnatal del cráneo y el estado de osificación observado en los neonatos de *B. nicefori* muestran dos importantes rasgos ontogenéticos: 1) un mosaico de rasgos craneales larvales, metamórficos y postmetamórficos en los neonatos, y 2) ausencia de elementos larvales en el cráneo y el aparato hiodeo. El particular estado de osificación en los neonatos de *B. nicefori* puede ser causado por cambios heterocrónicos en la secuencia de osificación comparado con la ontogenia de salamandras metamórficas. Los cambios heterocrónicos y la ausencia de rasgos larvales en la ontogenia postnatal craneal de *B. nicefori* son quizás debido a la presencia de un patrón ontogenético no recapitulatorio. Sin embargo, este patrón de desarrollo no tuvo un impacto sobre la morfología craneal adulta (ausencia de novedades morfológicas), las cuales están relacionadas a la existencia de un desarrollo compartimentalizado. Sin embargo, estudios futuros deben ser realizados con el fin de establecer la posible presencia de un patrón ontogenético no recapitulatorio o por el contrario una ontogenia recapitulatoria en la morfogénesis craneal de *B. nicefori* durante el desarrollo embrionario.

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ABSTRACT

TITLE: MORPHOLOGY AND POSTNATAL DEVELOPMENT OF THE SKULL OF *BOLITOGLOSSA NICEFORI* (CAUDATA: PLETHODONTIDAE).[*]

AUTHOR: Claudia Juliana Dulcey Cala[**]

KEY WORDS: cranial development; direct development; heterochrony; Plethodontidae; repatterning.

DESCRIPTION: The cranial morphology of the direct-developing salamander *B. nicefori* and its postnatal development are described and compared with that of other urodeles. The descriptions are based on a size series of dry skeletal preparations and cleared and double-stained specimens. Four stages of cranial development are defined on the basis of conspicuous events that occurred during postnatal ontogeny. The adult skull morphology of *B. nicefori* is similar to that of other plethodontids, however, some regions show interspecific variation. The postnatal ontogeny of the skull and the stage of ossification observed in the neonates of *B. nicefori* show two important ontogenetic features: 1) a mosaic of early larval, metamorphic and postmetamorphic skull features in neonates, and 2) absence of characteristic larval elements in skull and hyoid apparatus. The distinctive stage of ossification in the neonates of *B. nicefori* could be caused by heterochronic changes in the ossification sequence, compared to the ontogeny of metamorphic salamanders. The possible heterochronic changes and the absence of larval traits in the skull postnatal ontogeny of *B. nicefori* are perhaps due to the presence of an ontogenetic repatterning. Yet, this ontogenetic repatterning would not have an obvious impact on the adult skull morphology (absence of morphological novelties), which could be related to the existence of a compartmentalized development. However, future studies should be performed in order to establish the possible occurrence of recapitulatory patterns or ontogenetic repatterning in the skull morphogenesis of *B. nicefori* during the embryonic development.

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INTRODUCTION

The genus *Bolitoglossa* comprises nearly 93 species (Frost, 2007), which are distributed from the Atlantic region of south-western North America (San Luis Potosí, México) to the Amazon basin (Brazil) and the mountains of central Bolivia in South America (Parra-Olea, García-París & Wake, 2004). In spite of its great diversity, there are no detailed descriptions on the cranial morphology of *Bolitoglossa*. Morphological studies of the skull have been focused to describe some particular regions of dermatocranium, hyoid apparatus, and chondrocranium. General descriptions of the skull in 24 species of *Bolitoglossa* can be found in the survey of Wake (1966) regarding the comparative osteology of Plethodontidae. Likewise, other accounts about the skull morphology of *Bolitoglossa* either have a broad view or analyze particular regions of the skull (Restrepo, 1995; Bolivar, 1998; Ehmcke & Clemen, 2003; Acosta, 2007).

On the other hand, the cranial ontogeny in *Bolitoglossa* has also been scarcely studied. The embryonic morphogenesis of epibranchial cartilage of the hyoid apparatus (Alberch, 1987, 1989) and some aspects of its cranial postnatal development (Ehmcke & Clemen, 2000c) have been reported in *Bolitoglossa subpalmata*. In other species, have been only analyzed the postnatal development of the dermal bones of the nasal region and their morphological variation, such as: *B. occidentalis, B. rostrata, B. adspersa, B. altamazonica, B. dofleini, B. peruviana* and *B. platydactyla* (Alberch & Alberch, 1981; Alberch, 1983). Despite that the studies performed in *B. subpalmata* were general approximations, their results are noteworthy: 1) most of the cranial structures arise postnatally, 2) the distinctive larval traits of the skull and hyoid apparatus were absent (e.g., absence of coronoid, palatopterygoid and larval epibranchials), 3) some elements presented heterochronic development relative to the biphasic ontogeny in other urodeles (e.g., precocious development of the adult epibranchial cartilages) (Alberch, 1987, 1989; Ehmcke & Clemen, 2000c). In contrast to these ontogenetic modifications in *B. subpalmata*, the skull development in other direct developing salamanders of the family Plethodontidae shows the embryonic recapitulation of larval development in the hyobranchium (e.g., *Plethodon cinereus,* Dent 1942; *Aneides*, Wake, Wake & Wake, 1983; *Desmognathus wrighti,* Alberch 1989; *Desmognathus aeneus,* Marks 2000) and most of the cranial and hyoid elements appears during embryonic development, prior to hatching (see Dent, 1942; Wake, Wake & Wake, 1983; Alberch, 1987, 1989; Marks, 2000).

This study describes in detail the morphology and postnatal development of the dermatocranium, chondrocranium and hyoid apparatus of the Neotropical salamander, *Bolitoglossa (Eladinea) nicefori*. The goals of this study are to provide a complete description of the cranial morphology as a framework for the understanding of the ontogenetic changes during postembryonic development in a direct developing salamander and to determine whether there are morphological differences during the postnatal ontogeny compared to other direct developing and metamorphic salamanders.

MATERIALS AND METHODS

A total of 59 specimens of *Bolitoglossa nicefori* in different developmental stages were examined. These included 37 individuals collected in 2004 in disturbed forests of Vereda Las Amarillas, Microcuenca La Venta, Piedecuesta municipality (Santander, Colombia, N: 06°58’6" and W: 73°1’17.5", 1400 – 2000 m altitude), 19 specimens (2 of them embryos) captured during the years 2005 and 2006 in the Hacienda “El Roble”, Piedecuesta and Mesa de los Santos municipalities (Santander, Colombia N: 06°52´and W: 73°3´, 1500-1700 m altitude), and one embryo and two neonates collected in this last locality during the year 2000 (they were provided by the herpetological collection of the Universidad Javeriana de Bogotá, Colombia, MUJ, Appendix 1). All the individuals used in this study were deposited in the herpetological collection of the Museo de Historia Natural, Universidad Industrial de Santander (UIS-A) (Appendix 1).

The salamanders were fixed in 10% formalin and stored in 70% ethanol. A size series according to the snout-vent length (SVL) or standard length (SL) was established, with four stages ranged from 9.77 to 82.21 mm. Sex and sexual maturity were determined by macroscopic observation of the reproductive structures and presence of mental gland in males (Appendix 1). Three late embryos, two neonates and 49 individuals between juveniles and adults were cleared and double-stained following Wassersug (1976). Also 5 dry skulls were prepared; 4 of them were disarticulated.

The specimens were examined using an Olympus stereo microscope, and the photographs and drawings were made with the assistance of a digital camera. The anatomical terminology used herein follows de Beer (1937), Wake (1963) and Eyal-Giladi &

Zinberg (1964) for chondrocranial structures, Rose (1995) for nasal capsules and Wake (1966) for the osteocranium and hyoid apparatus. The cranial morphology and the postnatal development of the chondrocranium, dermatocranium and hyoid apparatus are described in detail. Some observations of the embryonic chondrocranium are also mentioned. For comparative purposes cleared and double-stained skulls of five salamanders of *B. vallecula* were also examined; they were provided by Museo de Herpetología de la Universidad de Antioquia, Colombia (MHUA).

RESULTS

Cranial morphology and its postnatal development in *B. nicefori* are described and compared with the cranial morphology of *B. vallecula.* Four stages of morphological development (adult, II, I and neonate stages) were established for *B. nicefori* taking into account distinct morphological changes during cranial postnatal ontogeny (Table 1).

In spite of the sexual dimorphism in body size (larger body size in females), the morphology and ontogeny of chondrocranium, dermatocranium and hyoid apparatus of *B. nicefori* are similar between females and males.

ADULT CHONDROCRANIUM

The chondrocranium is constituted by: nasal capsule, orbitosphenoid, pila antotica, trabecula, palatoquadrate, operculum, otic capsule, and Meckel's cartilage. In the adults, the orbitosphenoid, the otic capsule, the quadrate process of the palatoquadrate, and the mentomeckelian are ossified elements, whereas the nasal capsule, the most part of the palatoquadrate and the Meckel's cartilage remain cartilaginous.

NASAL CAPSULES

The **nasal capsules** have large fenestrae and posteriorly they are connected to one another by the tectum internasale dorsally, and the planum internasale ventrally; there is not nasal septum (Figs. 1a and 2a). The roof of the nasal capsule (*tectum nasi*) presents a large dorsal fenestra that is bordered anteriorly by the oblique and *alary* cartilages, laterally by the planum tectale, medially by the dorsal border of the planum verticale, and posteriorly by the sphenoseptal commissure (Fig. 1a). In the dorsal region is also observed the fenestra endonarina anterior (Fig. 1a). The floor of the nasal capsule (*solum nasi*) has a large basal fenestra; it is bordered anteriorly by the *alary* cartilage, laterally by the ectochoanal cartilage, medially by the ventral border of the planum verticale and posteriorly by the lamina orbitonasalis (Fig. 2a). The lateral region of the nasal capsule presents the fenestra endonarina anterior (external nares) anteriorly, and the fenestrae lateralis (anterior and posterior) posteriorly (Fig. 3a). The planum verticale is pierced by 3 small internal foramina (not shown). The posterior wall of the nasal capsule is formed by the lamina orbitonasalis, which forms the lateral border of the orbitonasal foramen (Fig. 3a). The nasal capsule is covered by the nasals, prefrontals, premaxilla, maxillae, anterior parts of the frontals and anterior vomers. Posteriorly, it contacts with the orbitosphenoid through the sphenoseptal commissure dorsally and the lamina orbitonasalis ventrally (Figs. 1a and 2a).

ORBITOTEMPORAL REGION

In the adult, the lateral walls of the orbitotemporal region are formed by the **orbitosphenoid** and the **pila antotica.**

The **orbitosphenoid** represents the endochondral ossification of the preoptic root, the pila metoptica and part of the trabecula. It forms the side of the neurocranium between the oculomotor foramen posteriorly and the orbitonasal foramen anteriorly, and it is pierced by the optic foramen (Fig. 3a). The orbitosphenoid contacts anteriorly with the nasal capsule, ventrally with the parasphenoid, dorsally with the frontal and the parietal, latero-ventrally with the posterior vomer and posteriorly with the pila antotica and part of the trabecula (Figs. 4a, 5a and 6a).

The **pila antotica** lies posterior to the orbitosphenoid. It is a cartilaginous rod that borders the posterior margin of the oculomotor foramen and the anterior limit of the foramen prooticum, and covers the descending process of the parietal laterally (Fig. 3a). The pila antotica is joined dorsally to the taenia marginalis, ventrally to the trabecula and it is connected with the ascending process of the palatoquadrate laterally (Fig. 6a).

PALATOQUADRATE

The **palatoquadrate** lies on the posterolateral corner of the skull, it is composed by 6 processes: pterygoid (anterolateral), ascending (anteromedial), otic (dorsal), basal (posteromedial), opercular (posterior) and quadrate (ventral) (Fig. 3a). The palatoquadrate is totally cartilaginous excluding the quadrate process. The pterygoid process is the most prominent region and extends anterolaterally to the posterior tip of the maxilla (Fig. 2a). The ascending process is a slender cylindrical bar connected to the dorsal part of the pila antotica (Fig. 3a). The basal and otic processes firmly join the palatoquadrate to the otico-occipital region; the basal process contact to the ventrolateral surface and the otic process the laterodorsal surface (Fig. 3a). The opercular process is bifurcated; it projects toward the posterolateral part of the otico-occipital complex, surrounding the foramen ovale dorsally and ventrally (Figs. 2a and 3a). The quadrate process is in vertical position and bears the articulation of the palatoquadrate with the Meckel’s cartilage, where the quadrate process has a concave surface (Fig. 3a).

OTICO-OCCIPITAL COMPLEX

The **otico-occipital complex** is composed by a pair of large otic capsules, which are joined synchondrotically, dorsomedially by the *tectum synoticum* and ventromedially by the *hypochordal* commissure (Figs.1a and 2a). In the dorsal surface of otico-occipital complex, the prominences of the semicircular canals are observed (Fig. 1a).Ventrally, close to the contact with the palatoquadrate, the otico-occipital complex is pierced by the facial foramen and foramen palatinum (Fig. 2a). Posteriorly the otico-occipital complex presents paired occipital condyles; they arise as cylindrical extensions of exoccipitals at the lateral margins of *foramen magnum* close to the post-otic foramina (Figs. 1a and 2a). Anterior and laterally, the otico-occipital region exhibit various small bony projections, which support some of the palatoquadrate processes. Internally, the otico-occipital region is perforated by three foramina including: auditory foramen (anteriorly), perilymphatic foramen (posteroventrally) and the tiny endolymphatic foramen (dorsally). The otico-occipital region articulates anterodorsally with the taenia marginalis, anteroventrally with the posterior part of trabeculae; it contacts with the parietal dorsally, the parasphenoid ventrally, the vomerine tooth patch ventrolaterally, the palatoquadrate and the squamosal laterally (Figs. 3a, 4a and 5a), and it articulates with the atlas by means of the occipital condyles and the walls of the *foramen magnum* (Fig 2a).

The adult **operculum** is placed near to the vestibular region; it is a small, circular and flattened plate that fills the foramen ovale. The operculum is ossified, although its border is cartilaginous (Fig. 3a).

MECKEL’S CARTILAGE

The **Meckel’s cartilage** is almost completely covered by dermal elements except at its posterior extreme where it is visible. It extends the full length of the jaw, and it is ossified anteromedially forming the mentomeckelian at the mandibular symphisis. At the articular region of the Meckel’s cartilage with the quadrate it has a dorsally convex articular surface. The Meckel’s cartilage is covered by the dentary bone in labial view and the prearticular bone in lingual view and articulates with quadrate posterodorsally (Figs. 7a-b).

POSTNATAL ONTOGENY OF CHONDROCRANIUM

The nasal capsule and the most part of the palatoquadrate are the only structures that remain cartilaginous during postnatal development; the exoccipital is the first endochondral element to ossify and the last is the quadrate process of palatoquadrate.

Neonate

Embryos at late stages of development, near to hatching, were observed. The chondrocranium is structurally similar to that of the neonates although it is completely cartilaginous. Therefore, the orbitosphenoid is absent and the otico-occipital region has not begun to ossify (Figs. 1b, 2b and 3b).

In the neonates, the nasal capsule is more compact than in the adults. The dorsal and basal fenestrae and the fenestrae endonarina anterior and posterior are smaller; the fenestra lateralis is not divided. The tectum internasale is absent, therefore the nasal capsules are joined to one another ventrally through the planum internasale but not dorsally (Fig. 4d). The sphenoseptal commissure is thinner (Fig. 6d). The orbitosphenoid begins its perichondral ossification on the preoptic root cartilage and part of the trabecular cartilage close to the pila metoptica but it does not articulate with any bony element. In the palatoquadrate all the processes are present, however the pterygoid process is small and the quadrate process is still cartilaginous; the articulation of the palatoquadrate with the Meckel's cartilage is placed forward relative to the adult condition (Fig. 6d). The otico-occipital region is cartilaginous in the anterior portion, the surfaces that contact with the palatoquadrate, the occipital condyles, and the floor of the occipital arch (Figs. 4d, 5d and 6d). The foramen palatinum and facial foramen are larger than in the adult, the facial foramen is bordered by the prefacial commissure anteriorly and the basitrabecular commissure posteriorly, the foramen palatinum is placed posteriorly with respect to the facial foramen and limits with basitrabecular commissure anteriorly and the basicapsular commissure posteriorly (Fig. 5d). The otic capsule floor is not completely chondrificated, leaving a fenestra basicapsular in ventral view, which is bordered by the parachordal cartilage medially, the basicapsular commissure anteriorly, and the basivestibular commissure posteriorly (Fig. 5d). The foramina on the medial walls of the otico-occipital region and the post-otic foramen are larger. The foramen ovale is beginning to be filled by the operculum; the foramen ovale is confluent with the fenestra basicapsular (Fig. 5d). In the neonates, the otico-occipital region is joined to the taenia marginalis dorsally, the trabecula ventrally, the palatoquadrate laterally, and it articulates with the atlas posteriorly. The operculum is small and ossified although some parts are still cartilaginous. The Meckel's cartilage is very similar to that of the adult; its anterior portion has already become ossified in the mentomeckelian bone, however the Meckel's cartilage is more exposed medially than in the adult (Fig. 7c).

Stage I

In the nasal capsule the tectum internasale arises and in some individuals the fenestra lateralis is now divided into the fenestrae lateralis anterior and posterior; the other fenestrae of the nasal capsule remain smaller than in the adults. The orbitosphenoid is ossified on the preoptic root, the trabecular crest, part of the pila metoptica and the trabecula. Dorsal to these endochondral ossifications the orbitosphenoid presents membranous appositional bone growth. The orbitosphenoid does not fill the lateral wall of the skull, thus leaving a large orbitotemporal fenestra (Figs. 5c and 6c). The pila antotica does not cover the descending process of the parietal completely yet (Fig. 6c). The palatoquadrate has a small pterygoid process; its quadrate process is ossified and presents an almost vertical orientation relative to the otico-occipital region (Fig. 6c). The otico-occipital region is completely ossified, the fenestra basicapsular is eliminated by the appearance of the mesotic cartilage, the latter ossifies forming part of the bony floor of the otico-occipital region (Fig. 5c). The operculum is larger than in the neonate but it does not fill the foramen ovale completely yet (Fig. 5c).

Stage II

The fenestrae of the nasal capsule are larger than in previous stages and now they show the adult shape. However, the nasal capsule as a whole has not attained the characteristic shape of adults. The orbitosphenoid grows dorsally by membranous appositional growth, therefore the orbitotemporal fenestra becomes smaller (Fig. 5b). The orbitosphenoid joins to the nasal capsule anteriorly and to the pila antotica posteriorly, and contacts with the parasphenoid and with the posterior vomer ventrally (Figs. 5b and 6b). The palatoquadrate has a large pterygoid process and its quadrate process has a vertical position with respect to the otico-occipital region (Figs. 5b and 6b). The palatoquadrate, the pila antotica, the otico-occipital region, and the operculum have acquired the adult shape (Figs. 4b, 5b and 6b).

ADULT DERMATOCRANIUM

The dermatocranium is formed by the dermal bones that constitute the palatal region and the bones that cover the frontoparietal fenestra, the fenestra basicranialis, the nasal capsule and the Meckel’s cartilage.

NASAL REGION

The anterior region of the dermatocranium is formed by the **premaxilla**, the **maxillae**, the **nasals** and the **prefrontals.**

The **premaxilla** is placed at the anteromedial region of the nasal capsules obliterating the internasal cavity (Fig. 4a). There are two main regions: the toothed portion (*pars dentalis*) and the paired frontal processes (*pars dorsalis*). The premaxillary *pars dentalis* is small and bears three to five long teeth curved lingually. The premaxillary *pars dorsalis* is formed by two completely separated processes directed posterodorsally overlapping the anterior portion of the frontals; there is not premaxillary *pars palatina.* The premaxilla contacts with the maxillae laterally and with the frontals dorsally (Fig. 4a).

The **maxilla** lies at the anterolateral region of the nasal capsules (Fig. 4a). Each maxilla consists of three regions: the toothed portion (*pars dentalis*), the facial process (*pars facialis*), and the palatal portion (*pars palatina*). The maxillar *pars dentalis* is large, it bears 15 to 28 short bicuspid teeth curved lingually. The maxillar *pars palatina* is a thin shelf, which is laterally thinner and medially becomes gradually ticker. The maxillar *pars facialis* is relatively large and overlies the lateral region of the nasal capsule. The maxillae articulate with the premaxilla, the nasals, the prefrontals, the vomers, and limit with the marginal part of the fenestra endonarina posterior (Figs. 4a, 5a and 6a).

The **nasal** forms the posterodorsal rim of the fenestra endonarina anterior, it overlies part of the dorsal surface of the nasal capsule and limits with the maxilla, the prefrontal, and the lateral margin of the fenestra endonarina posterior (Fig. 4a). In some individuals the nasals can be fused to the prefrontals.

The **prefrontal** lies over the posterolateral portion of the nasal capsule, it is small and it

has an oval-shape, and articulates with the frontals, the nasals, the maxillae, and forms the posterior border of the fenestra endonarina posterior (Fig. 6a).

PALATAL REGION

The palate is formed by the **anterior** and **posterior vomers** and the **parasphenoid**.

The **anterior vomer** presents a lateral plate that covers almost totally the basal fenestra of the nasal capsule and a toothed preorbital process which extends below the lamina orbitonasalis. The anterior vomer borders almost totally the internal nares, which are located between the lateral plate and the preorbital process (Fig. 5a). The preorbital process bears 11 to 28 bicuspid teeth curved lingually, organized in two or three lines. The anterior vomer contacts with the maxilla and the parasphenoid, and it is completely separated from the posterior vomer (Fig. 5a).

The **posterior vomer** supports the vomerine tooth patch, which presents numerous and large bicuspid teeth curved posteriorly. The posterior vomers cover almost totally the ventral surface of the parasphenoid. The posterior vomers contact with the orbitosphenoid, the trabeculae, and the otico-occipital region (Fig. 5a).

The braincase floor is formed by the **parasphenoid**, which closes the basicranial fenestra completely. It is a wide, triangular-shaped and laminar bone that ventrally supports the posterior vomer, and contacts the vomerine tooth patch, the orbitosphenoid, the trabeculae, and the otico-occipital region (Fig. 5A).

SKULL ROOF

The skull roof is formed by the **frontals** and **parietals**, which close the frontoparietal fenestra.

The **frontal** is large, it has three processes, two anterior processes and one posterolateral process. The frontals articulate with the nasals, the orbitosphenoid, and the prefrontals, and contact with the parietals through a W-shaped frontoparietal suture; the posterior region of the frontals overlaps the anterior portion of the parietals. The frontals can be fused medially in their anterior portion, or can be completely separated (Figs. 4a and 6a).

The **parietal** is a large element that has a long anterolateral process, which extends between the frontal and the orbitosphenoid, and a lateral descending process, which is laterally overlapped by the pila antotica. The parietals articulate with the otico-occipital region, the frontals and the orbitosphenoid (Figs. 4a and 6a).

TEMPORAL REGION

In the posterolateral region of the skull and closely associated with the palatoquadrate is the **squamosal**. The **squamosal** is oriented almost vertically and laterally overlies the otic process of palatoquadrate. Its anterior portion is rounded and its posterior end is acute (Fig. 6a). The squamosal contacts with the otico-occipital region and its posterior rim touches the ceratohyal cartilage of the hyoid apparatus.

MANDIBLE

The mandible is formed by the **dentary** and **prearticular**.

The **dentary** is a large and arc-shaped bone, which extends almost entirely along the mandibular arch and it is fused to the mentomeckelian medially. Its lingual face is grooved containing the Meckel’s cartilage. The dentary bears 32 to 44 bicuspid teeth of similar length to the maxillaries teeth. The dentary contacts with the prearticular and joins anteriorly to its contralateral twin at the cartilaginous mandibular symphisis (Fig. 7a-b).

The **prearticular** is located in the posterolingual region of the mandibular arch and extends along the posterior two thirds of the lower jaw; it is curved dorsomedially just anterior of the articulating surface with the quadrate, it tapers anteriorly and presents a well-developed coronoid process, which is the highest region of the mandibular arch. The prearticular covers the Meckel's cartilage lingually and is perforated posteriorly by a small facial foramen (Fig. 7a).

POSTNATAL ONTOGENY OF DERMATOCRANIUM

In neonates, most of the dermal bones have already appeared, however, many of them are observed as small ossification centers. The last elements to ossify are the nasals and prefrontals, which ossify during postnatal development.

Neonate

The nasals and prefrontals are absent and the premaxilla and the maxillae are present as small ossification centers, therefore, the nasal capsule is more exposed than in the adult.

The premaxilla is very small and its premaxillary *pars dentalis* does not have teeth (Figs. 4d and 5d). The maxilla is represented by a thin maxillary *pars dentalis* without teeth and a small maxillary *pars facialis* that has begun to ossify (Figs. 5d and 6d).

In the anterior vomer, the vomerine plate is scarcely discernible, the preorbital process is absent, and only two anterior vomerine teeth are present in the unossified preorbital region (Fig. 5d). The posterior vomer is a sliver-like ossification that bears only two teeth, the remaining vomerine teeth are placed over the ventral surface of the parasphenoid but they are not ankylosed to this element yet. The anterior vomer covers only a small portion of the basal fenestra of the nasal capsule (Fig. 5d). The frontals and parietals are ossified along the lateral margins of the skull roof, thus a large frontoparietal fenestra is observed in the skull roof; their distinctive processes present in the adult are absent (Fig. 4d). The parasphenoid fills almost completely the basicranial fenestra, reaching the floor of the occipital arch, it also contacts with the posterior vomer and with many vomerine teeth (Fig. 5d). The squamosal is a thin and oval ossification; it is in oblique position with respect to the otico-occipital region and covers a small portion of the otic and opercular processes of the palatoquadrate (Fig. 6d). The dentary is a prominent element, however it bears only one or two small teeth. It does not contact with the prearticular neither reaches the articular region (Fig. 7d). The prearticular presents a small coronoid process but it does not articulate with the dentary (Fig. 7c).

Stage I

The premaxillary teeth are still absent but the premaxillary *pars dorsalis* extend posterodorsally and now begins to cover the anterior margin of the frontals; the premaxilla does not articulate with the maxillae yet (Figs. 4c and 5c). All the processes of the maxilla are present, however, the maxilla does not reach any bone and the *pars dentalis* does not bear teeth yet (Figs. 4c and 5c). The nasals appear as small centers of ossification on the posterior part of the nasal capsules (Fig. 4c). In some individuals, small prefrontals have begun to ossify (Fig. 4c). In the anterior vomer the vomerine plate is longer and the preorbital process is present, it bears four to 11 teeth and covers part of the lamina orbitonasalis in ventral view; the anterior vomer does not cover the basal fenestra completely yet (Fig. 5c). The posterior vomer grows in medial, lateral, anterior and posterior directions above the parasphenoid. The posterior vomer now bears more teeth than in the neonate; however, there are some teeth that are not joined to the posterior vomer, which are located on the posterior region of the parasphenoid (Fig. 5c). The frontals grow in anterior, posterior, and medial directions, therefore the frontoparietal fenestra becomes smaller but the frontals do not contact each other along the midline. The frontal processes have appeared (Figs. 4c and 6c). The parietals grow medially but do not contact to each other yet, thus a small frontoparietal fenestra remains in the skull roof. The descending process of the parietal is present as a small bony extension behind pila antotica. The orbitosphenoid does not reach the skull roof but the orbitotemporal fenestra is smaller than in neonates (Fig. 4c). The parasphenoid closes the basicranial fenestra (Fig. 5c). The squamosals are oriented more vertically (Fig. 6c). The dentary bears six to 19 bicuspid teeth. The prearticular presents a prominent coronoid process and articulates with the dentary.

Stage II

The premaxilla does not contact with the maxillae and has a *pars dentalis* with 4 teeth (Fig. 5b). In each maxilla, the *pars dentalis* bears 11 to 23 teeth and the *pars palatina* is thin, it lacks the thicker medial border (Figs. 4b and 5b). The nasal is pentagonal shaped and it does not touch any bone (Fig. 4b). The prefrontals are small bony bars, they do not contact to any element (Fig. 4b). In the anterior vomer, the preorbital process bears 8 to 25 teeth. The anterior vomer does not contact any cranial element (Fig. 5b). The posterior vomer does not cover the parasphenoid completely but it is larger and bears numerous teeth; some teeth are located in the periphery of the vomer (Fig. 5b). The posterior vomer contacts the parasphenoid, the trabeculae, and the otico-occipital region (Fig. 5b). The dentary bears

16 to 30 bicuspid teeth. The frontals, parietals, parasphenoid, squamosals, and prearticulars are morphologically similar to the adult, however, the frontals and parietals do not contact to each other along midline (Figs. 4b, 5b and 6b).

MORPHOLOGY AND POSTNATAL ONTOGENY OF HYOID APPARATUS

In the adult, the hyoid apparatus is totally cartilaginous and it is formed by the first basibranchial with short and straight paired *cornua* located at its anterior margin. On each side of the basibranchial are the ceratohyals, first ceratobranchials, second ceratobranchials and long epibranchials (Fig. 8). From the last stages of the embryonic development, the hyoid apparatus is quite similar to the adult; therefore it does not show major morphological variation during the postnatal ontogeny.

CRANIAL MORPHOLOGY OF *Bolitoglossa vallecula*

The skull of *B. vallecula* is well ossified, and its cranial morphology is similar to that of *B. nicefori*. The premaxillary *pars dentalis* bears three to four monocuspid teeth and its premaxillary *pars dorsalis* are completely separated from one another. The nasals have irregular shape. The prefrontals are present in all skulls examined. The anterior and posterior vomers are separated, the anterior vomer does not contact the maxilla and the posterior vomer bears numerous bicuspid teeth curved lingually. The suture between frontals and parietals is W-shaped. The descending process of the parietal arises laterally overlapped by the pila antotica and the taenia marginalis. The orbitosphenoid is pierced by the optic foramen and borders the orbitonasal foramen anteriorly and the oculomotor foramen posteriorly. The parasphenoid is wider and larger than in *B. nicefori.* The squamosal and the quadrate process of the palatoquadrate are in vertical position. The palatoquadrate presents a prominent pterygoid process, a quadrate process totally ossified, and an opercular process bifurcated that surrounds the oval foramen dorsally and ventrally. The operculum is a bony plate. In the otico-occipital region, the prominences of the semicircular canals are evident. The hyoid apparatus is totally cartilaginous; there are a basibranchial with two small *cornua,* a pair of ceratohyals, two pair of ceratobranchials and a pair of epibranchials.

DISCUSSION

Dermatocranium

The dermatocranium of *Bolitoglossa nicefori* can be regarded as representative of the plethodontids (Wake, 1966; Duellman & Trueb, 1986; Rose, 1995; Ehmcke & Clemen, 2000c, 2003). It shows: completely separated anterior and posterior vomers, large number of vomerine teeth and absence of the palatine, lacrimal, pterygoid and angular bones. Also, it shares specific features with other species of *Bolitoglossa* (Wake, 1966; Duellman & Trueb, 1986; Restrepo, 1995; Bolívar, 1998; Ehmcke & Clemen, 2000c, 2003; Acosta, 2007), such as: unpaired premaxilla, lack of the premaxillary *pars palatina*, unfused premaxillaries *pars dorsalis,* reduced maxillaries *pars palatina,* W-shaped frontoparietal suture, smooth squamosals (without crests) and presence of the descending process of the parietal (parietal spur according to Wake, 1966).

In spite of the morphological similarities of the dermatocranium of *B. nicefori* with other species of *Bolitoglossa* some regions show interspecific variation, such as the presence or absence of the dermal bones prefrontal and septomaxilla. The prefrontals are present in *B. nicefori* and in other species of *Bolitoglossa* as well (e.g. *B. vallecula, B. adspersa* and *B. subpalmata*) either as a discrete elements or they are fused with the nasals (Wake, 1966;

Alberch & Alberch, 1981; Alberch, 1983; Restrepo, 1995; Ehmcke & Clemen, 2000c, 2003), whereas in *B. occidentalis* and *B. altamazonica*, these bones are never formed (Alberch & Alberch, 1981; Alberch, 1983). On the other hand, the septomaxillae are usually absent in the genus *Bolitoglossa* (Alberch, 1983), as in *B. nicefori* and *B. vallecula*, however, Wake (1966) reported small septomaxillae in the skull of some individuals of *B. rufescens, B. mexicana* and *B. platydactyla.* The morphological variation in the presence or absence of the prefrontals and septomaxillae in *Bolitoglossa* is apparently a product of paedomorphosis (Wake, 1966; Alberch & Alberch, 1981; Alberch, 1983), which results in the reduction or loss of these bony elements, as in the case of some species of the genera *Thorius, Oedipina, Batrachoseps* and *Chiropterotriton* (Wake, 1966; Hanken, 1984).

Chondrocranium

The chondrocranium of *B. nicefori* is similar to that of other urodeles. The nasal capsules have large fenestrae, which are placed on the surface of the *tectum nasi*, the *solum nasi* and the lamina orbitonasalis (de Beer, 1937; Eyal-Giladi & Zinberg, 1964; Duellman & Trueb, 1986; Trueb, 1993; Rose, 1995). The neurocranium is formed by paired orbitosphenoid that are pierced by the optic foramen and constitute the lateral margins of the frontoparietal and basicranial fenestrae and the otico-occipital complex where the otic capsules are located and the palatoquadrate is firmly joined (de Beer, 1937; Wake, 1963, 1966; Eyal-Giladi & Zinberg, 1964; Corsin, 1966; Duellman & Trueb, 1986; Trueb, 1993; Rose, 1995).

The morphology of chondrocranium in the genus *Bolitoglossa* has not been studied in detail, only a few general descriptions are known related to some elements such as the orbitosphenoid, the pterygoid process of the palatoquadrate and the opercular apparatus (Wake, 1966; Bolívar, 1998; Ehmcke & Clemen, 2000c, 2003). Compared to the chondrocranial morphology of other salamanders, the chondrocranium of *B. nicefori* shows some morphological differences, such as the number of foramina of the lamina orbitonasalis and the morphology of the braincase floor. The lamina orbitonasalis of *B. nicefori* is pierced medially by only one orbitonasal foramen, while in the plethodontid *Eurycea bislineata* (Rose, 1995) and in the salamandrids *Pleurodeles waltlii* and *Salamandra salamandra* (Eyal-Giladi & Zinberg, 1964; Duellman & Trueb, 1986), two (lateral and medial) orbitonasal foramina are present. On the other hand, in the ventral region of the braincase of *B. nicefori* there is a large fenestra basicranialis, however, in *P. waltlii* and in *S. salamandra*, there are two fenestrae basicranialis (anterior and posterior), which are divided by a cartilaginous bar, the *crista sellaris tranversa* (Eyal-Giladi & Zinberg, 1964; Duellman & Trueb, 1986), additionally in the genus *Cryptobranchus* there is only one fenestra basicranialis, but it is much more reduced than the present in *B. nicefori*, since a great portion of the basal plate is chondrified (de Beer, 1937). The chondrocranium of *B. nicefori* also presents some differences with respect to other species of *Bolitoglossa*, such as: presence or absence of the columella and ossification of the articular bone in the mandible. *B. nicefori* does not possess a columella and the articular region of the Meckel's cartilage is not ossified forming the articular bone, this is a similar condition to the present in most of the species of *Bolitoglossa* (Monath, 1965; Wake, 1966; Bolívar, 1998; Ehmcke & Clemen, 2000c, 2003), however, in *B. dunni* there is a vestigial columella joined to opercular plate (Wake, 1966), and in *B. subpalmata* there is an articular ossification articulating with the quadrate process of the palatoquadrate (Ehmcke & Clemen, 2000c, 2003).

The palatoquadrate of *B. nicefori* is formed by 6 processes: pterygoid, ascending, otic, basal, opercular, and quadrate. In some salamandrids (*Pleurodeles* and *Triturus*) and plethodontids (*Eurycea, Aneides, Plethodon* and *Ensatina*), the palatoquadrate have 5 processes, there is not an equivalent region corresponding to the opercular process presents in *B. nicefori* (Wake, 1963; Eyal-Giladi & Zinberg, 1964; Rose, 1995; Rocek, 1996). In *Bolitoglossa,* there are general descriptions of the suspensorium anatomy, but those descriptions are focused mainly on the pterygoid and quadrate processes (Wake, 1966; Ehmcke & Clemen, 2000c, 2003), and the opercular process has never been reported previously for any species of the genus. However it is evident as a bifurcated posterior portion that surrounds the oval foramen ventral and dorsally in the palatoquadrate of *B. vallecula* here reported and in *B. walkeri* (Bolívar, 1998). Thus, the opercular process of palatoquadrate is evident in the chondrocranium of some species of *Bolitoglossa*, although it is unknown whether it is a shared and derived character in all the species of the genus or if it has interespecific variation*.*

Hyoid apparatus

The hyoid apparatus of *B. nicefori* presents a similar morphology to that of other species of *Bolitoglossa*; therefore, the hyoid apparatus is totally cartilaginous, the second basibranchial is absent, the *cornua* are short and continue with the first basibranchial, the ceratobranchials II are longer than the ceratobranchials I, and the epibranchials are very long (Wake, 1966; Alberch, 1987; Bolívar, 1998).

Postnatal development

The skull of neonates of *B. nicefori* presents an advanced stage of ossification, therefore, most of the elements of the dermatocranium (except nasals and prefrontals) have already begun their ossification, the palate does not present palatopterygoid, the anterior and posterior vomers are completely separated, the nasal capsule and the hyoid apparatus are well formed, and there is not a coronoid bone in the mandible. The configuration of these regions resembles to those of biphasic salamanders in postmetamorphic stage (Eyal-Giladi & Zinberg, 1964; Bonebrake & Brandon, 1971; Reilly, 1986; Rose, 1995; Jöman, Clemen & Greven, 2005). On the other hand, the cranial roof has a large frontoparietal fenestra, the otico-occipital region is not completely ossified, the orbitosphenoid starts its perichondral ossification, and the maxillae and premaxilla do not bear teeth; the latter are similar features to those of metamorphic urodeles in early larval stage (Worthington & Wake, 1971; Bonebrake &

Brandon, 1971; Rose, 1995; Jöman *et al.,* 2005). Although in the palatoquadrate all its processes are present, the presence of the small and slender pterygoid process makes the palatoquadrate similar to that of the biphasic individuals in metamorphic stage, but at the same time the quadrate process is still cartilaginous and this is similar to the condition of metamorphic salamanders in early larval stage (Rose, 1995).

Hence, the morphology of the neonates of *B. nicefori* presents a mosaic of larval, metamorphic and postmetamorphic characters, and contrasts with the stage of ossification of the skull in the neonates of *B. subpalmata.* According to Ehmcke & Clemen (2000a, 2000b, 2000c, 2003) *B. subpalmata* hatches with a stage of ossification comparable to that of biphasic urodeles in postmetamorphic stage, with bicuspid vomerine teeth organized in a continuous column on the palate, yet the rest of the skull is poorly developed. Therefore, there are a few endochondral elements (quadrate process of palatoquadrate and otic capsules) in cartilaginous stage and the anlagen of the cartilage of the ethmoidal region (nasal capsules) and the derivates of the trabeculae are scarcely discernible. The interspecific variation of the cranial stage of ossification and the mosaic of larval, metamorphic and postmetamorphic skull features in neonates of *B. nicefori* could be caused by heterochronic changes in the ossification sequence, compared to ontogeny of metamorphic salamanders. However, whether some elements have accelerated or retarded its onset of ossification relative to the ossification sequences of biphasic salamanders is difficult to establish, given the absence of enough embryonic material and incomplete ossification sequences. Furthermore the comparative study of these ossification sequences should be analyzed in future studies within a phylogenetic framework (see Jeffery *et al*., 2005; and Schoch, 2006).

The absence of larval structures (coronoid, palatopterygoid, larval vomers and numerous epibranchials) during postnatal development and the existence of possible heterochronic changes in the skull ontogeny of *B. nicefori* is perhaps due to the presence of an ontogenetic repatterning (Hanken, 1992; Wake & Hanken, 1996), in contrast to a recapitulatory pattern, as has been reported in the cranial development of direct-developing amphibians, such as the urodele *Desgmognathus aeneus* (Marks, 2000) and the anuran *Eleutherodactylus coqui* (Hanken *et al.,* 1992) and in the development of the hyoid apparatus of *B. subpalmata* (Alberch, 1987, 1989).

In the plethodontids the ontogenetic repatterning has been associated to the appearance of structural innovations in adult morphology allowed by the loss of larval constraints (restrictions imposed by larval morphology on adult morphology) within the tribe Bolitoglossini (Roth and Wake, 1985; Wake and Roth, 1989), however, the possible modifications in the cranial ontogeny of *B. nicefori* would not have an obvious impact on the adult skull morphology, as was found by Hanken *et al.,* (1992) in the skull of the anuran *E. coqui.* The absence of morphological novelties in the adult skull morphology of *B. nicefori* could be related to the existence of a compartmentalized development, in which the precursors of larval and adult structures are physically decoupled allowing the elimination of "unnecessary" larval components in direct-developing amphibians, without affecting its adult morphology. The developmental compartimentalization of larval and adult structures has been observed in the ontogeny of the epibranchial cartilage of the plethodontids *E. bislineata* and *B. subpalmata* (Alberch, Lewbart & Gale, 1985; Alberch & Gale, 1986; Alberch, 1987, 1989) but seems to be absent in non plethodontid salamanders. Therefore, Alberch (1987, 1989) proposed that compartmentalized development evolved in the ancestral root of the plethodontid lineage. As such, the emergence of direct-development in Bolitoglossini salamanders such as *B. nicefori* do not represent the loss of larval constraints, at least regarding the skull ontogeny, rather such larval constraints do not exist in the cranial development of the family Plethodontidae due to the presence of a compartmentalized development of larval and adult structures (Alberch *et al.,* 1985; Alberch & Gale, 1986; Alberch, 1987, 1989). However, in contrast to the skull of *B. nicefori*, there are morphological novelties in the functional morphology of the tongue and in some structures related to feeding in the tribe Bolitoglossini, such as: reduction of mass of the tongue skeleton, reduction of the length of the two pairs of ceratobranchials, full elaboration of a complete muscular sheath around the epibranchials by the m. subarcualis rectus, increased eye frontality and increased number of ipsilateral retinal afferent projections (Lombard & Wake, 1977; Roth & Wake, 1985; Wake & Roth, 1989). These morphological novelties are probably attained through the circumvention of larval constraints (Roth & Wake, 1985; Wake & Roth, 1989).

It is possible to suggest the presence of an ontogenetic repatterning in the skull development of *B. nicefori,* yet it is important to remember that the ancestral biphasic pattern of cranial development can be also recapitulated during the embryonic ontogeny, as has been observed for the development of the hyoid apparatus of *D. aeneus* and *P. cinereus* (Dent, 1942; Alberch, 1989; Marks, 2000), for many cranial structures of direct-developing anuran, *Philautus silus* (Kerney *et al.,* 2007), and for some cranial components of *E. coqui* (Hanken *et al.,* 1992). Therefore, the possible occurrence of ontogenetic repatterning or recapitulatory processes, or even the mosaic of both patterns, can only be clearly established in future analysis of cranial morphogenesis during the embryonic development of *B. nicefori*.

The principal events occurring during postnatal development of the skull of *B. nicefori* are also observed during postnatal development in other metamorphic and direct-developing urodeles (Eyal-Giladi & Zinberg, 1964; Corsin, 1966; Bonebrake & Brandon, 1971; Alberch & Alberch, 1981; Alberch, 1983; Wake *et al*., 1983; Reilly, 1986; Reilly & Altig, 1996; Ehmcke & Clemen, 2000b; Jöman *et al.*, 2005): 1) closure of the frontoparietal fenestra and of the fenestra basicranialis, 2) ossification of the quadrate process of palatoquadrate, 3) emergence of maxillary teeth, 4) ossification of the nasals, and 5) growth and strengthening of the elements of the dermatocranium.

The morphology of the dermatocranium, chondrocranium and hyoid apparatus in *B. nicefori* and its postnatal development is similar to that of metamorphic and direct-developing plethodontids and urodeles in general. However, the neonatal stage of ossification shows a mosaic of traits that suggests the occurrence of a non recapitulatory ontogenetic repatterning, with loss of the characteristic larval structures and possible heterochronic changes affecting the sequence of ossification of some cranial structures.

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TABLE 1. Stages in cranial postnatal ontogeny of *Bolitoglossa nicefori*

Stage	**Morphological parameters**	**Size range** (mm)
Neonate	Appearance of orbitosphenoid.	9.77 – 10.92
I	Appearance of nasals and prefrontals. Ossification of the quadrate process of palatoquadrate.	19.58 – 26.53
II	Appearance of premaxillary and maxillaries teeth.	27.25 – 45.93
Adult	The nasal capsule is totally covered by dermal elements. Orbitosphenoid covers totally the orbitotemporal fenestra.	47.78 – 82.21

APPENDIX 1.

List of examined individuals. Specimen number is followed by snout-vent or standard length (mm) and sex (F, female and M, male, where known). *Bolitoglossa nicefori*. Embryos: UIS-A-3812; UIS-A-3813, 9.77; MUJ-2886-1. Neonate Stage: MUJ-2886-2, 10.4; MUJ-2886-3, 10.92. I Stage (juveniles): UIS-A-3804, 19.58; UIS-A-3452, 20.52; UIS-A-3805, 21.61; UIS-A-3806, 21.95; UIS-A-3802, 22.54; UIS-A-3808, 23.82; UIS-A-3453, 25.21; UIS-A-3807, 25.41; UIS-A-3803, 25.62; UIS-A-3168, 26.11; UIS-A-3170, 26.32; UIS-A-3169, 26.53. II Stage (subadults and small adults): UIS-A-3189, 27.25 (M); UIS-A-3454, 27.36; UIS-A-3234, 29.33 (F); UIS-A-3195, 30.59 (M); UIS-A-3226, 32.73 (F); UIS-A-3194, 32.79 (F); UIS-A-3203, 33.22 (F); UIS-A-3186, 33.69 (M); UIS-A-3233, 33.9 (M); UIS-A-3216, 35.27 (F); UIS-A-3202, 34.5 (F); UIS-A-3209, 35.06 (F); UIS-A-3199, 36.63 (F); UIS-A-3227, 37.1 (F); UIS-A-3198, 38.03 (M); UIS-A-3197, 38.39 (M); UIS-A-3460, 40.75 (M); UIS-A-3210, 41.6 (M); UIS-A-3222, 42 (M); UIS-A-3178, 42.4 (F); UIS-A-3810, 43.00 (F); UIS-A-3211, 43.13 (M); UIS-A-3458, 45.93 (M). Adult Stage: UIS-A-3191, 47.78 (M); UIS-A-3217, 48.7 (F); UIS-A-3179, 49.33 (M); UIS-A-3192, 50.63 (M); UIS-A-3200, 50.76 (M); UIS-A-3205, 50.8 (F); UIS-A-3214, 51.1 (F); UIS-A-3457, 51.63 (M); UIS-A-3201, 52.68 (F); UIS-A-3221, 53.4

(F); UIS-A-3811, 54.21 (F); UIS-A-3206, 54.4 (F); UIS-A-3171, 55 (F); UIS-A-3238, 58.1 (F); UIS-A-3220, 52.15 (M); UIS-A-3213, 61.31 (F); UIS-A-3219, 62.62 (F); UIS-A-3801, 82.21 (F); UIS-A-3809. *Bolitoglossa vallecula*. Adults: MHUA-1393, 76.14 (F); MHUA-0984, 58.92 (F); MHUA-2613, 69.17 (F); MHUA-1511, 41.04 (F); MHUA-0626, 31.5 (juvenil).

FIGURES LEGENDS

Figure 1. *Bolitoglossa nicefori*. Development of the chondrocranium from embryo to adult stages (dorsal views). **a.** Adult stage (UIS-A-3457). **b.** Embryo (UIS-A-3813). Cartilage is represented in gray and endochondral bone in white. ac *alary* cartilage; bf basal fenestra; df dorsal fenestra; fea fenestra endonarina anterior; fep fenestra endonarina posterior; ffrp frontoparietal fenestra; fo optic foramen; focn oculomotor foramen; forn orbitonasal foramen; fp foramen prooticum; lon lamina orbitonasalis; obc oblique cartilage; oc occipital condyle; oor otico-occipital region; pa ascending process of quadrate; pao pila antotica; pin planum internasal; pm pila metoptica; q quadrate; sc semicircular canal; ssc sphenoseptal commissure; t trabecula; tin tectum internasal; tm taenia marginalis; ts tectum synoticum. Scale bar = 1.8 mm for a, 0.7 mm for b.

FIgure 2. *Bolitoglossa nicefori*. Development of the chondrocranium from embryo to adult stages (ventral views). **a.** Adult stage (UIS-A-3457). **b.** Embryo (UIS-A-3813). Cartilage is represented in gray and endochondral bone in white. ac *alary* cartilage; bc basitrabecular commissure; bcc basicapsular commissure; bf basal fenestra; bpr basal process of quadrate; bvc basivestibular commissure; ec ectochoanal cartilage; fb fenestra basicranialis; fbc fenestra basicapsular; fea fenestra endonarina anterior; ff facial foramen; fo optic foramen; focn oculomotor foramen; fpa foramen palatinum; fpost post-otic foramen; hchco hypochordal commissure; lon lamina orbitonasalis; op operculum; oor otico-occipital region; osp orbitosphenoid; p parachordal; pao pila antotica; pfc prefacial commissure; pin planum internasal; por opercular process of quadrate; pro preoptic root; ptp pterygoid process of quadrate; t trabecula. Scale bar = 1.8 mm for a, 0.7 mm for b.

Figure 3. *Bolitoglossa nicefori*. Development of chondrocranium from embryo to adult stages (lateral views). **a.** Adult stage (UIS-A-3457). **b.** Embryo (UIS-A-3813). Cartilage is represented in gray and endochondral bone in white. df dorsal fenestra; fea fenestra endonarina anterior; fep fenestra endonarina posterior; fla fenestra

lateralis anterior; flp fenestra lateralis posterior; fo optic foramen; focn oculomotor foramen; fp foramen prooticum; lon lamina orbitonasalis; mc Meckel's cartilage; mm mentomeckelian; obc oblique cartilage; op operculum; pa ascending process of quadrate; pao pila antotica; pm pila metoptica; po otic process of quadrate; por opercular process of quadrate; pro preoptic root; ptp pterygoid process of quadrate; q quadrate; tc trabecular crest; tm taenia marginalis; ts tectum synoticum. Scale bar = 1.8 mm for a, 0.7 mm for b.

Figure 4. *Bolitoglossa nicefori*. Development of the skull from neonate to adult stages (dorsal views). **a.** Adult stage (UIS-A-3171). **b.** II stage (UIS-A-3194). **c.** I stage (UIS-A-3452). **d.** Neonate stage (MUJ-2886-3).Cartilage is gray, membranous ossifications and endochondral bones are white. df dorsal fenestra; ffrp frontoparietal fenestra; fro frontal; lon lamina orbitonasalis; max maxilla; mfp maxillary facial process; nas nasal; nc nasal capsule; oc occipital condyle; oor otico-occipital region; osp orbitosphenoid; par parietal; pmx premaxilla; prf prefrontal; ptp pterygoid process of quadrate; q quadrate; sc semicircular canal; squ squamosal; ts tectum synoticum. Scale bar = 2 mm for a, 1.4 mm for b, 0.9 mm for c, 0.4 mm for d.

Figure 5. *Bolitoglossa nicefori*. Development of the skull from neonate to adult stages (ventral views). **a.** Adult stage (UIS-A-3171). **b.** II stage (UIS-A-3194). **c.** I stage (UIS-A-3452). **d.** Neonate stage (MUJ-2886-3).Cartilage is gray, membranous ossifications and endochondral bones are white. bc basitrabecular commissure; bcc basicapsular commissure; bvc basivestibular commissure; fbc fenestra basicapsular; ff facial foramen; fpa foramen palatinum; max maxilla; nc nasal capsule; oor otico-occipital region; op operculum; osp orbitosphenoid ; p parachordal; pfc prefacial commissure; pmx premaxilla; psp parasphenoid; q quadrate; squ squamosal; t trabecula; voa anterior vomer; vop posterior vomer; vt vomerine tooth patch. Scale bar = 2 mm for a, 1.4 mm for b, 0.9 mm for c, 0.4 mm for d.

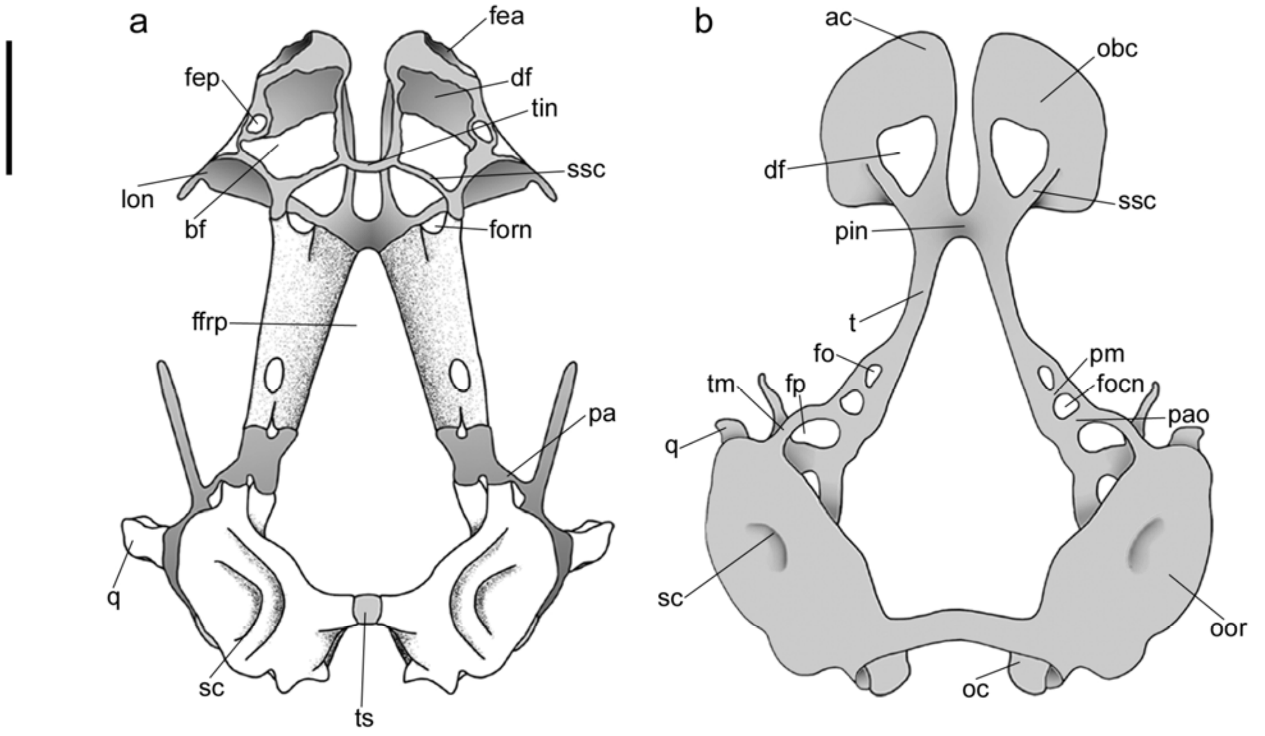
Figure 6. *Bolitoglossa nicefori*. Development of the skull from neonate to adult stages (lateral views). **a.** Adult stage (UIS-A-3171). **b.** II stage (UIS-A-3194). **c.** I stage (UIS-A-3452). **d.** Neonate stage (MUJ-2886-3).Cartilage is gray, membranous ossifications and endochondral bones are white. fea fenestra endonarina anterior; fep fenestra endonarina posterior; fl fenestra lateralis; fobt orbitotemporal fontanella; fov foramen ovale; fro frontal; lon lamina orbitonasalis; max maxilla; mfp maxillary facial process; nas nasal; nc nasal

capsule; oor otico-occipital region; op operculum; osp orbitosphenoid; par parietal; por opercular process of quadrate; prf prefrontal; psp parasphenoid; ptp pterygoid process of quadrate; q quadrate; squ squamosal; t trabecula; tc trabecular crest; tm taenia marginalis; voa anterior vomer vop posterior vomer. Scale bar = 2 mm for a, 1.4 mm for b, 0.9 mm for c, 0.4 mm for d.

Figure 7. *Bolitoglossa nicefori*. Development of the mandible from neonate to adult stages (lateral views). **a.** Adult stage, lingual view of left mandible (UIS-A-3171). **b.** Adult stage, labial view of left mandible (UIS-A-3171). **c.** Neonate stage, lingual view of left mandible (MUJ-2886-3). **d.** Neonate stage, labial view of left mandible (MUJ-2886-3). Cartilage is gray, membranous bones are white. den dentary; mc Meckel’s cartilage; mm mentomeckelian; ms mandibular symphysis; pra prearticular. Scale bar = 1.5 mm for a,b and 0.4 mm for c,d.

FIGURES

Figure 1



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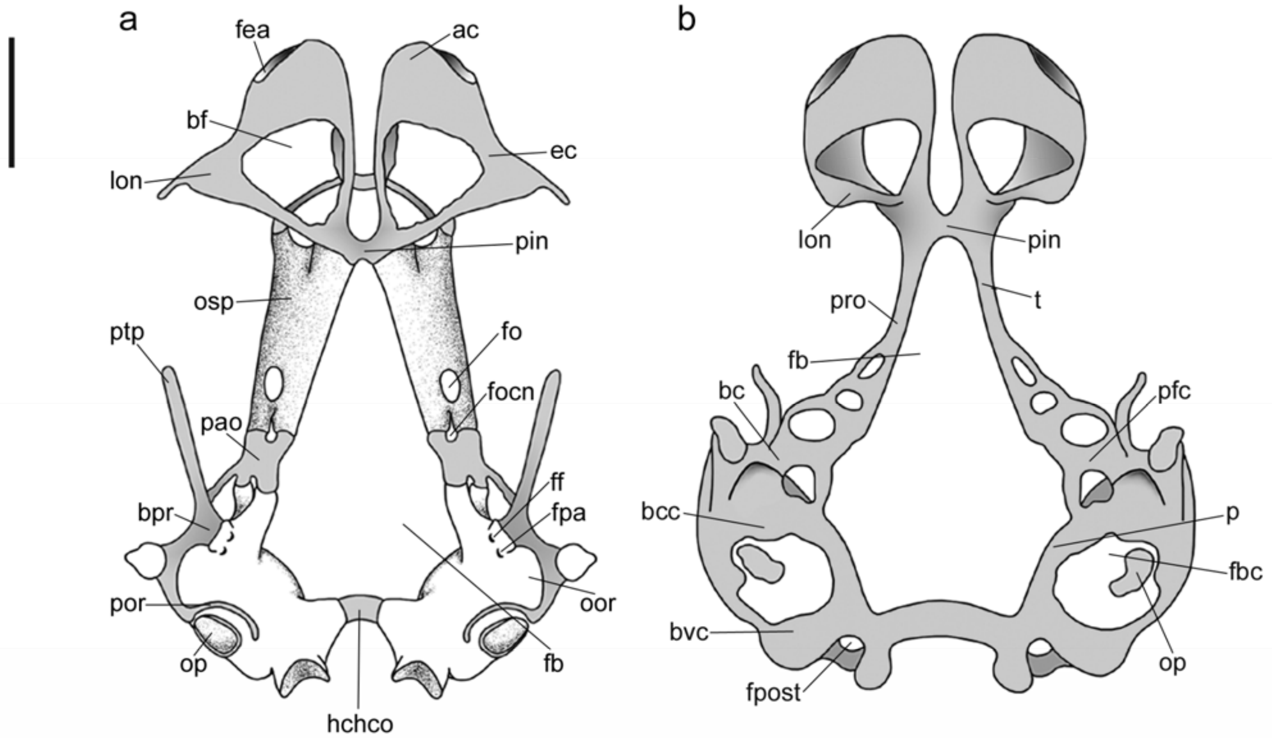

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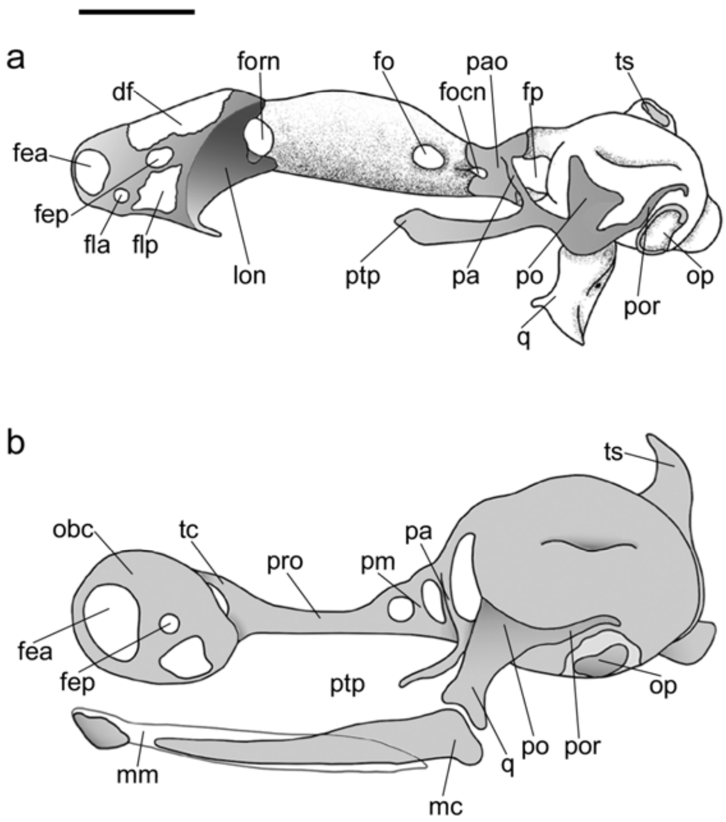
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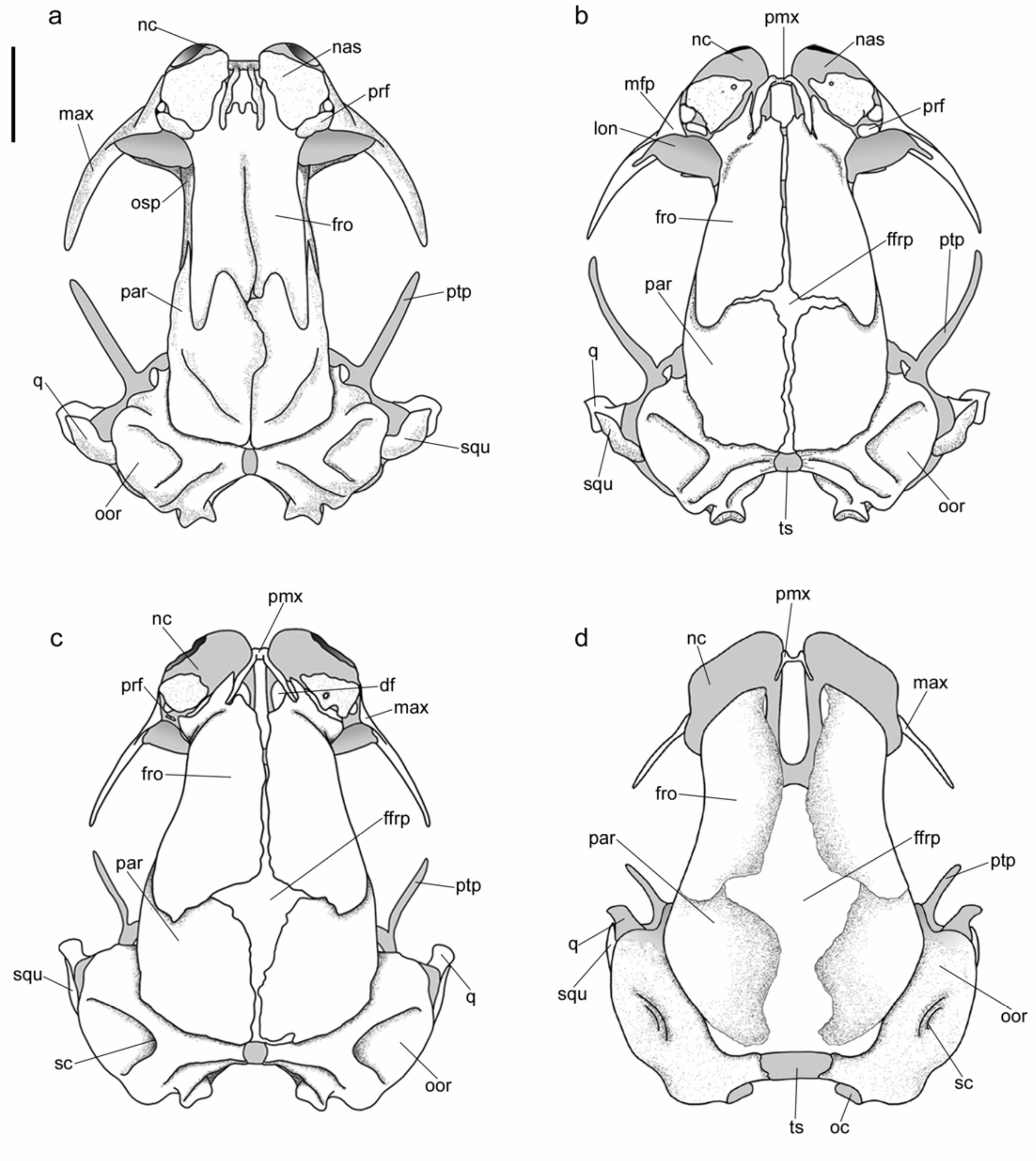
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Figure 5

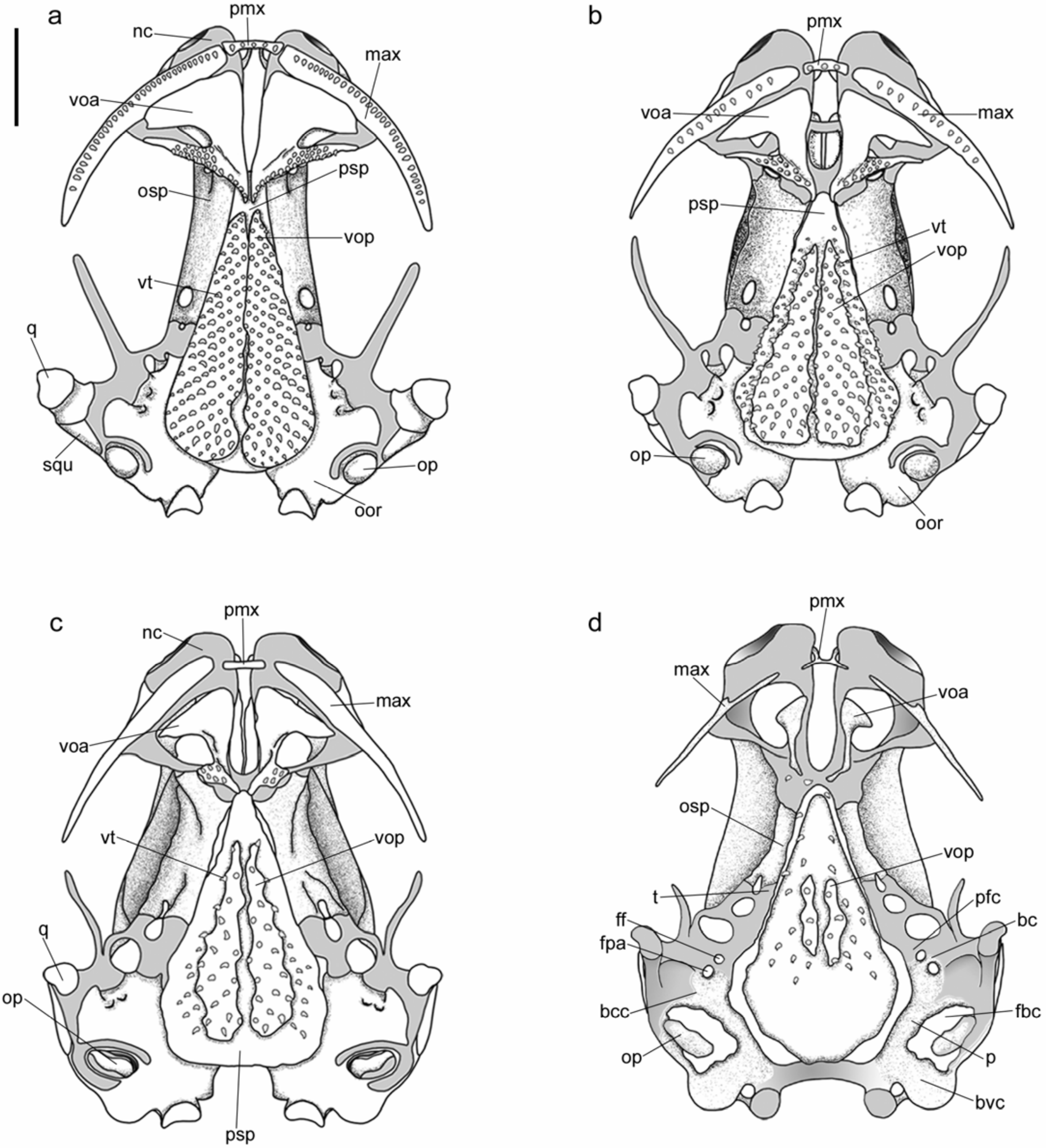
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Figure 6

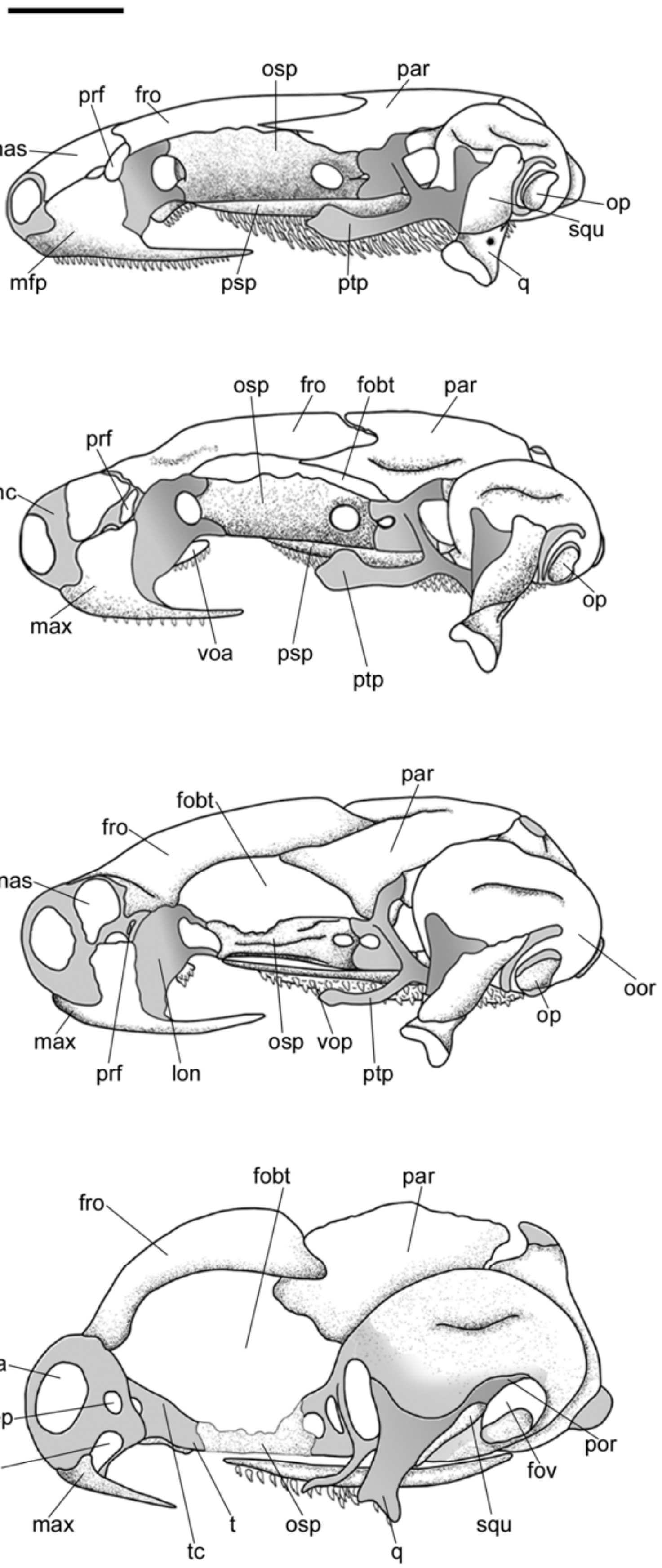
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Figure 7

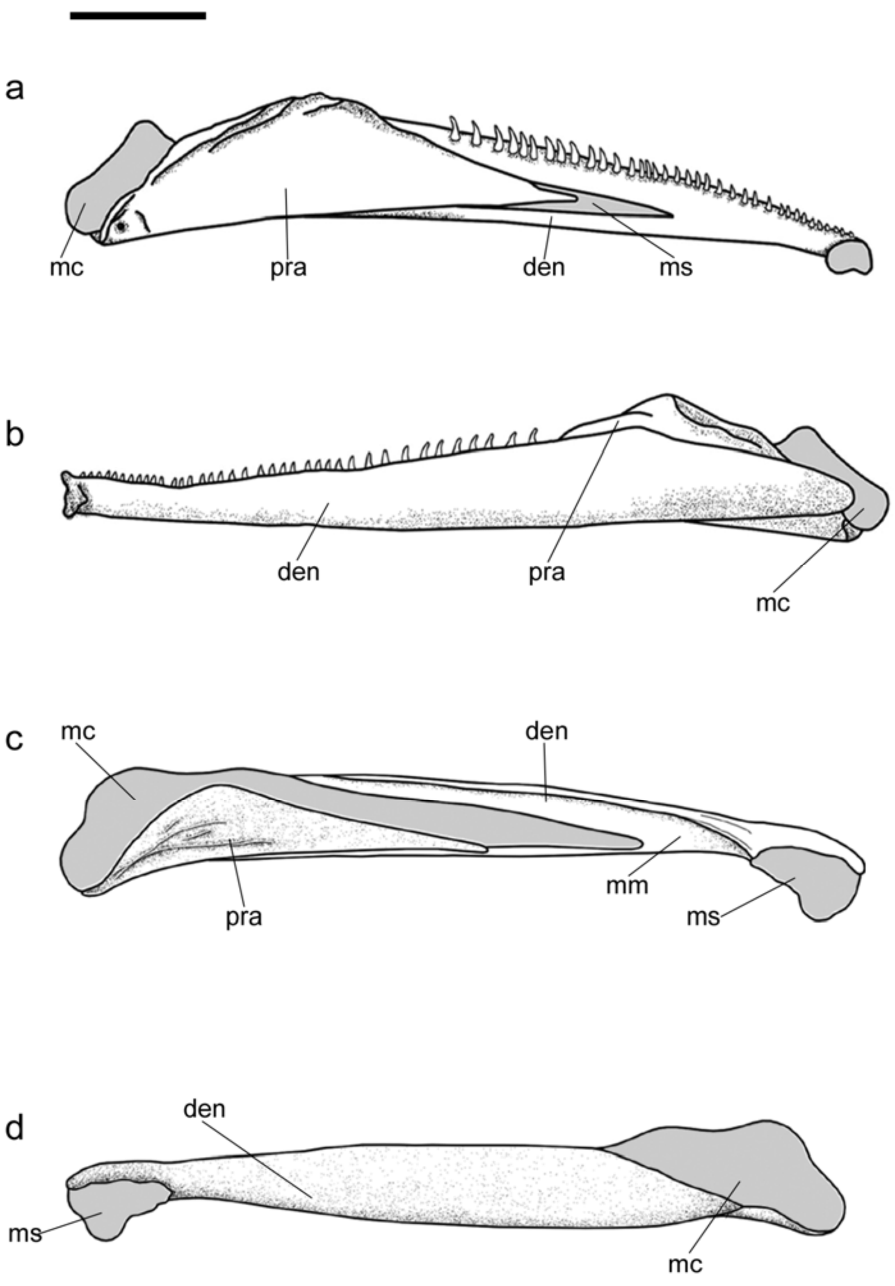

Figure 8