EMBRYONIC DEVELOPMENT OF THE SKULL OF THE ANDEAN LIZARD *Ptychoglossus bicolor* (SQUAMATA: GYMNOPHTHALMIDAE)

CARLOS ANDRÉS HERNÁNDEZ JAIMES

UNIVERSIDAD INDUSTRIAL DE SANTANDER
FACULTAD DE CIENCIAS
ESCUELA DE BIOLOGÍA
BUCARAMANGA
2012

EMBRYONIC DEVELOPMENT OF THE SKULL OF THE ANDEAN LIZARD *Ptychoglossus bicolor* (SQUAMATA: GYMNOPHTHALMIDAE)

CARLOS ANDRÉS HERNÁNDEZ JAIMES

Trabajo de Grado para optar por el título de
Biólogo

Directora
Ph.D. Martha Patricia Ramírez Pinilla

Co-Directora
Ph.D. Adriana Jerez

UNIVERSIDAD INDUSTRIAL DE SANTANDER
FACULTAD DE CIENCIAS
ESCUELA DE BIOLOGÍA
BUCARAMANGA
2012

A mi familia por su apoyo incondicional

AGRADECIMIENTOS

Agradecemos a Vivian Páez,y Juan M Daza de la Universidad de Antioquia, y Martha Calderón de la Universidad Nacional de Colombia, por el préstamo de los especímenes de gimnoftálmidos. De igual forma agradecemos a Francisca Leal y Oscar Tarazona quienes realizaron valiosas sugerencias y comentarios sobre el manuscrito. De igual forma presentamos nuestros agradecimientos a Leonardo Meza, Eliana Ramos, Fernando Cediel y Julián Lozano por su asistencia en la colecta de embriones de *Ptychoglossus*. El permiso de colecta fue tramitado con la Corporación para la Defensa de la Meseta de Bucaramanga (CDMB).

CONTENIDO

pág.

LISTA DE TABLAS

Pág.

LISTA DE FIGURAS

Pág.

RESUMEN

TITULO: DESARROLLO EMBRIONARIO DEL CRÁNEO DEL LAGARTO NEOTROPICAL *Ptychoglossus bicolor* (SQUAMATA: GYMNOPHTHALMIDAE)*

AUTORES: Carlos Andrés Hernández Jaimes, Adriana Jerez, Martha Patricia Ramírez Pinilla**

PALABRAS CLAVES: Desarrollo embrionario; condrocráneo; cráneo; Gymnophthalmidae; osificación

CONTENIDO: Las descripciones morfológicas del desarrollo embrionario del cráneo en Gymnophthalmidae son inexistentes. Adicionalmente, se conoce muy poco acerca del condrocráneo complete de la familia. En este trabajo se aborda el desarrollo del cráneo del lagarto Neotropical *Ptychoglossus bicolor* junto con un análisis del condrocráneo de otras especies de gimnoftálmidos y el teiido *Cnemidophorus lemniscatus*. La condrogénesis del cráneo comienza en el estado 31 con la condensación temprana de la región orbitotemporal, viscerocráneo, y las condensaciones precondrogénicas del septum nasal y cartilago parietotectal. La osificación del cráneo empieza en el estado 35 con algunos elementos del dermatocráneo (pterigoides, prefrontal, maxilar y yugal). Luego, en el estado 40, todos los elementos dermales restantes han comenzado su osificación. El orbitoesfenoides es el último hueso chondral en comenzar la osificación y se encuentra completamente formado en el neonate, junto con el resto del cráneo. En terminus generales, el condrocráneo de los Gymnophthalmidae se asemeja a la condición en *C. lemniscatus* así como otras especies de lagartos. Sin embargo, algunas catacterísticas de la cápsula nasal no fueron halladas en la literature como por ejemplo, el proceso rostral del planum antorbitale. Por otro lado, el patron de desarrollo del condrocráneo de *P. bicolor* difiere en algunos aspectos con el patrón descrito para otras especies de reptiles estudiadas hasta ahora como el Desarrollo d elos procesos basipterigoideos; por lo tanto, el eesarrollo embrionario del cráneo de Gymnophthalmidae merece mayor atención.

---

*Proyecto de Grado.

**Facultad de Ciencias. Escuela de Biología. Directora: Martha Patricia Ramírez Pinilla. Codirectora: Adriana Jerez.

ABSTRACT

TITLE: DESARROLLO EMBRIONARIO DEL CRÁNEO DEL LAGARTO NEOTROPICAL *Ptychoglossus bicolor* (SQUAMATA: GYMNOPHTHALMIDAE)*

AUTHORS: Carlos Andrés Hernández Jaimes, Adriana Jerez, Martha Patricia Ramírez Pinilla**

KEYWORDS: Embryonic development; chondrocranium; skull; Gymnophthalmidae; ossification

CONTENT: Complete morphological descriptions of the embryonic skull development within Gymnophthalmidae are nonexistent. Moreover, very little is known about the fully formed chondrocranium of the family. Hereby, the development of the skull of the Neotropical lizard *Ptychoglossus bicolor* is addressed along with an examination of the chondrocranium of other gymnophthalmid taxa and the teiid *Cnemidophorus lemniscatus*. Cranial chondrification starts at stage 31 with early condensations from the orbitotemporal region, viscerocranium, and the prechondrogenic condensations of the nasal septum and parietotectal cartilage. Ossification of the skull begins at stage 35 with elements of the dermatocranium (pterygoid, prefrontal, maxillary and jugal). Then, at stage 40, all of the remaining dermal elements appear ossified. The orbitosphenoid is the last chondral bone to ossify and is completely formed in the neonate, along with the rest of the skull. In general terms, the gymnophthalmid chondrocranium resembles the condition in *C. lemniscatus* and other lizard species. However, some features of the nasal capsule were absent in the literature as for instance, the rostral process of the planum antorbital. Furthermore, the pattern of development of the chondrocranium of *P. bicolor* differs in some respects to the pattern described for other reptilian species studied so far like the development of the basipterygoid processes; therefore, the embryonic development of the skull within Gymnophthalmidae deserve further attention.

---

*Proyecto de Grado.

**Facultad de Ciencias. Escuela de Biología. Directora: Martha Patricia Ramírez Pinilla. Codirectora: Adriana Jerez.

INTRODUCTION

The Gymnophthalmidae is composed of a morphologically and ecologically diverse group of lizards (Pianka & Vitt, 2003; Donnelly et al., 2006) comprising nearly 223 species and 45 genera (Uetz et al., 2011). Nonetheless, most of the biological information available for most of the species within this group is restricted to taxonomic descriptions (e.g., Rodrigues et al., 2007; Peloso & Avila-Pires, 2010; Sánchez-Pacheco, 2010), geographic distributions (e.g., de Moura et al., 2010; de Freitas et al., 2011), reproduction (e.g., Vitt, 1982; Ramos-Pallares et al., 2010), ecology (e.g., Vitt & Avila-Pires, 1998; Anaya-Rojas et al., 2010), evolution (Barros et al., 2011) and phylogenetic arrangements (Hoyos, 1998; Pellegrino et al., 2001; Castoe et al., 2004); therefore, detailed studies regarding the embryonic development of the skull are nonexistent. Previous works about the skull anatomy in this family emphasize in the structure of the adult dermatocranium (e.g., Montero et al., 2002; Bell et al., 2003; Tarazona et al., 2008; Guerra & Montero, 2009; Roscito & Rodrigues, 2010). Additionally, the scarce studies on the development of the skull within Gymnophthalmidae only involve a revision of postnatal stages in *Neusticurus ecpleopus* (Bell et al., 2003) and *Bachia bicolor* (Tarazona et al., 2008). However, a few recent contributions to the subject include a description of the orbitotemporal region of the chondrocranium in adult and late embryonic stages of the fossorial and burrowing lizard *Bachia bicolor* (Tarazona & Ramírez-Pinilla, 2008), and a significant account of the chondrocranium in adult stages of *Vanzosaura rubricauda* (Guerra & Montero, 2009), the latter being the first and only description of the entire chondrocranium of a gymnophthalmid lizard.

The most recent phylogenetic hypothesis pertaining to the Gymnophthalmidae places *Ptychoglossus* along with *Alopoglossus* in the basal clade (subfamily) Alopoglossinae (Castoe et al., 2004), a group of species with semifossorial habits and a lacertiform bodyplan. In general, the available phylogenetic studies rely on molecular data (Pellegrino et al., 2001; Castoe et al., 2004) and morphological characters for building tree topologies (Hoyos, 1998; Montero et al., 2002; Rodrigues et al., 2005). Because of its position within the gymnophthalmid phylogeny and the great ecological and morphological diversity of the family (from lacertiform to serpentiform bauplans), the study of the anatomy and development of the skull of *Ptychoglossus bicolor* can provide information about the general features of the gymnophthalmid chondrocranium in contrast to serpentiform gymnophtalmids.

The main goal of this paper is to describe the gross anatomy and development of the embryonic skull of *Ptychoglossus bicolor*. The neonate chondrocranium of *P. bicolor* is briefly examined and compared with the chondrocranium of other gymnophthalmid lizards. This information can provide an insight into the morphological diversification of the group, which can as well be relevant for future systematic and evolutionary works interested in the interspecies relationships among these taxa. Moreover, anatomical studies based upon embryonic series provide information regarding the developmental sequence of appearance of individual structures, which in turn, provide a basis for studies in the heterochronic changes among different taxa.

6. MATERIALS AND METHODS

The embryonic material was collected throughout the year, from a coffee shade plantation at La Hacienda El Roble from the municipality of Los Santos (Department of Santander; 06°52’N; 73°03’W), at an altitude of 1700m, on the western slopes of the Cordillera Oriental of the Colombian Andes. The embryos were either fixed on 10% neutralized formalin or Bouin’s fixative for the visualization of dermal and cartilaginous structures, respectively, afterwards, they were classified according to the staging table from Defaure & Hubert “D&H” (1961). Descriptions included 23 embryos from stages 31, 32-33, 33-34, 35, 39, 39-40, 40 D&H, and 4 hatchlings; these were processed by clearing and double staining of cartilage and bone following Wassersug (1979) and examined through a Nikon 20X-dissecting microscope. For each embryonic stage we only mentioned major morphological changes in relation to previous stages. Anatomical descriptions followed the nomenclature from Bellairs and Kamal (1981) for the chondrocranium and Bell et al. (2003) for the dermal structures. Collected specimens were deposited in the Colección Herpetológica of the Museo de Historia Natural, Universidad Industrial de Santander (UIS-R).

The chondrocranium of *P. bicolor* neonates was compared with that of other eighteen-gymnophthalmid species which were classified into four subfamilies according to the phylogenetic classification provided by Castoe et al. (2004) (Alopoglossinae, Cercosaurinae, Ecpleopinae and Gymnophthalminae) and with *Cnemidophorus lemniscatus* (Teiidae), to obtain a general view of the gymnophthalmid chondrocranium in contrast with the chondrocranium of Teiidae, its closest phylogenetic relative. We organized the data and compiled it in table 1. The specimens were obtained for loan from the Museo de Herpetología of the Universidad de Antioquia (MHUA), the Colección de Reptiles of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN), and the Colección Herpetológica of the Universidad Industrial de Santander. Photographs were taken with a Canon PowerShot A630 and the schemes were drawn using CorelDraw X5 and Adobe Illustrator CS5.

7. RESULTS

Descriptions follow a proximal to distal direction dividing the chondrocranium into three regions: an anterior ethmoid region, a medial orbitotemporal region, and a distal occipital region.

7.1 SKULL DEVELOPMENT

Chondrification of the skull starts with the early condensations of elements from the orbitotemporal region, viscerocranium, and the prechondrogenic condensations of the nasal septum and parietotectal cartilage. Later, in the neonate, the chondrocranium is fully formed. Cranial ossification begins at stage IV (D&H 35) with the formation of the prefrontal, maxillary, jugal and pterygoid bones. Subsequently, at stage VII (D&H 40), all of the remaining dermal elements appear ossified.

7.1.1 STAGE I (D&H 31, FIG. 1, A, B).

In this stage, the ethmoid region of the chondrocranium consists of a very thin prechondrogenic condensation of the nasal septum and the rudiment of the developing parietotectal cartilage enclosing most of what will become the *fenestra superior*; we were unable to identify these prechondrogenic structures in the following two stages.

Posteriorly, and continuous with the prechondrogenic nasal septum, the *trabeculae cranii* are merged together (*trabecula communis*) between the orbits referred as the tropitrabic (tropibasic) condition, consistent with the situation of most reptiles. In dorsal view, the anterior region of the *trabecula cranii* appears as a broad cartilaginous *plate* (trabecular plate). Posteriorly, the *trabecula cranii* diverge freely into two *trabeculae*. Moreover, the *pila metoptica* is present at this early stage of development on each side of the *trabecula cranii*, yet both are separated from each other.

In the occipital region, the skull floor consists of a slim and concave basal plate and, a separate long and narrow transversal bar in front of the basal plate, just behind and above the *trabecula cranii* corresponding to the acrochordal cartilage (posterior orbital cartilage). In the basal plate, the basicranial fenestra is underway; only the posterior and lateral margins are present. In the acrochordal cartilage, the lateral edges are rostrally oriented, parallel to the *trabecula cranii*. Also, the notochord appears embedded in the medial aspect of the basal plate, projecting rostrally into the basicranial fenestra without contacting the acrochordal cartilage. Distally, the basal plate is continuous with the developing occipital arch; also in this region the first of the three openings for the roots of the hypoglossal nerves (i.e. the first hypoglossal foramen) is open at the back of the basal plate, on each side of the notochord. Laterally, the sidewall of the skull is partly formed by the early condensation of the cochlear portion of the auditory (otic) capsule, which chondrifies independently from the basal plate and in this stage remains separate from one another. Also laterally, the small spherical rudiment of the *columella auris* rests just below the developing otic capsule, on each side of the skull.

Considering the elements of the mandibular arch: Meckel’s cartilage and the palatoquadrate (pterygoquadrate) complex are present. Although, the pterygoquadrate (or intermediate part) that connect the quadrate with the rest of the complex is regressed and so the quadrate cartilage is separated. Therefore, at this stage the palatoquadrate complex comprises only the ascending process dorsally, a reduced pterygoid process rostrally, and posteriorly what appears to be the remains of the intermediate part.

7.1.2 STAGE II (D&H 32-33, FIG. 1, C, D).

In the orbitotemporal region, chondrification of the *planum supraseptale* is now underway, projecting dorsally from the lateral flanks of the anterior aspect of the *trabecula communis* as two separate narrow cartilaginous bars, one on each side of the skull. Also, the *trabecula communis* has further elongated and now appears narrower. In regard to the pterygoquadrate complex, the processus ascendens is now more prominent while the pterygoid process and the remains of the intermediate part have further shortened. Furthermore, the basal plate has partly fused rostrally with the medial portion of the acrochordal cartilage thus closing the anterior border of the basicranial fenestra.

Additionally, the lateral edges of the acrochordal cartilage remain rostrally oriented in an almost vertical position forming the basipterygoid processes*.* Also in this stage, an extra pair of short horizontal processes has appeared below the basipterygoid processes also projecting forward so that the anterior tips lie just behind the hind end of each *trabecula,* namely the trabecular processes*;* these trabecular processes must not be confound with the basipterygoid or basitrabecular processes*.* The cochlear portion of the auditory capsule has expanded and in this stage appears fused with the anterior lateral margins of the *basal plate* at the basicapsular commissure but leaving a gap behind known as the *fissura metotica*.

7.1.3 STAGE III (D&H 33-34, FIG. 2).

As development proceeds, the interorbital septum appears continuous with the *trabecula communis* and extends into the ethmoid region of the chondrocranium, thus forming the rudiment of the nasal septum, which becomes high by means of a prechondrogenic dorsal expansion. Additionally, the two halves of the developing *planum supraseptale* resemble a slim plate and persist as separate structures. Also in this stage, a pair of arched slender cartilaginous rods corresponding to the rudiment of the *sphenethmoid commissures* is continuous with the rostral aspect of each half of the *planum supraseptale* while anteriorly they end freely. The dorsal aspect of the interorbital septum has increased in height now forming a thin prechondrogenic wall in the midline of the skull, which is evident in dorsal view between the two halves of the *planum supraseptale*. Further behind, the rudiments of the *taenia marginalis* and *pila accesoria* appear separated from every element of the chondrocranium. In the occipital region, the acrochordal cartilage appears completely fused with the basal plate. Furthermore, the medial portion of the acrochordal cartilage has regressed a little bit due to cartilage resorption so that the basicranial fenestra is open again anteriorly in the midline. Also, in the rostral aspect of the basal plate (previously acrochordal cartilage), the foramina for the abducens nerve are evident. The trabecular processes have extended rostrally, and the lateral projections of the acrochordal cartilage form the rudiments of the basipterygoid processes. In the occipital region of the basal plate, the three hypoglossal foramina are now open. In the developing auditory capsule the foramen for the facial nerve is open on both sides and is evident in lateral view. The processus ascendens has further increased in size, and now the anterior and posterior processes from the pterygoquadrate complex are not evident anymore. Meckel's cartilage has extended anteriorly and at this time, the articular process projects dorsally from the posterior region.

7.1.4 STAGE IV (D&H 35, FIG. 3).

In this stage, the elements of the chondrocranium belonging to the orbitotemporal and occipital regions are more developed while the structures of the ethmoid or nasal region are still very rudimentary. The nasal capsule is underway showing a large *fenestra superior* surrounded by the early parietotectal and paranasal cartilages, which are continuous with the nasal septum forming part of the roof and lateral wall, respectively. The *foramen epiphaniale* is open behind the *fenestra superior* and lateral to this foramen, the paranasal cartilage extends ventrally to form the anterior contour of the *fenestra lateralis*. Anteriorly, the dorsal extension of the nasal septum has now chondrified, projecting towards the roof of the capsule forming a consistent wall, which contacts the parietotectal cartilage in the region between the paired *fenestra superior*. Lateral to the nasal septum, the rudiments of the paired *lamina transversalis anterior* and *planum antorbitale* appear as two slender cartilaginous condensations. The lamina transversalis anterior lies at the floor of the nasal capsule, it is continuous with the lateral wall of the capsule and is separated from the nasal septum. Ventrally and medially the *lamina transversalis anterior* shows the cartilage of Jacobson's organ densely chondrified. On the other hand, the *planum antorbitale* appears as a short independent condensation in the back of the nasal capsule. Posteriorly, the nasal capsule contacts the anterior portion of the *sphenethmoid commissures* forming a large *fenestra olfactoria* for the olfactory and vomeronasal nerves.

In the orbitotemporal region, the *taenia marginalis* contacts the dorsal surface of the otic capsule posteriorly, the dorsal aspect of the *planum supraseptale* anteriorly and the *pila accesoria* ventrally. Also, the *taenia medialis* is continuous with the *pila accesoria*, the *pila metoptica* and the posterior border of the *planum supraseptale*. Moreover, the *pila metoptica* has joined its counterpart forming the *subiculum infundibuli*, which contacts the dorsal margin of the trabecula communis by means of the *cartilago hypochiasmatica*. The *planum supraseptale* is completely formed and subtlety contacts the interorbital septum rostrally and caudally, leaving a large space between the dorsal margin of the interorbital septum and the ventral surface of the *planum supraseptale*, namely the fenestra in interorbital septum. Posteriorly, the trabeculae are complete, contacting the rostral aspect of the basal plate, specifically the trabecular processes of the acrochordal cartilage. Furthermore, the pituitary fossa (hypophyseal fenestra) is now complete, formed anteriorly and laterally by the trabeculae and posteriorly by the rostral aspect of the basal plate.

The roof of the occipital region of the cartilaginous skull shows a closed occipital arch forming the *tectum posterius* and the otic capsules fused together dorsally forming the *tectum synoticum*. The *tectum posterius* projects forward and contacts the *tectum synoticum* anteriorly forming a single *tectum* (*tectum synoticum plus posterius*), from which a cartilaginous *processus anterior tecti* (ascending process) projects rostrally. The quadrate is complete and the *extracolumella* is now formed. Ventrally, the basicranial fenestra has become reduced and split into two by chondrification from the medial region of the basal plate.

7.1.5 STAGE V (D&H 39, FIG. 4)

In the nasal capsule, the parietotectal cartilage has broadened, extending further over the nasal septum. In the sidewall, the nasal concha is completely formed by the paranasal cartilage and opens to the outside through the aditus concha, which abuts with the lateral aspect of the *lamina transversalis anterior*. Also, on the lateral aspects of the paranasal cartilage the *processus alaris superior* is well formed. Posterolaterally, the *fenestra lateralis* is completely formed. The *planum antorbitale* is continuous medially with the paraseptal cartilage and laterally it forms the posterior maxillary process. Also, the planum antorbital now forms a small wall in the back of the nasal capsule, and contacts the posterior and lateral margins of the nasal concha. Mesially, the *planum antorbitale* has a short posterior and rostral processes.

In the orbitotemporal region, the ascending process of the pterygoquadrate is quite long now extending dorsally near the *taenia marginalis*. In addition, the basipterygoid processes have increased in length.

Posteriorly, the rostral aspect of the basal plate has now ossified into *crista sellaris* including the trabecular processes of the acrochordal cartilage. The otic capsule, occipital arch and basal plate have begun to ossify forming the prootic, supraoccipital, exoccipital, basioccipital and basisphenoid, respectively, which are joined together and with the *crista sellaris* by synchondrosis. The intercalary cartilage appears as a small structure whose apical tip lies dorsal to the *extracolumella* and is joined at its base to the *crista parotica*.

7.1.6 STAGE VI (D&H 39-40, FIG. 5)

Regarding the chondrocranium, the most important events evident at this stage are restricted to ossification events; everything else resembles the previous stage. In the orbitotemporal region, the ascending process has ossified into the epipterygoid bone with its epiphyses still cartilaginous. Also, the basipterygoid processes appear ossified, except for their articular edges. Moreover, the quadrate appears partly ossified medially and Meckel’s cartilage has become invested by the membrane bone of the lower jaw (mandible).

7.1.7 STAGE VII (D&H 40, FIG. 6)

In this stage, the major changes correspond to the development of the orbitosphenoid, which begins to form by ossification of the anterior part of the *pila metoptica* near the region of junction between this cartilage, the *taenia medialis* and the *pila accesoria*, yet it is not fully developed. Also, the posterior bases of the bifurcated *trabecula* ossify forming the trabecular crest.

7.1.8 NEONATE (FIG. 7)

This developmental stage corresponds with the fully formed chondrocranium of *Ptychoglossus bicolor*.

7.1.8.1 NASAL CAPSULE

The parietotectal cartilage roofs the elements of the nasal capsule; it is continuous medially with the nasal septum and laterally with the paranasal cartilage. Dorsally, a large rostral fenestra superior and a small posterior *foramen epiphaniale* are present over the parietotectal cartilage on each side. The sidewall of the *capsule* is pierced on both flanks of the skull by two large openings, which lie on opposite extremes, an anterior *fenestra narina* and a posterior *fenestra lateralis*. The anterior region of the *fenestra narina* shows the *processus alaris inferior* and *processus alaris superior*. The nasal capsule is divided medially by a high slender nasal septum, which is continuous posteriorly with the interorbital septum. The backside of the nasal capsule consists of the *planum antorbitale*, which forms a very thin and low cartilaginous wall. Additionally, the middle portion of the *planum antorbitale* bears two paired processes on its base: one short posterior process, and one long and slender anterior process; the latter projects rostrally in an oblique direction until they contact the dorsal aspect of the vomer. Medially, the *planum antorbitale* is continuous with the paired paraseptal cartilages, which run anteriorly and parallel to the nasal septum, bearing one short rostral process at the anterior tip. An additional process namely the secondary lateral process of paraseptal cartilage was also found connecting the paraseptal cartilage with the rostral process of the *planum antorbitale* thus forming a fenestra; nevertheless, this condition was only documented in the right side of the skull of some embryos and is depicted as such in Fig. 7. Behind the *planum antorbitale*, the paired, narrow sphenethmoid commissures outline a large *fenestra olfactoria*. On each side, the floor of the *nasal capsule* consists of the *lamina transversalis anterior*, which is continuous with the anterior sidewall of the paranasal cartilage, forming a complete cartilaginous ring (*zona annularis*). Also in the *lamina transversalis anterior*, the cartilage of Jacobson's organ appears medially as well as the ectochoanal cartilage, which looks as a large cartilaginous process projecting posteriorly.

7.1.8.2 ORBITOTEMPORAL REGION

The orbitotemporal region of *Ptychoglossus bicolor* consists of the *planum supraseptale* and a scaffolding of narrow cartilaginous bars. The *planum supraseptale* bends in the midline dividing the structure into two distinct regions: (i) an anterior cylindrical and slender portion, which contacts the interorbital septum at the point where the paired sphenethmoid commissures converge; and (ii) a posterior broad shield-shaped region, which contacts the interorbital septum and is posteriorly continuous with the *taenia medialis*. A short rostrally-oriented lateral process arises from both sides of the *planum supraseptale*, namely the rostral process of the *planum supraseptale*. The long *taenia marginalis* contacts the roof of the auditory capsule posteriorly and the lateral margin of the *planum* *supraseptale* anteriorly. The interorbital septum is continuous anteriorly with the nasal septum and posteriorly with the *trabecula communis*. In lateral view, the interorbital septum looks like a thin, high longitudinal wall, pierced by three membrane-filled fenestrae of different size. Moreover, the orbitosphenoid is now a tripartite element, formed by endochondral ossification where the *pila accesoria*, *taenia medialis* and *pila metoptica* converge. The paired *pila metoptica* contact each other medially forming the *subiculum infundibuli*, which joins the interorbital septum by means of the *cartilago hypochiasmatica*. Posteriorly, the two trabeculae contact the ossified trabecular processes at the rostral aspect of the basal plate delineating the pituitary fossa. The epipterygoid appears almost fully ossified, with the epiphyses still cartilaginous.

7.1.8.3 OTICO-OCCIPITAL REGION

The otico-occipital region of *Ptychoglossus bicolor* is almost entirely ossified in the neonate, and the prootic, supraoccipital, exoccipital, basioccipital and basisphenoid, are present; however, some areas remain cartilaginous and a portion of the basicranial fenestra persists. Posteriorly, the roof of the occipital region derives from the fusion between the *tectum posterius* and the *tectum synoticum* of the *otic capsule*. Therefore, a single *tectum* (*tectum synoticum plus posterius*) is formed outlining the dorsal aspect of the *foramen magnum*; this *tectum* is also ossified at this stage forming the supraoccipital. The *anterior process of tectum* (*processus anterior tecti*) rests in the anteriormost margin of the *tectum* and extends rostrally. The otic capsule is ossified forming the prootic, which is joined ventrally by synchondrosis to the exoccipital and basioccipital, and thus the *fissura metotica* is completely closed. The cartilaginous footplate of the *columella auris* rests over the *fenestra ovalis*, which lies on the sidewall of the *otic* *capsule*. Ventrally, the basipterygoid process, which remains cartilaginous at its articular region, rises at each side of the basisphenoid.

7.2 OSSIFICATION SEQUENCE

The sequence of ossification events is presented in table 2. Ossification starts at stage IV embryos (D&H 35) with four dermal elements: prefrontal, maxillary, jugal and pterygoid. In more advanced stages, the elements of the braincase form by endochondral ossification of the prootic, supraoccipital, exoccipital, basioccipital and basisphenoid, all of which are joined by synchondrosis. At stage VI (D&H 39-40) the mandible starts to ossify. The orbitosphenoid and lacrimal are respectively, the last chondral and dermal bones to start the ossification process. Later, in the neonate dermatocranium, all of the elements show distinct degrees of ossification, but most are almost completely formed (Fig. 8). The frontal and parietal bones are not yet fully differentiated (i.e., only the margins show some ossification); therefore, a large frontoparietal fenestra (frontoparietal fontanelle) remains opened.

8. DISCUSSION

8.1 DEVELOPMENT OF THE CHONDROCRANIUM OF *Ptychoglossus bicolor*

The most relevant features concerning the embryonic development of the chondrocranium of *Ptychoglossus bicolor* are the following: 1. The development of the basipterygoid processes from the acrochordal cartilage. 2. The formation and ossification of the trabecular processes from the acrochordal cartilage. 3.

Concomitant development of the viscerocranium and chondrocranium. 4. The division between the quadrate and the palatoquadrate complex from stage I. 5. The tripartite architecture of the orbitosphenoid and its development during late embryonic stages. 6. The independent origin of the cochlear part of the otic capsule.

Commonly in lizards, the basipterygoid processes originate either from the pterygoid process of the pterygoquadrate complex as in *Trachylepis* (*Mabuya*) *capensis* (Skinner, 1973), or from the posterior ends of the trabeculae, where they join the basal plate as in *Lacerta agilis* (de Beer, 1930) and *Acanthodactylus boskiana* (Kamal & Abdeen, 1972). Nonetheless, In *Ptychoglossus bicolor* the basipterygoid processes have a different origin; they are formed from the rostrally oriented lateral edges of the acrochordal cartilage (posterior orbital cartilage), these processes are present as rudiments before the acrochordal cartilage fuses with the rostral aspect of the basal plate. Additionally, the acrochordal cartilage of *P. bicolor* presents another uncommon feature, which consists in the development of short, paired trabecular processes during early stages; these are situated below each of the basipterygoid processes and appear after the acrochordal cartilage has fused with the basal plate. These trabecular processes ossify along with the *crista sellaris* and later they fuse to the posterior ends of the *trabeculae*. We were unable to find these trabecular processes elsewhere in the literature.

Considering the evidence found in the earliest embryonic stage analyzed, we can include *Ptychoglossus bicolor* within those lizards in which all of the elements of the viscerocranium develop concomitantly with the neurocranium resembling the condition at stage I of the sea turtle *Caretta caretta*, where the palatoquadrate complex, columella auris and Meckel’s cartilage are already present (Kuratani, 1999). In contrast, in some lizards only two of the components of the mandibular arch (i.e. Meckel’s cartilage and pterygoquadrate complex) are present at stage I concomitantly with the neurocranium (e.g., *Chalcides ocellatus*, El-Toubi & Kamal, 1959; *Acanthodactylus boskiana*, Kamal & Abdeen, 1972; *Trachylepis capensis*, Skinner, 1973), whereas in some other lizard embryos Meckel's cartilage chondrifies much earlier than the neurocranium as in *Lacerta* (*Zootoca*) *vivipara* (de Beer, 1937) and in *Calotes versicolor* (Ramaswami, 1946).

Regarding the palatoquadrate complex, in *Ptychoglossus bicolor* the quadrate is separated from the complex at the earliest stage analyzed and, the intermediate element, normally connecting the quadrate cartilage with the rest of the complex is greatly reduced. This situation is similar to the one observed at stage 33 D&H of *Mabuya* sp (Jerez, 2007) and at stage III of *Chalcides ocellatus* (El-Toubi & Kamal, 1959) in which the quadrate is first seen as an element isolated from any other cartilage in the chondrocranium, except for the fact that at stage IV of *Chalcides ocellatus* the *processus ascendens* becomes attached to the quadrate and then both become separated again at stage V, whereas in *P. bicolor* this connection is never established at any of the stages analyzed. In contrast, in other lizard taxa (e.g., *Ptyodactylus hasselquistii*, El-Toubi and Kamal, 1961; *Acanthodactylus boskiana* Kamal & Abdeen, 1972; *Trachylepis capensis*, Skinner, 1973) the quadrate is continuous with the pterygoquadrate complex via the intermediate element from the first stages analyzed.

The orbitosphenoid of *Ptychoglossus bicolor* is formed by endochondral ossification and begins to ossify during late embryonic development (Stage VII: D&H 40); starting with the ossification of the anterior surface of the *pila metoptica* and then extending into a portion of the *taenia medialis* and *pila accesoria*, forming a small triradiate bone. The orbitosphenoid of *Mabuya* sp. (Jerez, 2007) and *Bachia bicolor* also appears at late embryonic stages, while the orbitosphenoid of *Trachylepis capensis* ossifies in adult stages (Skinner, 1973). In contrast, in the gymnophthalmid *Bachia bicolor*, the orbitosphenoid is formed both by chondral and membranous contributions (Tarazona & Ramírez-Pinilla, 2008) and is markedly broader than that of *P. bicolor* and all other gymnophtalmids. The broad orbitosphenoid of *B. bicolor* resembles structurally and ontogenetically the orbitosphenoid of amphisbaenians and thus it has been hypothesized that the morphology and origin of this bone is related to fossorial habits (Tarazona & Ramírez-Pinilla, 2008); nevertheless, the orbitosphenoid of other snakelike fossorial gymnophtalmids such as *Scriptosaura catimbau* and *Nothobachia ablephara* (Roscito & Rodrigues, 2010) resembles that in *P. bicolor*.

There is significant variation concerning the orbitotemporal cartilages involved in the development of the orbitosphenoid; for instance, in most lizards, the orbitosphenoid is formed by ossification of the *pila metoptica* (de Beer, 1937) as occurs in *Trachylepis capensis* (Skinner, 1973), *Liolaemus scapularis* (Lobo et al., 1995), *Stenocercus guentheri* (Torres-Carvajal, 2003) and *Mabuya* sp. (Jerez, 2007) among others; nonetheless, a different case occurs in some lizards where "parts of the *taeniae mediales*, *pila metoptica* and perhaps of adjacent regions may ossify (or at least calcify) in mature individuals to form a small orbitosphenoid" (Bellairs and Kamal, 1981, p. 23). In this sense, within the gymnophthalmid species hereby studied (table 1, traits 24, 28 & 37), most showed small orbitosphenoid ossifications extending over some portion of the *pila metoptica*, *taenia medialis* and *pila accesoria*, roughly similar to the condition in *P. bicolor* and *Cnemidophorus lemniscatus*. On the other hand, a bunch of other species showed the orbitosphenoid formed by ossification of a portion of the *pila metoptica* and *taenia medialis*. In *Vanzosaura rubricauda*, the orbitosphenoid of is formed only by the ossification of the *taenia medialis* (Guerra & Montero, 2009); nevertheless, since we only studied a few number of gymnophthalmid species, it remains unclear whether this condition in *Vanzosaura rubricauda* is common or rare among the Gymnophthalmidae. In contrast, the orbitosphenoid of *Bachia bicolor* involves the ossification of the *taenia medialis* and *pila metoptica*, as well as other 2 to 3 additional orbitotemporal cartilages hardly comparable to other orbitotemporal cartilages such as the *pila accesoria* and *pila antotica* (Tarazona & Ramírez-Pinilla, 2008).

Bellairs and Kamal (1981) suggested that, in lizards generally, the *taenia marginalis* arises from the back of the *planum supraseptale* and then elongates in a posterior direction to contact the roof of the otic capsule. On the other side, de Beer (1930) observed the *taenia marginalis* projecting rostrally from the otic capsule to the *planum supraseptale* in *Lacerta vivipara*. However, our evidence suggests that in *P. bicolor* the *taenia marginalis* originates independently near the *planum supraseptale* and then elongates posteriorly and rostrally to contact the dorsal aspect of the *otic capsule* and the *planum supraseptale*, respectively. Such condition is somehow similar to stage V of *Trachylepis capensis*, where the *taenia marginalis* is initially separated from the otic capsule and *planum supraseptale*, although it closely approaches the dorsal surface of the otic capsule at this stage. The above indicates that there is more than one pattern regarding the development of the *taenia marginalis*, and that further evidence may throw light into the more generalized pattern in lizards.

“In lizards generally, the cochlear part of the otic capsule is never separated from the basal plate” (Bellairs and Kamal, 1981, p. 75). In this sense, the chondrocranium from stage II embryos of *Acanthodactylus boskiana* (Kamal & Abdeen, 1972) and stage I embryos of the African skink *Trachylepis capensis* (Skinner, 1973) shows the basal plate and otic capsule in contact with each other via the anterior basicapsular commisure (basicochlear commisure), consistent with the common pattern in lizards. In contrast, in regard to the origin of the otic capsule in *Ptychoglossus bicolor*, we observed that the otic capsule originates independently, starting at stage I with the cochlear portion, which is formed from a chondrification center separated from the basal plate (parachordal), and appears like a small isolated cartilage near the *columella auris* on each side. It would be interesting to see if this condition is also valid for other gymnophthalmid species.

8.2 THE GYMNOPHTHALMID CHONDROCRANIUM

The more generalized gymnophthalmid chondrocranium shares many characteristics with the chondrocranium of the teiid *Cnemidophorus lemniscatus* (table 1). The following discussion summarizes a) the characteristics of the chondrocranium shared by *Ptychoglossus bicolor* with most (more than 70%) of the other gymnophthalmid species included in this study, compared to other lizard groups, and b) the most relevant features of the gymnophthalmid chondrocranium that showed variation among the taxa. When pertinent, we emphasize in the characteristics of *Ptychoglossus bicolor, Bachia bicolor*, a fossorial snakelike burrowing lizard from the subfamily Cercosaurinae; and the terrestrial *Cnemidophorus lemniscatus*, a species from the gymnophthalmid sister family Teiidae, as well as other teiids and lizards from the literature, all of which are relevant for comparative purposes.

Most of the overall features of the gymnophthalmid chondrocranium correspond with elements of the *nasal capsule*: 1. In the lateral wall of the nasal capsule, a cartilaginous invagination corresponding to the nasal concha is opened to the outside through the *aditus conchae*. 2. A long and broad ectochoanal cartilage projects from the *lamina transversalis anterior* and prolongs distally near the *planum antorbitale*. 3. A small *foramen epiphaniale* is present on each side of the nasal septum near the *aditus conchae*. 4. As in the teiids *Ameiva undulata*, *Teius teyou*, *Cnemidophorus sexlineatus* (Malan, 1946) and *Cnemidophorus lemniscatus*, the nasal septum is prolonged forwards as a rostral process which varies in size and is largest in *Bachia bicolor* (table 1). 5. The paraseptal cartilage is present running parallel to the nasal septum and extending ventrally forming a thin wall; posteriorly it is continuous with the *planum antorbitale*. In some lizard groups like *Anolis* (Polychrotidae), the paraseptal cartilage is vestigial (Bellairs & Kamal, 1981). 6. The *lamina transversalis anterior* is wide and large; it contacts the lateral wall of the nasal capsule, it appears to be in contact with the nasal septum thus forming a complete *zona annularis*. 7. The *fenestra superior* consists of a large space present in the roof of the nasal capsule. In contrast, the fenestra superior is absent in *Tupinambis* (Bellairs & Kamal, 1981) and in *C. lemniscatus*. 8. The cartilage of Jacobson's organ is well developed. 9. As in the teiids *Tupinambis* (Bellairs & Kamal, 1981) and *C. lemniscatus*, a large *fenestra lateralis* is present. 10. A paired, long, rod-like rostral process projects from the *planum antorbitale* and abuts with the dorsal aspect of the vomer ventrally. This process was found in each of the gymnophthalmid species studied and in *C. lemniscatus*, except that, in the latter, it is short and fails to reach the vomer, thus it was hereby considered incomplete. In some species (*Ptychoglossus bicolor*, *Leposoma southi* and *Tretioscincus bifasciatus*), this *process* abuts with the vomer, and additionally contacts the *paraseptal cartilage* laterally forming a fenestra; however, in *P. bicolor*, this condition was not always evident, and when it was, it was always observed only on the left side of the nasal septum. We were unable to find this *rostral process* elsewhere in the literature, and thus it deserves further attention in order to see whether this is a shared trait between Teiidae and Gymnophthalmidae. 11. Within Gymnophthalmidae, similar to *C. lemniscatus*, the size of the *fenestra olfactoria* (*advehens* and *evehens*) was generally large, consistent with the large size of the main and accessory olfactory bulbs of the species studied (pers. obs.). The *fenestra olfactoria* was smallest in *Echinosaura horrida* due to the comparatively smaller olfactory bulbs in comparison with the other gymnophthalmid taxa. In contrast, in species of Chamaeleonidae, Polychrotidae and Iguanidae, the sensory olfactory apparatus (Jacobson's organ and olfactory bulbs) is poorly developed (Bellairs & Kamal, 1981), resulting in a *fenestra olfactoria* comparatively smaller than in Gymnophthalmidae.

Additionally, in the orbitotemporal region of the gymnophthalmid chondrocranium, we find some general features as well: 12. The *planum supraseptale* bears two laterally oriented wings, as described by Guerra & Montero (2009) for *Vanzosaura* *rubricauda*, which project dorsally and contact the rostral ends of the *taenia marginalis*; these lateral wings are largest in *B. bicolor* due to a low *planum supraseptale* given the absence of interorbital septum, consistent with the condition in other snakelike burrowing lizards (Tarazona & Ramírez-Pinilla, 2008). In addition, the anteriormost portion of the *planum supraseptale* consists of a long and slender trough-like process, almost as thin as the *sphenethmoid commissures*; however, in *B. bicolor* the planum supraseptale as a whole is very narrow in contrast to the other gymnophthalmids. 13. The *sphenethmoid commissures* contact the *planum supraseptale* posteriorly and the nasal capsule rostrally. However, in some species the *sphenethmoid commissures* fail to reach either the *planum supraseptale* or the nasal capsule. 14. Dorsally, an anteriorly oriented process projects from the rostral border of the lateral wings of the *planum supraseptale* as described for instance in *Mabuya* sp. (Jerez, 2007).

There appears to be significant variation within Gymnophthalmidae in respect to some chondrocranial features such as the orbitosphenoid and the *pila antotica*. The gymnophthalmid orbitosphenoid shows three conditions or states; it can be formed by ossification of a segment of: 1. The *pila metoptica*, *taenia medialis* and *pila accesoria*, which ossify in the region where the three are connected forming a bone with triangular shape as is the case of 50% of the species studied herein, including *Ptychoglossus bicolor* and the other three species from the Alopoglossinae subfamily, and in two fossorial snakelike lizards (*Nothobachia ablephara* and *Scriptosaura catimbau*, Roscito & Rodrigues, 2010). 2. The *pila metoptica* and *taenia medialis* as in 40% of the taxa. 3. The *taenia medialis* alone, as in *Vanzosaura rubricauda* (Guerra & Montero, 2009). 4. As regards the condition in *Bachia bicolor*, the orbitosphenoid consists of an unusually expanded bone, similar to amphisbaenians, composed of 4-5 cartilages of which only two can be topologically homologized with any lizard orbitotemporal cartilages, the *pila metoptica* and *taenia medialis*, while the remaining processes (*pila antotica* and *pila accesoria*) can not be accurately identified (Tarazona & Ramírez-Pinilla, 2008).

The condition of the *pila antotica* within Gymnophthalmidae is also variable, when present, it can be long or reduced but it is always separated from the basal plate, or it may be absent as in *B. bicolor* and *P. bicolor*; in the latter, the *pila antotica* was absent even in early stages of development. Such cartilaginous bar is also absent in late embryonic stages of the terrestrial scincid *Plestiodon fasciatus* (Rice, 1920) and in *Cordylus* (Cordylidae, Van Pletzen, 1946), as well as in some fossorial snake-like scincid lizards like *Acontias meleagris* (Brock, 1941). Furthermore, the *pila antotica* may appear early during embryonic development and be absent in later stages as is the case in *Plestiodon latiscutatus* (*Eumeces quinquelineatus,* Rice, 1920). This situation indicates that the condition of the *pila antotica* is variable among groups and is subjected to change during ontogeny.

8.3 OSSIFICATION SEQUENCE OF *Ptychoglossus bicolor*

The ossification of the skull of *Ptychoglossus bicolor* consists of two different processes: the development of the dermatocranium and the ossification of the chondrocranium.

In *Ptychoglossus bicolor* as well as in other lizard species, the pterygoid is the first or among the first bones to ossify in the skull (e.g., *Trachylepis capensis*, Skinner 1973; *Liolaemus scapularis,* Lobo et al., 1995; *Liolaemus quilmes*, Abdala et al., 1997; *Tupinambis rufescens*, *Tupinambis merianae,* Arias & Lobo, 2006; *Lacerta agilis,* Rieppel, 1994; *Elgaria coerulea*, Good, 1995; *Liopholis whitii* Hugi et al., 2010). Also, similar to the condition in *T. merianae*, *T. rufescens* (Arias & Lobo, 2006), *Liolaemus scapularis* (1995), *Liolaemus quilmes* (Abdala et al., 1997) among others, the lacrimal, postorbital and postfrontal, are among the last elements of the dermatocranium to start to ossify during embryonic development, while the last dermal bones to fully differentiate are generally those from the frontoparietal region which remain incompletely differentiated in the neonate (e.g., *Elgaria coerulea*, *Neusticurus ecpleopus*, *Dipsosaurus dorsalis*, Maisano, 2001; *Mabuya* sp, Jerez, 2007; *Bachia bicolor*, Tarazona et al., 2008), this suggests that the onset and termination of the ossification sequence of the dermatocranium is somewhat conserved among the lizards studied so far. In *P. bicolor* the postorbitofrontal ossifies as a single bone; also, in the gymnophthalmid *Calyptommatus nicterus* (Roscito & Rodrigues, 2010) there is also a single bone, whereas in other gymnophthalmid species, the postfrontal and postorbital bones are distinct (e.g., *Euspondylus acutirostris*, Montero et al., 2002; *Neusticurus ecpleopus*, Bell et al., 2003; *Vanzosaura rubricauda*, Guerra & Montero, 2009; *Nothobachia ablephara*, *Scriptosaura catimbau*, Roscito & Rodrigues, 2010).

The size of the lizard neonate frontoparietal fontanelle is variable among groups and depends upon the differentiation of the frontals and parietals; thus, it may be large, small or closed at the time of birth (Maisano, 2001). A large frontoparietal fontanelle was characteristic of *Ptychoglossus bicolor* neonates, in which the frontals remain unfused and the parietals are ossified only along their lateral margins. This condition is similar to the anguid *Elgaria coerulea* (Maisano, 2001). Differently, in the neonate skull of other lizards, ossification of the frontals and parietals is further advanced, as in the gymnophthalmids *Bachia bicolor* (Tarazona et al., 2008) and *Neusticurus ecpleopus*, and the iguanid *Dipsosaurus dorsalis* (Maisano, 2001) the closure of the frontoparietal fenestra is more advanced than in *P. bicolor*.

In respect to the ossification of the chondrocranium, the orbitosphenoid of *Ptychoglossus bicolor* is the last chondral bone of the skull to start the ossification process, a condition similar to that in *Elgaria coerulea* (Good, 1995), *Liolaemus scapularis* (Lobo et al., 1995) *Liolaemus quilmes* (Abdala et al., 1997), *Trachylepis capensis* (Skinner, 1973) and *Mabuya* sp (Jerez, 2007). On the other hand, the last chondral bones to completely differentiate in the skull of *P. bicolor* correspond to the basisphenoid and basioccipital similar to *Trachylepis capensis* (Skinner, 1973) and *Mabuya* sp (Jerez, 2007), among other lizards species.

9. CONCLUSION

The fully formed chondrocranium of *Ptychoglossus bicolor* and the overall ossification sequence pattern of the skull resemble that of other lizard species, especially that of teiids; however, certain features regarding the development of the chondrocranium during early embryogenesis such as the development of the basipterygoid processes from the acrochordal cartilage, the early ossification of the crista sellaris and the formation and ossification of the trabecular processes also from the acrochordal cartilage, differ from other reptilian embryos in the literature.

When looking at the gymnophthalmid orbitosphenoid we find different states in respect to its origin and the orbitotemporal cartilages that comprise this bone, with *Vanzosaura rubricauda* at one extreme and *Bachia bicolor* at the other. In most of the other gymnophthalmid species, including *Ptychoglossus bicolor* (table 1), we meet an intermediate state, suggesting that there might be a tendency within Gymnophthalmidae towards the expansion of the orbitosphenoid by means of the ossification of neighboring orbitotemporal cartilages.

The *nasal capsule* of *P. bicolor* and the other gymnophthalmids studied is hereby considered as complete and structurally complex relative to other lizards, where the nasal capsule is comparatively smaller and simplified, as from arboreal species with visual prey detection who has poorly developed olfactory and vomeronasal senses (e.g., Chamaeleonidae, Polychrotidae, Iguanidae, Bellairs & Kamal, 1981). In contrast, the family Gymnophthalmidae is characterized by a well developed olfactory and vomeronasal systems used in chemical detection and discrimination, related to its position within the scleroglossans (Pianka & Vitt, 2003), and thus, the chondrocranium presents some features, associated with the ethmoid region, which are either well developed or unique, compared to other lizards.

10. REFERENCES

Abdala F, Lobo F, Scrocchi G (1997) Patterns of ossification in the skeleton of *Liolaemus quilmes* (Iguania: Tropiduridae). *Amphib-Reptil* **18**, 75-83.

Anaya-Rojas JM, Serrano-Cardozo VH, Ramírez-Pinilla MP (2010) Diet, microhabitat use and thermal preferences of Ptychoglossus bicolor (Squamata, Gymnophthalmidae) in an organic coffee shade plantation in Colombia. *Pap Avulsos Zool* **50**, 159-166.

Arias F, Lobo F (2006) Patrones de osificación en *Tupinambis merianae* y *Tupinambis rufescens* (Squamata, Teiidae) y patrones generales en Squamata. *Cuad Herpetol* **20**, 3-23

Barros FC, Herrel A, Kohlsdorf T (2011) Head shape evolution in Gymnophthalmidae: does habitat use constrain the evolution of cranial design in fossorial lizards?. *J Evol Biol* **24**, 2423-2433.

Bellairs Ad'A, Kamal AM (1981) The chondrocranium and the development of the skull in recent reptiles. *In Biology of the Reptilia, vol. 11. Morphology F* (eds Gans C, Parsons T), pp. 1-263. New York: Academic Press.

Bell CJ, Evans SE, Maisano JA (2003) The skull of the gymnophthalmid lizard *Neusticurus ecpleopus* (Reptilia: Squamata). *Zool J Linn Soc* **139**, 283-304.

Brock GT (1941) The skull of *Acontias meleagris*, with a study of the affinities between lizards and snakes. *Zool J Linn Soc* **41**, 71-88.

de Beer GR (1930) The early development of the chondrocranium of the lizard. *Q J Microsc Sci* **73**, 707-739.

de Beer GR (1937) The development of the vertebrate skull. Oxford, Clarendon Press. 552 pp.

de Freitas MA, Fagundes de França DP, Veríssimo D (2011) First record of *Cercosaura eigenmanni* (Griffin, 1917) (Squamata: Gymnophthalmidae) for the state of Acre, Brazil. *Check List* **7**, 516.

de Moura MR, Dayrell JS, de Avelar São-Pedro V (2010) Reptilia, Gymnophthalmidae, *Micrablepharus maximiliani* (Reinhardt and Lutken, 1861): Distribution extension, new state record and geographic distribution map. *Check List* **6**, 419-426.

Defaure JP, Hubert J (1961) Table de development du lezard vivipare: *Lacerta* (Zootoca) *vivipara* Jaquin. *Arch Anat Micr Morph Exp* **50**, 309–328.

Donnelly MA, MacCulloch RD, Ugarte CA, Kizirian D (2006) A new riparian gymnophthalmid (Squamata) from Guyana. *Copeia* **3**, 396-403.

El-Toubi MR, Kamal AM (1959) The development of the skull of *Chalcides ocellatus*. I. The development of the chondrocranium. *J Morphol* **104**, 269-306.

El-Toubi MR, Kamal AM (1961) The development of the skull of *Ptyodactylus hasselquistii*. I. The development of the chondrocranium. *J Morphol* **108**, 63-94.

Good DA (1995) Cranial ossification in the northern alligator lizard, *Elgaria coerulea* (Squamata, Anguidae). *Amphib-Reptil* **16**, 157-166

Guerra C, Montero R (2009) The skull of *Vanzosaura rubricauda* (Squamata, Gymnophthalmidae). *Acta Zool* **90**, 359-371.

Hoyos JM (1998) A reappraisal of the phylogeny of lizards of the family Gymnophthalmidae (Sauria, Scincomorpha). *Rev Esp Herp* **12**, 27-43.

Hugi J, Mitgutsch C, Sánchez-Villagra MR (2010) Chondrogenic and ossification patterns and sequences in White's skink *Liopholis whitii* (Scincidae, Reptilia). *Zoosyst Evol* **86**, 21-32.

Jerez A (2007) Desarrollo del Plan Corporal en *Mabuya mabouya*. Doctoral dissertation. Facultad de Ciencias Naturales e Instituto Miguel Lillo. Universidad Nacional de Tucumán, Argentina.

Kamal AM, Abdeen AM (1972) The development of the chondrocranium of the lacertid lizard, *Acanthodactylus boskiana*. *J Morphol* **137**, 289-334.

Kuratani S (1999) Development of the chondrocranium of the Loggerhead Turtle, *Caretta caretta*. *Zool Sci* **16**, 803-818.

Lobo F, Abdala F, Scrocchi G (1995) Desarrollo del esqueleto de *Liolaemus scapularis* (Iguania: Tropiduridae). *Boll Mus reg Sci nat Torino* **13**, 77-104.

Maisano JA (2001) A survey of state of ossification in neonatal squamates. *Herpetol Monogr* **15**, 135-157.

Montero R, Moro SA, Abdala V (2002) Cranial anatomy of *Euspondylus acutirostris* (Squamata, Gymnophthalmidae) and its placement in a modern phylogenetic hypothesis. *Russ J Herpetol* **9**, 215-228.

Peloso PLV, Avila-Pires TCS (2010) Morphological variation in *Ptychoglossus brevifrontalis* Boulenger, 1912 and the status of *Ptychoglossus nicefori* (Loveridge, 1929) (Squamata, Gymnophthalmidae). *Herpetologica* **66**, 357-372.

Pianka ER, Vitt LJ (2003) Lizards: windows to the evolution of diversity, 1 edition. University of California Press.

Pratt CWM (1948) The morphology of the ethmoidal region of *Sphenodon* and lizards. *Proc zool Soc Lond* **118**, 171-201.

Ramaswami LS (1946) The chondrocranium of *Calotes versicolor* (Daud.) with a description of the osteocranium of a just-hatched young. *Q Jl microsc Sci* **87**, 237-297.

Ramos-Pallares EP, Serrano-Cardozo VH, Ramírez-Pinilla MP (2010) Reproduction of *Ptychoglossus bicolor* (Squamata, Gymnophthalmidae) in an Andean Coffee Shade Plantation in Colombia. *South Am J Herpetol* **5**, 143-150.

Rice EL (1920) The development of the skull in the skink *Eumeces quinquelineatus*. *J Morphol* **34**, 120-243.

Rieppel O (1994) Studies on skeleton formation in Reptiles. Patterns of ossification in the skeleton of *Lacerta agilis exigua* Eichwald (Reptilia, Squamata). *J Herpetol* **28**, 145-153.

Rodrigues MT, Freire EM, Pellegrino KC, Sites JW (2005) Phylogenetic relationships of a new genus and species of microteiid lizard from the Atlantic forest of north-eastern Brazil (Squamata, Gymnophthalmidae). *Zool J Linn Soc* **144**, 543–557.

Rodrigues MT, Pavan D, Franco-Curcio F (2007) Two new species of lizards of the genus *Bachia* (Squamata, Gymnophthalmidae) from Central Brazil. *J Herpetol* **41**, 545–553.

Roscito JG, Rodrigues MT (2010) Comparative cranial osteology of fossorial lizards from the Tribe Gymnophthalmini (Squamata, Gymnophthalmidae). *J Morphol* **271**, 1352-1365.

Sánchez-Pacheco SJ (2010) A new “microteiid” lizard (Squamata, Gymnophthalmidae) from Southwestern Colombia. *Herpetologica* **66**, 349-356.

Skinner MM (1973) Ontogeny and adult morphology of the skull of the South African skink, *Mabuya capensis* (Gray). *Ann Univ Stellenbosch* **48**, 1-116.

Tarazona OA, Ramírez-Pinilla MP (2008) The unusual orbitosphenoid of the snakelike lizard *Bachia bicolor*. *J Anat* **213**, 120-130.

Tarazona OA, Fabrezi M, Ramírez-Pinilla MP (2008) Cranial morphology of *Bachia bicolor* (Squamata, Gymnophthalmidae) and its postnatal development. *Zool J Linn Soc* **152**, 775-792.

Torres-Carvajal O (2003) Cranial osteology of the Andean lizard *Stenocercus guentheri* (Squamata: Tropiduridae) and its postembryonic development. *J Morphol* **255**, 94-113.

Van-Pletzen R (1946) The cranial morphology of *Cordylus* with special reference to cranial kinesis. *Ann Uni Stellenbosch* **24**, 41-68.

Vitt LJ (1982) Reproduction and sexual dimorphism in the microteiid lizard, Gymnophthalmus multiscutatus. *J Herpetol* **16**, 325-329.

Vitt LJ, Avila-Pires TCS (1998) Ecology of two sympatric species of *Neusticurus* (Sauria: Gymnophthalmidae) in the western Amazon of Brazil. *Copeia* **1998**, 570-582

Wassersug RJ (1976) A procedure for differential staining of cartilage and bone in whole formalin-fixed vertebrates. *Stain Technol* **51**, 131-134.

Uetz P, Goll J, Hallermann J (2011) The Reptile Database, http://www.reptile-database.org, accessed Feb 5, 2011.

Table 1. Chondrocranial trait distribution in four subfamilies of gymnophthalmid lizards and their sister taxon. **Alopoglossinae:** 1, *Ptychoglossus bicolor*; 2, *Ptychoglossus vallensis*; 3, *Ptychoglossus festae*; 4, *Alopoglossus copii*. **Cercosaurinae:** 5, *Anadia ocellata*; 6, *Anadia bogotensis*; 7, *Cercosaura vertebralis*; 8, *Cercosaura* cf *ampuedae*; 9, *Echinosaura horrida*; 10, *Riama striata*; 11, *Bachia bicolor*; 12, *Potamites cochranae*; 13, *Pholidobolus montium*. **Ecpleopinae:** 14, *Leposoma rugiceps*; 15, *Leposoma southi*. **Gymnophthalminae:** 16, *Gymnophthalmus speciosus*; 17, *Iphisa elegans*; 18, *Tretioscincus bifasciatus*; 19, *Vanzosaura rubricauda* (Guerra & Montero, 2009). **Teiidae:** 20, *Cnemidophorus lemniscatus*. The gray scale is hereby used to cluster the species into the groups mentioned above. x, present; ?, without data.

Trait	Species																				% spp
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
1. aditus conchae	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	100
2. ectochoanal cartilage	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	100
3. foramen epiphaniale	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	100
4. nasal septum forms a rostral process	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	100
5. paraseptal cartilage	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	100
6. planum supraseptale with anterior portion narrow	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	100
7. planum supraseptale with two laterally oriented wings	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	100
8. lamina transversalis anterior wide and large, forming a complete zona annularis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	100
9. cartilage of Jacobson's organ well developed	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	?	x	95
10. fenestra lateralis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	?	x	95
11. planum antorbital with a rod-like rostral process complete (i.e., abuts with vomer)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	?		90
12. sphenethmoid commisures	x	x	x	x	x	x		x		x		x	x	x	x	x	x	x	x	x	85
13. sphenethmoid commisures reach planum supraseptale	x	x	x	x	x	x	x	x		x			x	x	x	x	x	x	x	x	85
14. paraseptal cartilage extends ventrally forming a thin wall parallel to nasal septum	x	x	x	x	x	x		x	x	x		x	x	x	x	x	x	x	?		80
15. fenestra superior	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x				75
16. foramen in nasal concha (distinct from the foramen epiphaniale)	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x				75
17. sphenethmoid commisures contact the roof of the nasal capsule	x	x	x	x			x	x		x		x	x	x	x	x	x		x	x	75
18. lateral wings of planum supraseptale with an anteriorly oriented process	x	x	x	x	x		x						x	x	x	x	x	x	x	x	70
19. large fenestra olfactoria	x	x	x	x	x	x	x	x	x	x	x	?			x		x		?		65
20. foramina in planum supraseptale		x	x			x		x			x			x						x	65
21. planum antorbital with a posteriorly oriented process	x		x		x	x	x		x			x			x	x	x	x	?		55
22. rostral process of planum antorbital with an expanded ventral face			x		x	x			x	x		x	x	x	x		x	x	?		55
23. foramen apicale	x				x	x	x	x	x	x		x			x					x	50
24. orbitosphenoid formed by: pila accesoria, pila metoptica and taenia medialis	x	x	x	x	x	x	x				?	x				x				x	50
25. paraseptal cartilage with a laterally oriented anterior process	x	x	x	x								x	x	x	x	?		x	?	x	50
26. pila antotica							x	x		x			x	x	x	x	x	x	x		50
27. planum antorbital with a medial dorsal process high					x	x		x	x						x	x	x	x		x	45
28. orbitosphenoid formed by pila metoptica and taenia medialis								x	x	x	?		x	x	x		x	x			40
29. foramen for duct of lateral nasal gland							x	x	x	x	x	x			x				?		35
30. planum antorbital with a medial dorsal process low	x						x			x	x		x	x					x		35
31. foramen in medial region of dorsal process of planum antorbital				x	x	x	x						x					x	?		30
32. paraseptal cartilage extends behind the planum antorbital forming a process	x				x	x			x					x		x			?		30
33. anterolateral process of paraseptal cartilage with central foramen	x			x					x					x	x				?		25
34. paraseptal cartilage contacts rostral process of planum antorbital forming a fenestra	x															x		x	?		15
35. foramen in nasal capsule in front of the rostral end of sphenethmoid commisures				x												x			?		10
36. anterior maxillary process protuberant												x							?		5
37. orbitosphenoid formed by a portion of the taenia medialis											?								x		5
38. planum antorbital with rostral process incomplete (i.e., not abuts with vomer)																				x	5
39. posterior maxillary process contacts paranasal cartilage dorsally forming a fenestra								x													5

Table 2. Ossification sequence of the skull of *Ptychoglossus bicolor*.

Ossification Sequence	Stage				
	IV D&H 35	V D&H 39	VI D&H 39-40	VII D&H 40	Neonate
prefrontal	▨	▨	▨	▨	▨
maxillary	▨	▨	▨	▨	▨
jugal	▨	▨	▨	▨	▨
pterygoid	▨	▨	▨	▨	▨
frontal		▨	▨	▨	▨
parietal		▨	▨	▨	▨
squamosal		▨	▨	▨	▨
premaxillary		▨	▨	▨	▨
mandible		▨	▨	▨	▨
nasal		▨	▨	▨	▨
prootic		▨	▨	▨	▨
supraoccipital		▨	▨	▨	▨
exoccipital		▨	▨	▨	▨
basioccipital		▨	▨	▨	▨
basisphenoid		▨	▨	▨	▨
epipterygoid		▨	▨	▨	▨
ectopterygoid		▨	▨	▨	▨
vomer		▨	▨	▨	▨
postorbitofrontal		▨	▨	▨	▨
crista sellaris		▨	▨	▨	▨
quadrate		▨	▨	▨	▨
lacrimal			▨	▨	▨
orbitosphenoid (pila metoptica)			▨	▨	▨
orbitosphenoid (complete)				▨	▨
frontoparietal fenestra				▨	▨
basicranial fenestra				▨	▨

Figure 1. Chondrocranium of *Ptychoglossus bicolor* at stages I (D&H 31), and II (D&H 32-33). Stage I: A, Dorsal view, B. Lateral view. Stage II: C, Dorsal view, D. Lateral view. Abbreviations: acc, acrochordal cartilage; bf, basicranial fenestra; bpl, basal plate; bpt, ca, columella auris; fhn, hypoglossal foramen; fm, fissura metotica; Mc, Meckel’s cartilage; n, notochord; ns, nasal septum; oa, occipital arch; oc, otic capsule; pas, processus ascendens; pm, pila metoptica; ptc, parietotectal cartilage; ps, planum supraseptale; q, quadrate; t, trabecula; tc, trabecula communis; tp, trabecular process of acrochordal cartilage. Scale bar 0.5 mm.

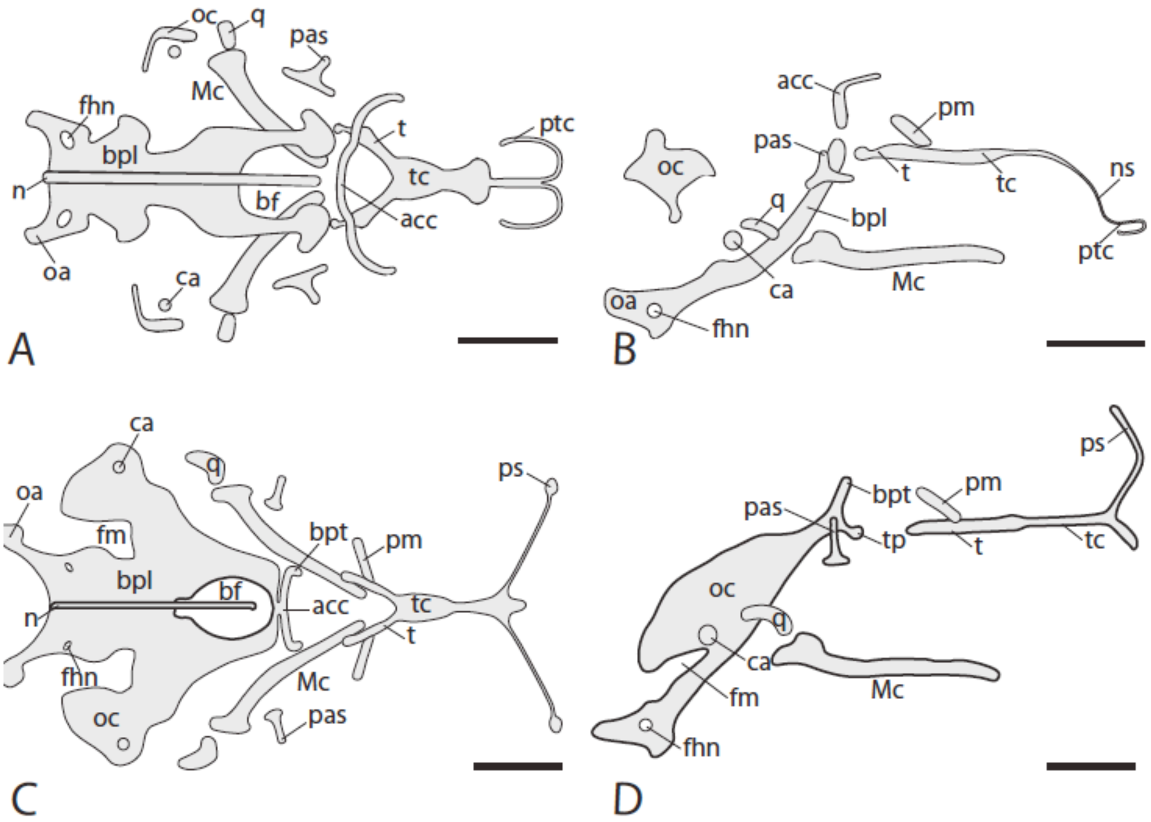

Figure 2. Chondrocranium of *Ptychoglossus bicolor* at stage III (D&H 33-34). A. Dorsal view. B. Lateral view.

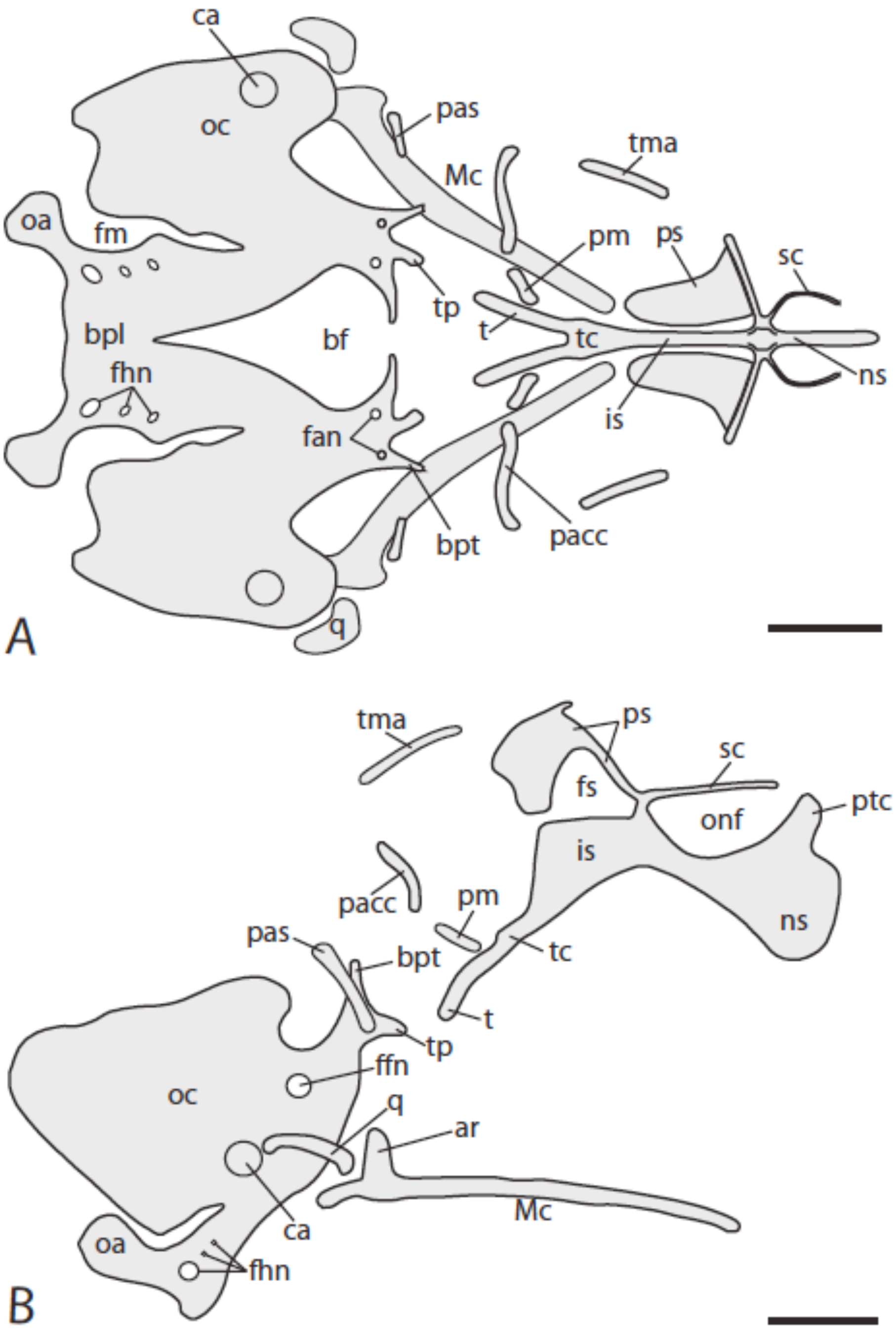

Figure 3. Chondrocranium of *Ptychoglossus bicolor* at stage IV (D&H 35). Dashed lines denote subjacent cartilage. A. Dorsal view. B. Lateral view.

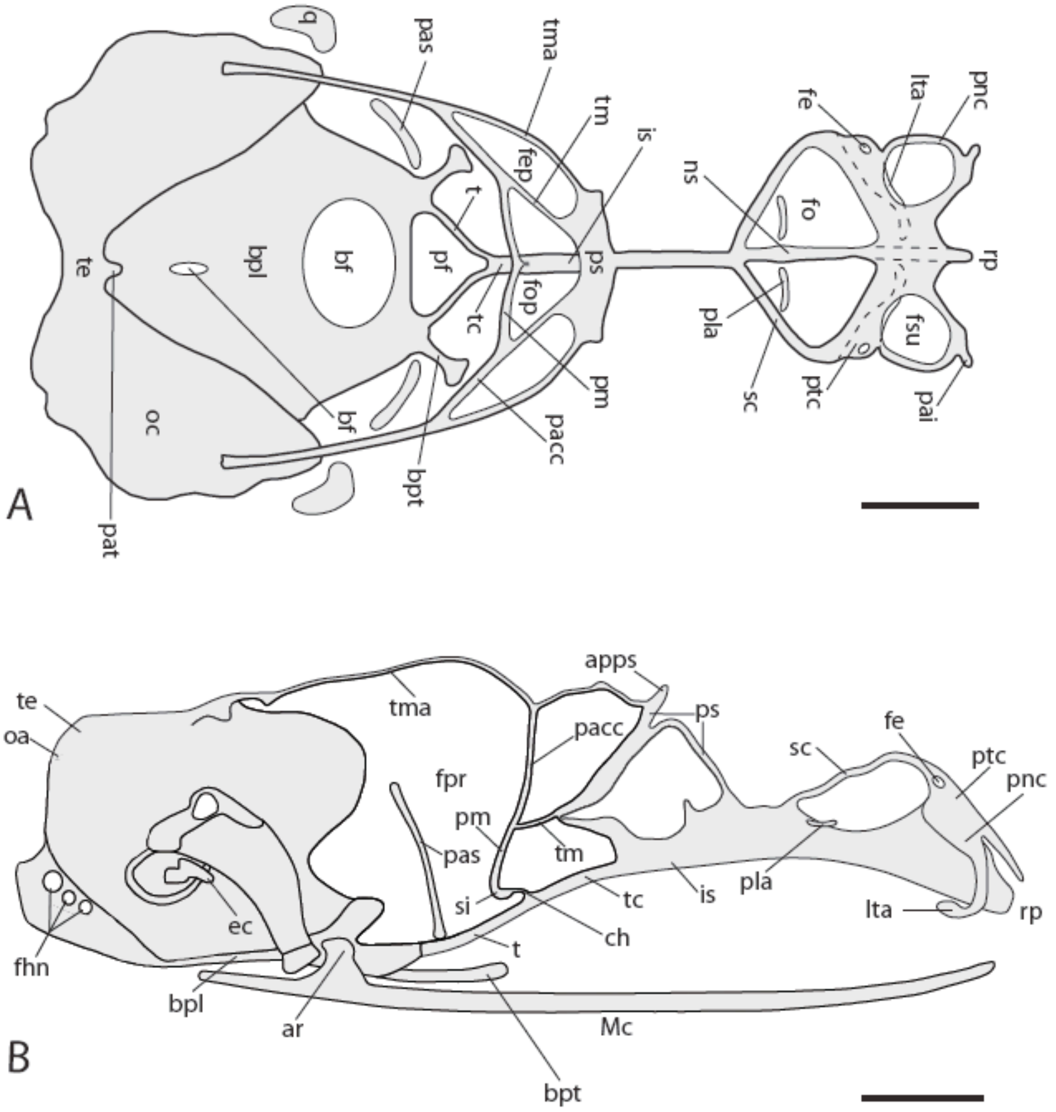

Figure 4. Chondrocranium of *Ptychoglossus bicolor* at stage V (D&H 39). Dashed lines denote subjacent cartilage and dark-grey structures denote ossified cartilage. A. Dorsal view. B. Lateral view.

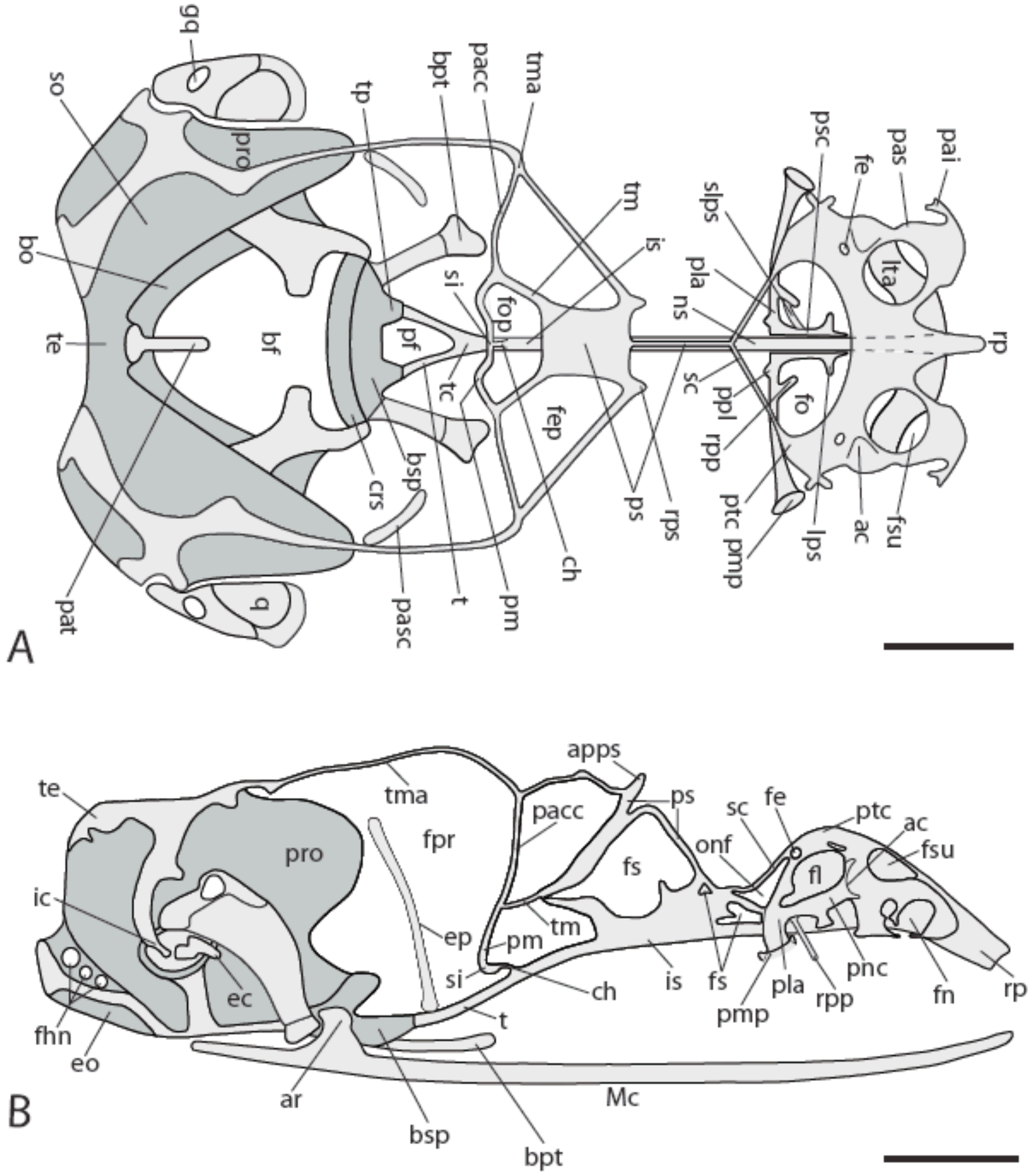

Figure 5. Chondrocranium of *Ptychoglossus bicolor* at stage VI (D&H 39-40). Dashed lines denote subjacent cartilage and dark-grey structures denote ossified cartilage. A. Dorsal view. B. Lateral view.

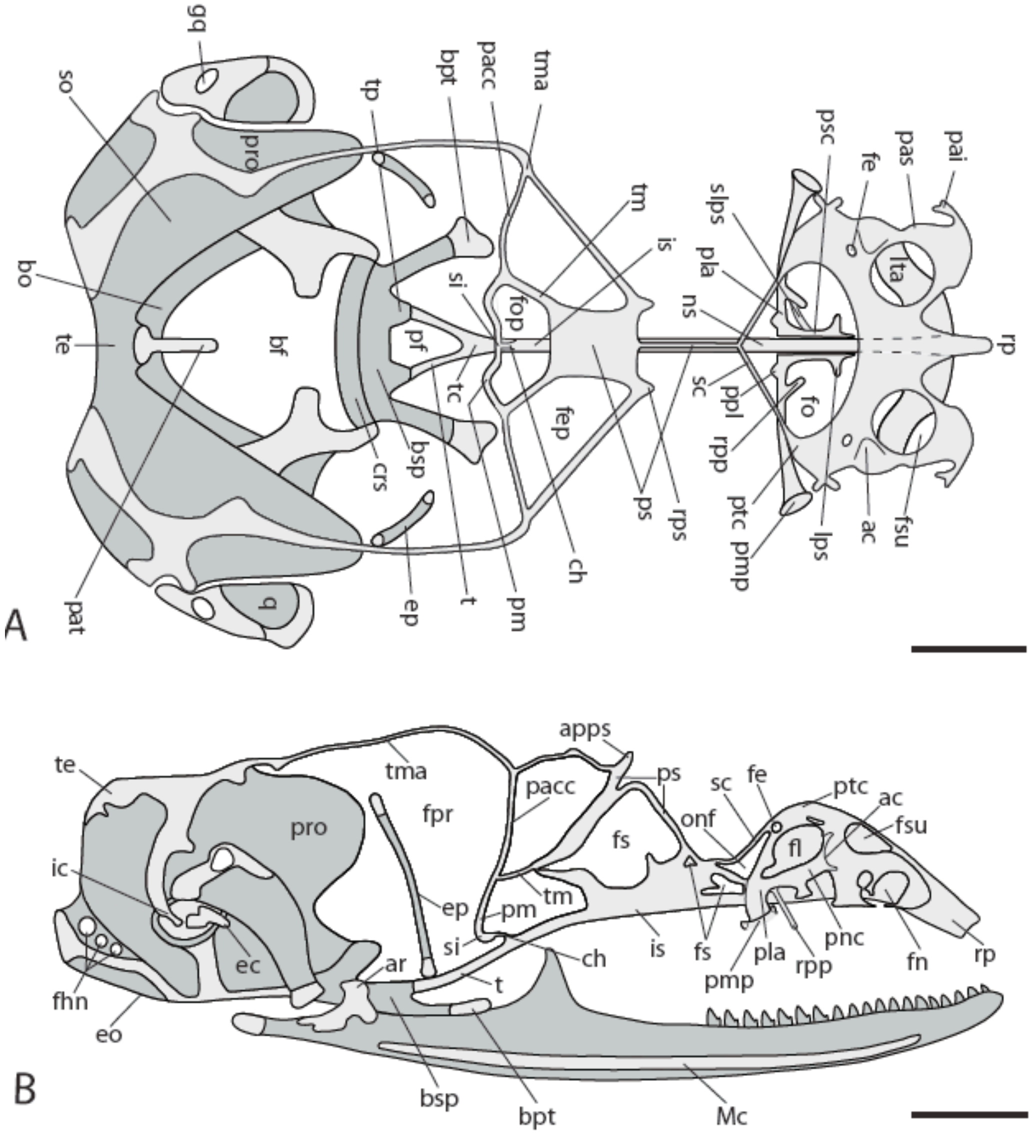

Figure 6. Chondrocranium of *Ptychoglossus bicolor* at stage VII (D&H 40). Dashed lines denote subjacent cartilage and dark-grey structures denote ossified cartilage. A. Dorsal view. B. Lateral view.

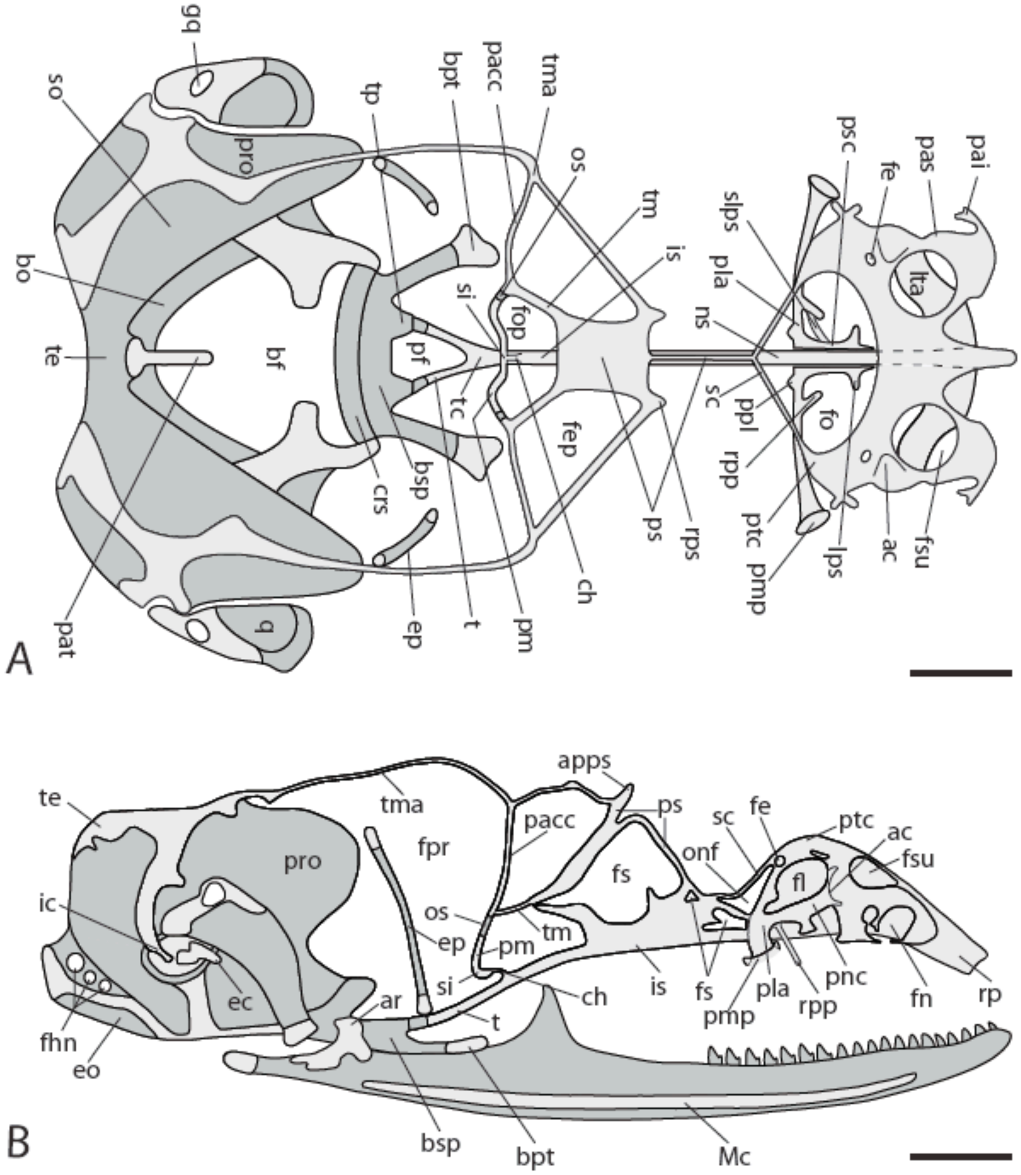

Figure 7. The fully formed chondrocranium of *Ptychoglossus bicolor* neonate. Dashed lines denote subjacent cartilage and dark-grey structures denote ossified cartilage. A. Dorsal view. B. Lateral view.

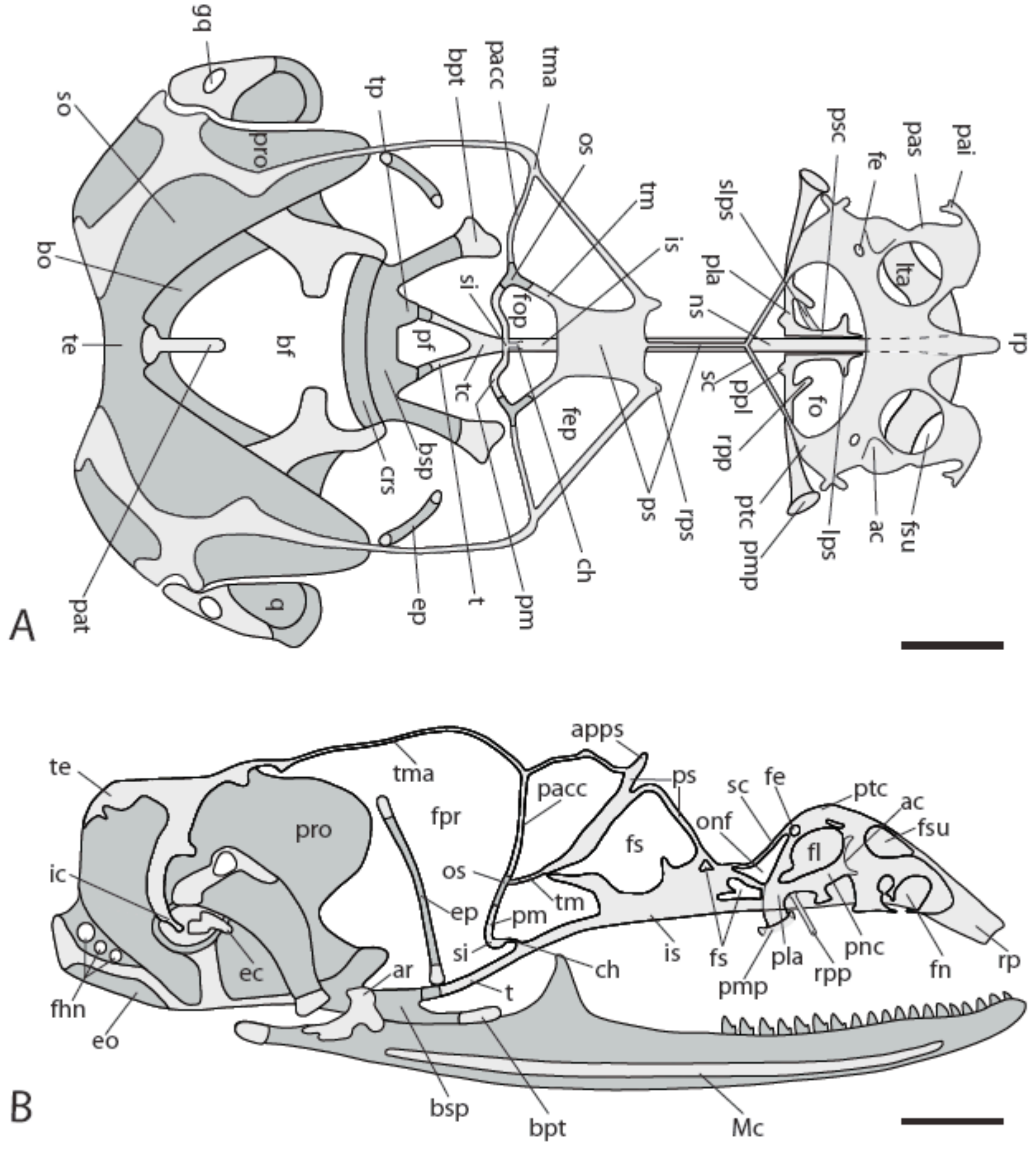

Figure 8. The dermatocranium of *Ptychoglossus bicolor* neonate. A. Dorsal view. B. Ventral view. C. Lateral view. Abbreviations: ec, ectopterygoid; fpf, frontoparietal fenestra; fr, frontal; jg, jugal; md, mandible; mx, maxillary; na, nasal; pal, palate; pof, postorbitofrontal; prf, prefrontal; prm, premaxillary; pt, pterygoid; sp, supratemporal; sq, squamosal; vo, vomer. Scale bar 0.5 mm.