Cranial morphology of *Bachia bicolor* (Squamata: Gymnophthalmidae) and its postnatal development

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Autor: Oscar Alejandro Tarazona Rey **
Palabras clave: osteología, ontogenia, orbitoesfenoides, *trabecula communis.*

Bachia bicolor muestra modificaciones en su plan corporal respecto a un lagarto típico, que pueden ser vistas como un estado intermedio en la evolución del plan corporal serpentiforme. En la búsqueda de cambios en la estructura craneal que puedan revelar modificaciones mas allá de las observadas en el esqueleto postcraneal, este estudio describe la osteología craneal de *B. bicolor* y su variación durante el desarrollo postnatal. Se usaron series de tamaño de preparados esqueléticos, incluyendo esqueletos secos y especimenes doblemente coloreados para hueso y cartílago. La morfología adulta de *B. bicolor* es similar a la de otros gymnophthálmidos; sin embargo, presenta algunos caracteres particulares convergentes con varios lagartos serpentiformes. El diseño craneal de *B. bicolor* presenta dos modificaciones craneales sobresalientes: 1) La presencia del proceso rostral del basiesfenoides, producto de la osificación del cartílago *trabecula communis* durante el desarrollo postnatal y 2) un orbitoesfenoides amplio, este último es un hueso compuesto (endocondral y membranoso) que forma parte del piso de la bóveda craneana. Algunas de las modificaciones craneanas observadas en *B. bicolor* se originan durante el desarrollo postnatal, sugiriendo un efecto importante de posibles cambios heterocrónicos postnatales en la modificación estructural del diseño craneal.

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ABSTRACT

Title: Cranial morphology of *Bachia bicolor* (Squamata: Gymnophthalmidae) and its postnatal development *
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Key words: osteology - ontogeny - orbitosphenoid - *trabecula communis.*

Bachia bicolor shows body plan modifications with respect to typical lizards that can be regarded as an intermediate state in the evolution of the serpentiform body plan. In the search for cranial structural changes that might reveal modifications beyond the observed in the postcranial skeleton, this study describes the adult cranial osteology of *B. bicolor* and its variation during postnatal development. Descriptions are based on a size series of osteological preparations, including dry skeletons and cleared and double-stained specimens. The adult skull morphology of *B. bicolor* is similar to that of other gymnophthalmids; however, it shows some particular characters that are convergent with those of several serpentiform lizards. The skull design of *B. bicolor* has two remarkable structural modifications: 1) The presence of the basisphenoid rostral process by the ossification of the cartilage *trabecula communis* during the postnatal development and 2) the broad orbitosphenoid bone, the latter is a compound bone (chondral and membranous) that forms part of the braincase floor. Some of the cranial modifications observed in *B. bicolor* arise during postnatal development, suggesting an important role for possible heterochronic changes.

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INTRODUCTION

In squamate lizards, several studies have found that morphological patterns like limb reduction/loss, body elongation and cranial modifications (loss of skull elements and reduction of head diameter) converge on evolutive processes such as miniaturization and/or fossoriality (Lee, 1998; Rieppel, 1984, 1996). Those patterns are more frequently observed in Scleroglosa, having multiple independent origins in unrelated groups like Amphisbaenia, Dibamidae, Ophidia, Pygopodidae, Anguidae, Scincidae and Gymnophthalmidae (Lee, 1998, Wiens & Slingluff, 2001, Estes *et al.*, 1988).

Some Gymnophtyhalmidae lizards exhibit morphological patterns that at first glance can be regarded as intermediate in the evolution of a serpentiform body plan, which seemingly would be involved in processes such as miniaturization and/or fossoriality (Presch, 1980; Presch, 1975, Dixon, 1973, Pellegrino *et al.*, 2001). Among the members of this group there are forms of small body size, elongated trunks, reduced limbs, and with loss of external ear openings; they are frequently burrowers or fossorials. The recent molecular phylogenetics analysis of Gymnophthalmidae supports the multiple independent origins of those characters (Pellegrino *et al.*, 2001), resembling the morphological convergence observed in Squamata (Lee, 1998).

Bachia is a genus of gymnophthalmid lizards that shows several degrees of limb reduction with a wide range of limb morphologies (Presch, 1975; Dixon, 1973; Kizirian & McDiarmid, 1998); the species with a major degree of limb reduction show more elongated trunks and an increased number of presacral vertebrae (Presch, 1975). *Bachia bicolor* (Cope, 1896) is found in Northern and Central Colombia, and Western Venezuela. These lizards have elongated trunk and tail, forelimbs with four digits, and hindlimbs reduced to the stylopodium; the body and head are narrow, and the external ear openings are absent (Dixon, 1973; Presch, 1975). Among 17 species of the genus, *B. bicolor* shows an intermediate degree of limb reduction (Dixon, 1973; Presch, 1975; Kizirian & McDiarmid, 1998). Thus, it represents an interesting species to analyze morphological features in regards to its ontogenetic basis.

Information about the skull morphology in the species of *Bachia* has focused on adult forms (MacLean, 1974; Presch, 1980; Soares, 2000); therefore, detailed studies of skull features would allow the recognition of morphological variation during ontogeny and adult character states. Also, the identification of structures with heterochronic patterns during ontogeny is an important tool in the determination of the structural liberties and constraints in *B. bicolor* skull morphology, and in the identification of “mature” and “immature” traits in a comparative analysis.

Here we present a detailed description of the cranial morphology in adult individuals of *B. bicolor* and its variation during postembryonic development. Since most of the evolutionary hypothesis leading to the origin of the serpentiform body plan states that cranial modifications occur in a modular form and are subsequent to those related to the trunk and limbs (Rieppel, 1996), our objective focuses on finding cranial traits that may indicate changes in the structural skull design, which can reveal modifications beyond the observed in the postcranial skeleton.

MATERIALS AND METHODS

All the specimens used in the study were obtained from the Colección Herpetologica of the Museo de Historia Natural, Universidad Industrial de Santander (UIS-R). Lizards were collected in the gardens of Bucaramanga city (Santander, Colombia, 07°07'28.7” N, 73°06'41.6” W, 1040 m altitude), fixed in 10% formalin, and stored in 70% ethanol. Thirty-eight adults and juvenile individuals of *B. bicolor* were selected; two of the juveniles hatched in the laboratory. A size series according to the snout-vent length (SVL) was established, with five stages ranged from 25.48 to 71.39 mm. Sex and sexual maturity were determined by macroscopic observation of the gonads (Appendix 1). The skeletal material was prepared by two methods: 1) dry skulls (six adult skulls), four of them were disarticulated, and 2) cleared and double-stained specimens following the protocol of Wassersug (1976). The specimens were examined through an Olympus stereo microscope, and the photographs and drawings were made with the assistance of a digital camera. Cranial osteology of dermatocranium and otico-occipital regions was described in detail for each bone. The most significant events in the skull morphology variation during postnatal development were described. The anatomical terminology used herein follows Oelrich (1956), Bellairs & Kamall (1981) and Bell *et al.* (2003).

RESULTS

SKULL

The adult skull of *Bachia bicolor* (Fig. 1) is typical of tetrapod lizard skulls and very similar to that of other gymnophthalmids (MacLean, 1974; Montero, Moro & Abdala, 2002; Bell *et al.*, 2003). It is between 7 to 8 mm in length depending on its SVL, corresponding to nearly 12 % of the body length (SVL). Intraspecific variation due to sexual dimorphism was not observed. The preorbital region is short, ending in a slightly rounded snout. The orbits are small. The supratemporal fossa is opened and is bordered by a complete supratemporal arch. The otico-occipital (Fig. 2) region is very large in comparison to the rest of the skull, reaching the skull table, closing the post-temporal fossa, and posteriorly protruding from the skull. The middle ear is modified, it shows an extremely reduced extracolumella and the stapes is short with a huge oval foot plate. The skull shows a secondary palate and a small suborbital fenestra. The hyoid apparatus is formed by a *processus lingualis* separated from the basihyal, hyoid cornus, small epihyals, and first ceratobranchials.

The following osteological description was ordered according to the location of each bone in the skull roof, orbital, temporal, otico-occipital, palatal, and mandible regions:

PALATAL REGION

The ***vomers*** contact each other along the midline. The vomer is anteriorly narrow and markedly extended backward, but less than the maxilla in palatal view. The lateral margin of the vomer, the maxillary palatal shelf and the palatine maxillary process close the *fenestra exochoanalis* forming a secondary palate (*sensu* Presch, 1976); therefore, the choana is opened posteriorly on the palatine.

Anteriorly, the vomer forms the medial border of the fenestra for the Jacobson's organ. The vomer has two processes in its anterior tip: the anterior process, which laterally contacts the maxillary anteromedial process; and the anterolateral process that rests slightly on the maxillary palatal shelf and is grooved ventrally by the lacrimal groove. Ventrally, underlying the anterolateral process of the vomer is the ventral crest and dorsally to it the medial border rises in a dorsal crest. In the dorsal surface of the vomer lies a transverse flange, posteriorly and very close to the dorsal crest. The cavity for the Jacobson's organ is enclosed by the dorsal crest, transversal flange and the septomaxilla. The vomer projects backward in the posterolateral and posteromedial processes. The posteromedial process is short and narrow, and reaches the palatine.

Dorsal to the anterior part of the vomer lays the concave ***septomaxilla***, that forms the roof of the cavity for the Jacobson's organ. The septomaxilla has a flat lateral process with irregular borders that rests on the maxillary palatal shelf. Ventrally, the septomaxila covers the laterodorsal border of the vomerine transversal flange.

The ***palatine*** ventral surface is concave forming the palatal groove, although it is gradually less grooved posteriorly. It has two anterior processes: a narrow vomerine process; and a broad maxillary process. Posteriorly, there is an expanded pterygoid process. The vomerine process is laterally sutured to the vomer and contacts medially the contralateral palatine, the maxillary process dorsally overlaps the maxillary palatal shelf, and the pterygoid process rest on the dorsal surface of the pterygoid bone. Dorsally, the anterior border of the palatine bone, between the vomerine and the maxillary process, contacts the medial portion of the prefrontal placed dorsal to the palatine. The posterolateral border of the palatine limits medially the suborbital fenestra.

The lateral border of the suborbital fenestra is formed by the ***ectopterygoid***. It is a laminar bone with two processes in its tips: the anterior maxillary process joined to the maxilla; and the posteromedial process joined to the pterygoid; the ectopterygoid also contacts dorsally with the jugal.

The ***pterygoid*** forms the posterior border of the suborbital fenestrae. It has two anterior processes: the broad medial palatine process that overlaps ventrally the palatine; and a transverse process, which is acute and overlaps laterally the ectopterygoid. Posteriorly, the pterygoid has a quadrate process, which in its posterior end articulates laterally with the quadrate. On the dorsal surface the epipterygoid articulates in a columellar fossa of the pterygoid. Medially, at the base of the quadrate process, the pterygoid articulates with the basipterygoid process of the basisphenoid.

SKULL ROOF

The anterior region of the skull roof is formed by the ***frontals***, which are strongly fused in the midline without an evident suture. There are two short anterolateral and two triangular medial processes divided by a slit. The lateral margins descend and form the ventral processes that are slightly curved, without reaching the midline. Two small posterolateral processes and two large and rounded posteromedial processes (parietal tabs) are projected in its posterior margin. Posteriorly, the frontal contacts the parietal through a complex W-shaped frontoparietal suture; here, the posteromedial processes overlaps the parietal, and the posterolateral processes laterally underlie the parietal; this complex suture would prevent cranial mesokinesis as in other gymnophtalmids (Bell *et al.*, 2003). Anteriorly, the frontal contacts the nasals laterally and medially with the premaxilla. The premaxilla overlaps the medial triangular processes, hidden them in articulated skulls, whereas the short anterolateral processes lie between the nasals and prefrontals. The frontal contacts the prefrontal along its lateral border, from the anterior corner to the base of the ventral process. The ventral process also contacts with the medial portion of the prefrontal, in its anterior and ventral margin. The orbitotemporal cartilage *planum supraseptale* extends between the extremes of the ventral processes; then, the olfactory peduncles are enclosed by the *planum supraseptale* and the frontal. Below each posterolateral process of the frontal is observed what seems to be the free-end of orbitotemporal cartilage *taenia marginalis*; it is continuous with the *planum supraseptale* by a cartilaginous sigmoid bar.

The azygous ***parietal*** is roughly rectangular in shape. Its posterior margin contacts the otico-occipital region closing completely the post-temporal fossa. The lateral descending processes of the parietal forms a lateral wall which partially closes the braincase and posteriorly contacts the alar process of the prootic. Laterally, the descending process is in light contact with the epipterygoid. The parietal anterior border shows an anterolateral process that covers the frontal posterolateral process. In its posterior border the supratemporal processes project in a ventrolateral direction, and the parietal fossa is found between them. A ventral crest extends throughout the base of each supratemporal process, from the parietal fossa in anterolateral direction to the base of the descending process. The parietal attaches to the otico-occipital region by connective tissue along the ventral crest and in the ventral surface of the supratemporal process, which overlaps the supraoccipital and partially the prootic. The posterior parietal border articulates with the cartilaginous ascending process of the otico-occipital region.

NASAL REGION

The ***premaxilla*** limits the dorsomedial rim of the nares and extends posterodorsally reaching the frontal bone. The nasal process of the premaxilla overlaps posteriorly the frontal and laterally the nasals. It has a ventral alveolar region, where it bears 7 to 9 unicuspid pleurodont teeth. Dorsally, the premaxilla shows the nasal process that is narrow posteriorly and widens anteriorly, but narrowing between the nares. Above the nares a small lateral process arises from the lateral border of the nasal process. Laterally, the base of the premaxilla has a maxillary process which is continuous with the alveolar region. In the ventral face of the premaxilla a pair of palatal shelves extends separated by a medial slit. The premaxilla meets the maxilla at the maxillary process and the palatal shelf of each side. The cartilaginous rostral tip of the *Septum nasale* is exposed between the palatal shelve and the posteriorly placed vomers.

Most of the dorsal margin of the nares is formed by the ***nasal***. The nasal is a roughly rectangular element, slightly wider in its anterior portion. Each nasal is separated from its opposite in the midline by the nasal process of the premaxilla. The medial border of the nasal has a shelf, dorsally covered by the premaxilla. The posterior border and most of the medial border of each nasal meets the anteromedial process of the frontal; however the contact of the nasal medial shelf with the frontal is hindered in dorsal view by the overlapping premaxilla. The nasal laterally contacts with the maxilla.

The ***maxilla*** is a trirradiate element; it forms the posterolateral and ventral margins of the nares, the ventral margin of the orbit, and the lateral margin of the fenestra for the Jacobson's organ. Ventrally, it has an alveolar region that bears 11 to 12 unicuspid pleurodont teeth. There are three large processes: the premaxillary (anterior), the facial (dorsal) and the orbital (posterior). Medially, there is a palatal shelf continuous to the alveolar region, beginning at the premaxillary process and ending at the orbital process. On the palatal shelf, close to the base of the facial process, an horizontal crest is present where the lateral process of the septomaxilla dorsally rests.

In its anterior end the premaxillary process bifurcates in a short and slender anterolateral process that slightly bends dorsally, and a larger and wider anteromedial process. Both processes overlap the premaxilla, the anterolateral process overlaps the maxillary process and the anteromedial process overlaps dorsally the palatal shelf of the premaxilla. The anteromedial process tip also touches the anterior process of the vomer. The facial process of the maxilla meets the nasal in its anterior margin, posteriorly lies over the prefrontal, and at its junction with the orbital process contacts with the lacrimal. The maxilla contacts with the palatine on the palatal shelf; posterior to that contact the maxilla forms the anterior margin of the suborbital fenestra. The posterior end of the orbital process of the maxilla is joined medially to the ectopterygoid and dorsally to the jugal. The maxilla is pierced by the alveolar canal that anteriorly opens at the premaxillary process and posteriorly at the orbital process. The lateral surface of the maxilla is perforated by several labial foramina (one to four), with intraspecific variation and often bilaterally asymmetric.

ORBITAL REGION

Each ***prefrontal*** shows a broad ventral region and a slender dorsal region that tapers forming the supraorbital process; medially, the prefrontal shows a transversal lamina that forms the posterior wall of the nasal cavity. The medial border of the prefrontal together with the palatine and the frontal limits the orbitonasal fenestra. Two processes arise from the transversal lamina; the palatine process at the ventromedial corner, and another process at the dorsomedial corner that is posteriorly directed. The palatine process forms the medial margin of the lacrimal foramen. The prefrontal is in tight joint with the frontal, dorsally it reaches the anterolateral border of the frontal, and medially the transversal lamina meets the anterior and the ventral borders of the frontal ventral process. Between the palatine process and the dorsomedial processes of the prefrontal there is a contact with the convex anterior border of the palatine. Anteriorly, the prefrontal meets ventrally the maxilla and dorsally the nasal. Posterolateraly, the prefrontal shows a small notch where the lacrimal fits.

The ***lacrimal*** is a small and slightly enlarged element, broader in its anterior tip and it borders the anteroventral orbital margin. It limits the lateral rim of the lacrimal foramen and joins in its anterior extreme with the prefrontal and ventrally with the maxilla.

The posterior and ventral borders of the orbit are formed by the ***jugal***. It is a sigmoid shaped bone that is ventrally expanded on its maxillary process and tapers posteriorly towards the temporal process. The jugal touches the maxilla and the ectopterygoid at the maxillary process; whereas the temporal process joins syndesmotically with the postorbital bone. At the base of the jugal a foramen is present.

TEMPORAL REGION

The temporal region, located between the orbit and the otico-occipital region, shows the ***postfrontal*** which forms the dorsal and posterior margin of the orbit and the anterior limit of the supratemporal fossa. It is flat, slightly arched and embraces laterally the frontoparietal suture. The lateral margin of the postfrontal joins syndesmotically to the postorbital and in its medial margin with the frontal and parietal in the same way.

The lateral border of the supratemporal fossa is formed by the ***postorbital***, which also limits the orbit dorsally and posteriorly. It is an elongate bone, slender and almost straight but with a slight curvature. Its anterior end is slightly expanded and the posterior end is acute. Laterally, the postorbital joins in its anterior extreme with the jugal by syndesmosis, and its posterior extreme rests on the squamosal.

The posterior region of the supratemporal arch is formed by the ***squamosal*** that borders the posterior and lateral region of the supratemporal fossa. It is a laminar bone, elongated, and posteriorly bends ventrally. Its anterior process is acute and joins to the postorbital. It joins with the supratemporal by syndesmosis and articulates ventrally with the quadrate.

The ***quadrate*** is placed in ventral position with respect to the squamosal, it shows a slight lateral concavity, a gentle pronounced tympanic crest, a broad cephalic condyle, and a narrower mandibular condyle. It has two crests as well, one posterior and another medial. The articulation with the squamosal lies in a dorsally placed notch, anterior to the cephalic condyle. The cephalic condyle articulates with the paraoccipital process and is very close to the columella. The mandibular condyle is involved with the ventral mandible articulation. The quadrate articulates with the pterygiod bone medially, near the mandibular condyle.

The ***supratemporal*** is placed among the squamosal, the cephalic condyle of the quadrate and the paraoccipital process of the otico-occipital region. It is very small and oval-shaped. The supratemporal is connected to the squamosal and the quadrate by connective tissue.

Between the pterygoid and the parietal lies the ***epipterygoid*** in a vertical position. It is a cylindrical element that does not reach the skull roof in its dorsal tip. Ventrally, it articulates with the pterygoid by a condylar extreme. The dorsal tip laterally touches the descending process of the parietal bone.

OTICO-OCCIPITAL REGION

The ***basisphenoid*** is posteriorly wide and anteriorly narrow (Fig. 2A-B), and shows a smooth internal surface that is slightly concave. The posterior edge of the basisphenoid raises in a weak *crista sellaris*, as a consequence it has a shallow *dorsum sella*. Laterally and posteriorly, a stout, triangular and anterolateraly directed alar process arises. On the lateral face of the alar process extends the anterior portion of the crista prootica, which ends at a small anterior process on the lateral border of the basisphenoid. Anteriorly, the basisphenoid rises dorsally forming a slender rostral process, which shows a smooth dorsal surface without *crista trabecularis*. The basipterygoid processes arise in the ventrolateral margins of the basisphenoid, they are widely separated, anterolaterally directed and they have an almost horizontal position. Each basipterygoid process is crossed by two crests: a ventrolateral crest, which extends reaching the exterior opening of the posterior foramen of the vidian canal; the other crest rises on the dorsal face of the basipterygoid process. The *recessus vena jugularis* lies between the ventrolateral crest and the crista prootica. The basiesphenoid is pierced by four foramina belonging to the vidian canal. The posterior foramen is found near the suture with the prootic; it communicates internally with the carotid foramen in the base of the alar process. In front of the carotid foramen the basisphenoid shows another foramen in which the vidian canal continues; finally, the vidian canal ends in a medial foramen at the base of the basipterygoid process. The openings for the abducens canal are found posterior to the *crista sellaris* and anteriorly in the base of the alar process. The basisphenoid is fused with the basioccipital posteriorly and dorsally with the prootic at the posterior margin of the alar process. The anterior tip of the rostral process is continuous with the cartilage *trabecula communis*; the parasphenoid process is absent. The anterolateral margin of the rostral process is very close to the ventral border of the orbitosphenoid bone. The basisphenoid articulates with the pterygoid by means of the anterior tips of the basipterygoid process in the palatobasal articulation.

The anteroventral limit of the braincase is formed by the ***orbitosphenoid*** (Fig. 2A and Fig. 3), it is a broad and laminar element, very close to its opposite, and shows a tilted position in a similar angle as the rostral process of the basisphenoid. Its medial margin is interrupted by a large notch for the optical foramen. The lateral margin is irregular and it is attached to short cartilaginous orbitotemporal remnants. In front of the medial notch the orbitosphenoid attaches to the posterior region of the orbotitemporal cartilage *planum supraseptale*.

The ***prootic*** forms the anterior part of the otic capsule (Fig. 2); it is mainly shaped by the *osseous labyrinth*. The prootic shows a bulked dorsal region, which encloses the vestibular cavity, and a ventral region that encloses the lagenar cavity. A constriction is present between the vestibular and lagenar cavities, it is formed in its front by the trigeminal notch and posteriorly by the foramen ovale. The prootic extends posteriorly as far as the foramen ovale. The alar process forms the lateral wall of the braincase together with the parietal, and the inferior process lies ventrally to the alar process. On the lateral surface of the prootic bulges the prominences of the anterior and horizontal semicircular canals, and its ampular recess, as well as the prominence of the lagenar recess ventrally. The crista prootica is present in the ventral region on the prootic; it begins at the basisphenoid, continues on the inferior process of the prootic, and ends at the facial foramen. The latter is close to the foramen ovale and is at the same level as the trigeminal notch. The *recessus vena jugularis* lies below the crista prootica and continues in the basiesfenoid bone. On the internal surface at the same level as the trigeminal notch, the utricular prominence is observed as a wide horizontal ridge. Ventral to the utricular prominence and anterior to the prominence of the lagenar recess, the acoustic recess is present with two foramina: the posterior auditory foramen and the anterior auditory foramen. The internal facial foramen is placed anteroventrally with respect to the acoustic recess. The prootic shows synostosic unions with the basisphenoid anteriorly, with the exoccipital and basioccipital posteriorly, and with the supraoccipital dorsally.

The ***exoccipital*** forms the posterior part of the otic capsule (Fig. 2). Similar to the prootic, the exoccipital enclose a large dorsal vestibular cavity and a ventral lagenar cavity that dictate its shape. With its opposite, the exoccipitals form the lateral portions of the occipital condyle and between them lies the basioccipital. Laterally each exoccipital borders the foramen magnum. Anteriorly, the exoccipital forms the posterior margin of the foramen ovale and behind the foramen ovale lies the short and anteriorly directed paraoccipital process. On its lateral face, the exoccipital shows the prominences of the horizontal and posterior semicircular canals, and the prominence of the posterior ampullar recess. The jugular recess is found below the prominence of the posterior ampullar recess, where the exterior vagus foramen opens; ventral to the vagus foramen, three hypoglossal foramina are present lined in anteroventral direction. Internally, posterior to the prominence of the vestibule (tympanic bulla) is found the internal vagus foramen, below it there are three openings for the internal hypoglossal foramina. The perilymphatic foramen is placed in the backside of the prominence of the lagenar recess (opening into the lagenar cavity), and the internal opening of the foramen rotundum is present in close proximity. There is a deep occipital recess, which opens in a narrow and elongated (slit like) foramen rotundum with a tilted position. The occipital recess is posteriorly limited by the *crista tuberalis*, which arises at the base of the paraoccipital process and reaches the anteroventral margin of the exoccipital (on the spheno-occipital tubercle). The *crista interfenestralis* also arises at the base of the paraoccipital process; it forms the posteroventral margin of the faramen ovale, reaches the spheno-occipital tubercle, and limits the occipital recess anteriorly. In posterior view, the *crista interfenestralis* and the *crista tuberalis* are not at the same level, since the *crista interfenestralis* is more pronounced with respect to the *crista tuberalis*.

The ***supraoccipital*** extends between the otic capsules (Fig. 2A-B), forms the dorsal closure of the neurocranium (enclose the otic capsule) and borders dorsally the foramen magnum. In the midline, the supraoccipital shows a constriction that separates the vestibular cavities of each side. The supraoccipital has a small *processus ascendens* anteriorly, with a slightly calcified cartilaginous tip. The supraoccipital shows a depression on the midline between the vestibular cavities, extending between the foramen magnum and the *processus ascendens*; the prominences of the anterior and posterior semicircular canals are observed on the dorsal surface as well. The supraoccipital is crossed dorsally by a transversal crest, which arises above the paraoccipital process of the exoccipital, parallel to the the exoccipital-prootic suture, reaching the *processus ascendens*. The tympanic bullae bulge ventral to the supraoccipital, each one is pierced by the endolymphatic foramen. The supraoccipital is ventrally fused with the prootic anteriorly and with the exoccipital posteriorly. It is sutured to the parietal anterior to the transversal crest. The cartilaginous tip of the *processus ascendens* fits into the parietal fossa.

The braincase floor is formed mainly by the ***basioccipital*** (Fig. 2A-B); it is pentagonal-shaped with a long and slender posterior apex, which is dorsally curved and forms part of the occipital condyle. Its ventral and dorsal surfaces are smooth, and the dorsal one is slightly concave. It fuses with the basisphenoid anteriorly, with the prootic anterolaterally and with the exoccipital posterolaterally. Where the basioccipital, the prootic, and the exoccipital meet, the spheno-occipital tubercle is found, which forms the ventral margins of the occipital recess and the foramen rotundum.

The ***columella*** is very short and its shaft is nodular shaped (Fig. 2B); laterally it bears an extremely reduced extracolumella and medially the foot plate is very large; almost fitting the foramen ovale completely. The columella is placed very close to the paraoccipital process posteriorly and to the cephalic condyle of the quadrate anteriorly.

MANDIBLE

The ***dentary*** is crossed by Meckel's canal, which is posteriorly closed by the splenial, but is open at the anterior extreme where Meckel's cartilage is visible. The alveolar region of the dentary bears 13 to 15 unicuspid pleurodont teeth. The dentary articulates with its opposite in its anterior end, in the mandibular symphisis. The dentary contacts with the coronoid dorsally, and covers the postdentary compound bone in labial view and the angular ventrally.

The ***angular*** is placed posterior to the dentary; it is small and forms the ventrolateral angle of the mandible.

The ***splenial*** is found in lingual view. It is oval-shaped with sharp extremes, and partially closes Meckel's canal. Posteriorly the splenial contacts with the postdentary compound bone and the angular, dorsally and ventrally respectively. Two anterior foramina are present, one large and dorsal, and another small and ventral.

The ***coronoid*** lies dorsally and forms the coronoid process. It is rounded and has three processes: the posteromedial, the anteromedial, and the anterolateral processes. The coronoid lies dorsal to the postdentary compound bone and the splenial; it contacts the dentary anteriorly and also contacts the dentary with its anterolateral process.

The posterior half portion of Meckel's canal is formed by a ***postdentary compound bone*** product of the postnatal fusion of the articular and surangular, and it has a large adductor fossa. The articular surface of the mandible is present behind the adductor fossa, which has a tilted position. Posteriorly there is a narrow retroarticular process. On the lingual face of the postdentary compound bone, anterior to the retroarticular process, is present a slightly pronounced angular process, although it resembles like a crest rather than a process. The postdentary compound bone contacts all the elements of the inferior mandible, dorsally with the coronoid, ventrally with the angular, laterally with the dentary, and medially with the splenial.

POSTNATAL DEVELOPMENT

NEONATES

All the bones that compound the adult skull are present in the neonates. Some of the chondrocranium and splachnocranium components are partially ossified. The skull roof is ossified only at the posterior and lateral margins of the parietal and the lateral margins of the frontal, thus leaving a large frontoparietal fontanelle on the roof. The post-temporal fossa is open. The dorsal and ventral extremes of the epipterygoid and the quadrate bones are caped by cartilage; the articular surface and the extreme of the retroarticular process in the mandible are covered also by cartilage. There are some apophyseal ossifications: on the cephalic condyle of the quadrate, on the dorsomedial portion of the articular surface and on the retroarticular process. The elements of the otico-occipital region are sutured synchondrotically; the extremes of the basipterygoid processes and paraoccipital processes are caped by cartilage, and the *processus ascendens* of the supraoccipital is cartilaginous. The spheno-occipital tubercles are barely observed; they are covered by a large apophyseal ossification that lies over them. The anterior border of the basisphenoid is not well defined, it lacks the rostral process, and instead of it is the pituitary fossa (Fig. 3). Between the basisphenoid and the basioccipital there is a basicraneal fenestra. The prootic lacks the alar crest and the parietal descending processes are short and slender, leaving the lateral wall of the braincase open. The orbitosphenoid is less broad than in the adult, but it is ossified and sketches the shape and position of the adult. In neonates the orbitosphenoid is present as a compound bone; it has a core endochondral ossification with membranous growths around it (Fig. 4). Table 1 and 2 summarize the most significant events in postnatal development.

DISCUSSION

The skull of *Bachia bicolor* is very similar to the skull of other gymnophthalmid lizards (MacLean, 1974; Montero *et al.*, 2002; Bell *et al.*, 2003) and to the skull of some studied species of *Bachia* (MacLean, 1974; Soares, 2000). However, the skull of *B. bicolor* also shows convergent morphological similarities with other fossorial/bourrowing serpentiform lizards.

The evolution of a serpentiform body plan seems to be a frequent event, which has occurred independently within squamate lizards (Estes *et al.*, 1988; Lee, 1998). Several authors point out that characters like limb reduction, body elongation, miniaturization and cranial modifications would be functionally correlated as an adaptation to fossoriality (Lee, 1998, Rieppel, 1981, 1984, 1996). Rieppel (1981, 1984, 1996) states that those characters were integrated in the origin of the serpentiform body plan; the cranial skeleton was modified in parallel to the postcranial skeleton, following a trend within an adaptative scenario (burrowing habits), and ending in a serpentiform lizard with particular cranial modifications. These modifications would be associated with evolutionary processes like miniaturization, with reduction in head and body diameter.

In the genus *Bachia* Presch (1975; see also Dixon, 1973) claims that limb reduction, body elongation, and reduction in head and body diameter are correlated with the evolution of this group towards fossorial habits, which suggest that *B.*

bicolor can be regarded as a transitional lizard between the saurian and the serpentiform ecomorphs. *B. bicolor* shows convergent craneal characters with different serpentiform lizards of Scincidae, Amphisbaenia, Dibamidae, Ophidia, Pygopodidae (Rieppel, 1981, 1984; Rieppel & Zaher, 2000; Lee, 1998; Greer 1985; Montero & Gans, 1999; Kearney, 2003): short preorbital region, large oticooccipital region, closed post-temporal fossa, closed lateral wall of the braincase, slit-like foramen rotundum, complex frontoparietal suture, large footplate of the columella, reduced tympanic crest of the quadrate, reduced parietal supratemporal process, short epipterygoid, broad orbitosphenoid, short and anteriorly directed paraoccipital processes, an almost plane basiesphenoid internal surface, very low *dorsum sellae*, extended but barely pronounced *crista sellaris,* and low interorbital septum.

Hence, lizards like *B. bicolor* show the coexistence of several of those body plan modifications, such as: body elongation, limb reduction, short snout and enlarged skull posterior region (increased oticooccipital region relative to the dermatocranium); however, the morphological cranial modifications of *B. bicolor* relative to most squamate lizards are discrete, since they are displayed on isolated traits, apparently not integrated, and apparently related to the small size. Considering that limb reduction and body elongation is evident within the genus *Bachia*, the interspecific variation suggests that the postcranial body plan has more liberties, whereas the cranial structural design shows more restriction.

There are some shared similarities in the skull of *B. bicolor* with other species of *Bachia* (Bell *et al.*, 2003; Soares, 2000; Presch, 1980; Hoyos, 1998, MacLean, 1974): preorbital shortening, descendent frontal lateral margins without touching each other medially, W-shaped frontoparietal suture, reduced maxillar teeth number, free lacrimal, small quadrate, small ends of the basipterygoid process, reduced columella shaft with increased footplate size, opened Meckel's canal, and an enlarged splenial. Some regions show interespecific variation: presence of a premaxillar nasal process reaching the frontal and separating the nasals in the midline, vertical or tilted epipterygoid, open or closed supratemporal fossa.

Bachia bicolor share more general characters with other gymnophthalmid lizards like: fused frontals, lack of pineal foramen, frontal tabs overlaping the parietal, secondary plate, compound postdentary element (Presch, 1976; Estes *et al.*, 1988; Bell *et al.*, 2003; Montero *et al.*, 2002). Furthermore, the skull of *B. bicolor* shows some derived morphological similarities present in particular groups within Squamata (Estes *et al.*, 1988) as described below. The vidian canal is open on the basiesfenoid dorsal surface, as described in Ophidia (Estes *et al.*, 1988; Rieppel & Zaher, 2000) and Dibamidae (genus *Anelytropsis* and *Dibamus*) (Greer, 1985); however, the position of the external foramina (anterior and posterior) are similar to that of other lizards (Oelrich, 1956) rather than those present in Ophidia and Dibamidae. The trabecular cartilages and a portion of the cartilage *trabecula communis* ossify during postnatal development forming the basiesfenoid rostral process, that condition has been only observed in Pygopodidae (Stephenson, 1961; Underwood, 1957). The name septosphenoid has been recommended for that process (Bellairs & Kamal, 1981); however, that ossification is flat in *B.bicolor* rather than tubular as described in Pygopodydae. The sphenooccipital tubercles ventral surface are caped by a broad apophisis; in adults that apophisis fuses to the oticoocciptal region, as described in

Amphisbaenia (Kearney, 2003; Montero & Gans, 1999) and the skinks *Acontias* and *Feylinia* (Rieppel, 1981).

A remarkable feature of the skull of *B. bicolor* is the orbitosphenoid bone. In most squamate lizards the orbitosphenoid is small, arch-shaped, it is formed by the ossification of orbitotemporal cartilages (*taenia medialis*, *pila metoptica* and neighboring regions) (Bellairs & Kamall, 1981), and it borders the optic foramen posterolaterally. As described before, the orbitosphenoid in *B. bicolor* is paired, broad and plane, in close proximity with its opposite in the midline and it shows a tilted position in an angle similar to the basisphenoid rostral process. In *B. bicolor* the orbitosphenoid closes the braincase anteroventraly, but it does not touch any skull element. In Amphisbaenia the orbitosphenoid is very different to other squamates, since it is unpaired, azygous, and closes the braincase anteroventrally. In contrast to *B. bicolor* in Amphisbaenia the orbitosphenoid shows a tight contact with the parabasisphenoid, frontal and parietal (Montero & Gans, 1999; Maisano *et al.*, 2006). The analyses of embryological material in Amphisbaenia (Bellairs & Gans, 1983; Montero, Gans & Lions, 1999) reveals that the orbitosphenoid bone is a compound bone (chondral [of dubious identity] and membranous ossifications), for that reason the name “tabulosphenoid” was recommended in view of its unique morphology not homologous to the orbitosphenoid bone of most squamates (Montero & Gans, 1999; Montero, Gans & Lions, 1999). On the other hand, Kritzinger (1946) described in the amphisbaena *Monopeltis capensis* paired orbitosphenoids, anteriorly fused to its opposite and posteriorly diverged in two lateral wings. In addition, recent work based on high-resolution X-ray computed tomography, revealed that in the amphisbaenid fossil *Rhineura hatcherii* no tabulosphenoid-like element exists, instead it shows a paired element, relatively broad and close to its opposite medially, identified by Kearney *et al.* (2005) as the orbitosphenoid. The latter is roughly similar to the orbitosphenoids in *B. bicolor*, however the orbitosphenoids in *R. hatcherii* are inside the braincase, enclosed by the frontals, and lacks an optic foramen.

In contrast to other lizards, the orbitosphenoid of *B. bicolor* is not expanded by the ossification of orbitotemporal cartilages during postnatal development (Bellairs & Kamall, 1981). The neonates of *B. bicolor* present an ossified orbitosphenoid, which shape and position are similar to the adult morphology, but it expands nearly closing the braincase anteroventrally without the ossification of adjacent orbitotemporal cartilages during postnatal development. In neonates the orbitosphenoid is observed as a compound element, since it has the endochondral ossification of the orbitotemporal cartilages connected to the *planum supraseptal,* and membranous ossifications around and continuous to those cartilages, giving it a broader shape in neonates, and growing during postnatal development until it reaches the adult shape/size.

In summary, the orbitosphenoid in *B. bicolor* is a broad element that forms part of the braincase floor; although it is not as enlarged as in most amphisbaenians, it resembles the element observed in *R. hatcherii*. The orbitosphenoid in *B. bicolor* is attached to the *planum supraseptal* but does not contact any other skull elements; whereas in most amphisbaenians it does, but it does not attach to any orbitotemporal cartilages. The orbitosphenoid is a compound bone in *B. bicolor*, it has a chondral nucleus (attached to the *planum supraseptal*) with membranous growths around it, which expand during postnatal development, similar to the ontogenetic origin of this element in Amphisbaenia. An exhaustive analysis on the orbitosphenoid variation during ontogeny within Squamata would establish the equivalence or homologies of the orbitosphenoid components in *B. bicolor.* At the moment it can only be claimed that the orbitosphenoid in *B. bicolor* shows unique and distinctive features with respect to most Squamata, and that is structurally similar to Amphisbaenia.

Excluding the observed conditions in the orbitosphenoid and basisphenoid rostral process, the neonatal state of ossification and the pattern of postnatal development follow the general pattern described until now in other squamates (Rieppel 1992; Maissano; 2001, Barahona & Barbadillo, 1998): there is a large frontoparietal fontanelle on the skull roof, which ossifies towards the midline fusing the parietals and the frontals (azygous in Gymnophthalmidae; Estes *et al.*, 1988; Maissano, 2001), open basicranial fenestra in neonates, and the fusion of neurocranial elements, apophyses and ossified secondary centers.

Some of the convergent features observed in the skull of *B. bicolor* with respect to other serpentiform lizards, arise entirely during postnatal development, such as: the lateral wall of the braincase, the closure of postemporal fossa, the anteroventral closure of the braincase by the expansion of the orbitosphenoid, and the ossification of the basisphenoid rostral process. Other characters showing interspecific variation within Gymnophthalmidae arise during postnatal development as well (as noted by Barahona & Barbadillo, 1998 for some Lacertid lizards, and Bell *et al.*, 2003 for *Neusticurus ecpleopus*) like the complex W-shaped frontoparietal suture and the frontal ventral process. Therefore, an important role for the postnatal heterochronic changes in the modification of cranial structural design within Gymnophthalmidae and Squamata can be suggested, as mentioned by Rieppel (1993, 1996) for the origin of the Ophidian skull morphology.

The data presented in this work, in relation to morphologies in postnatal development (basisphenoid and orbitosphenoid ossification, for instance), would be significant when considering the interspecific variation related to heterochronic patterns in a phylogenetic analysis of the species of *Bachia*.

Bachia bicolor is an elongated, limb reduced and small sized lizard; traits that at first glance place *B. bicolor* among the transitional forms in the evolution of serpentifom body plans. The structural design of *B.bicolor* skull has shared features with other species of *Bachia* and with other gymnophthalmid lizards as well. However, some isolated features such as the basisphenoid rostral process only described in serpentifom lizards of Pygopodidae and the compound orbitosphenoid bone (chondral and membranous), insinuate important structural changes in cranial anatomy, which highlights the need to explore other species of *Bachia* and Gymnophthalmidae within a phylogenetic framework.

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FIGURES.

FIGURE 1.

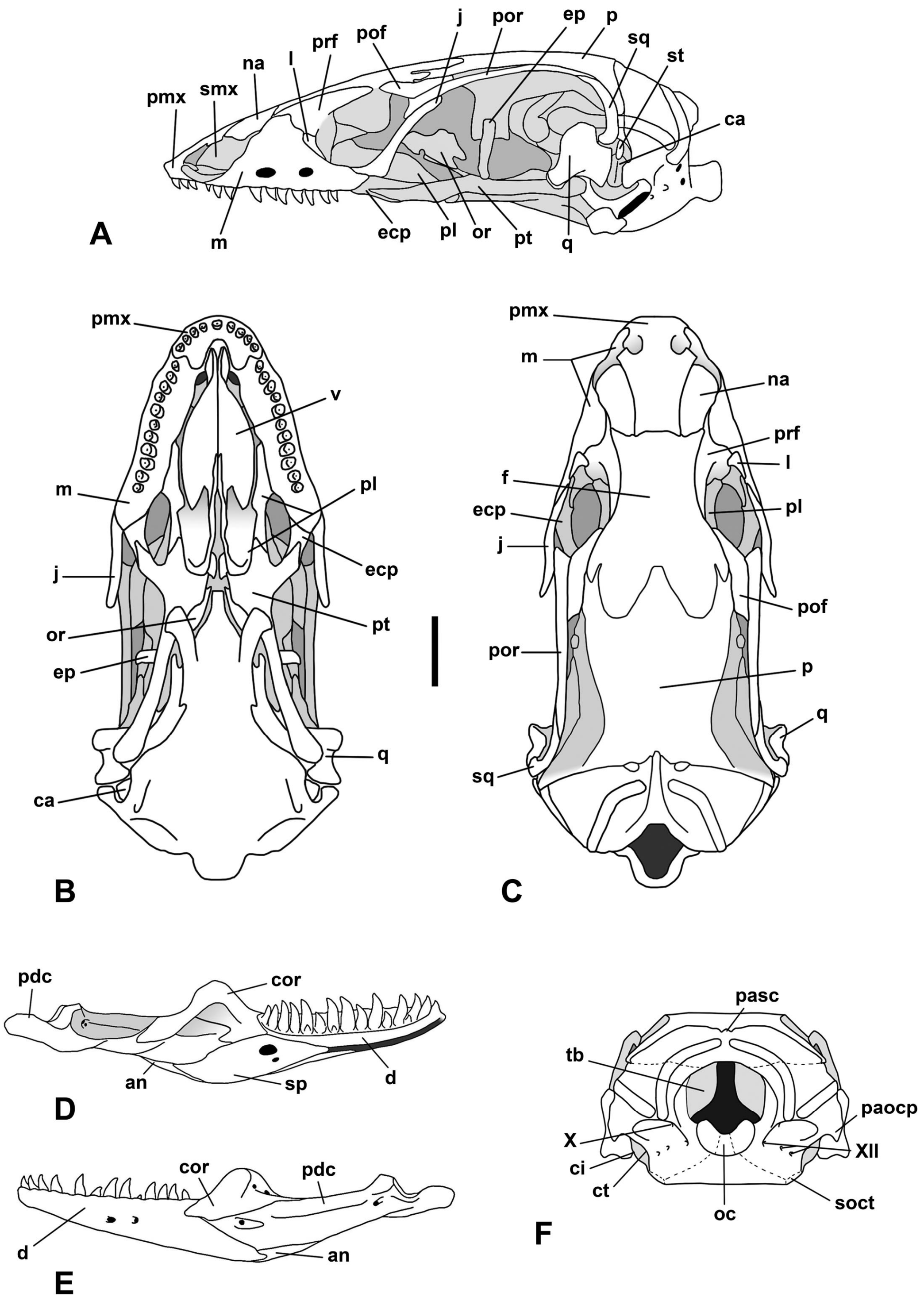

FIGURE 2.

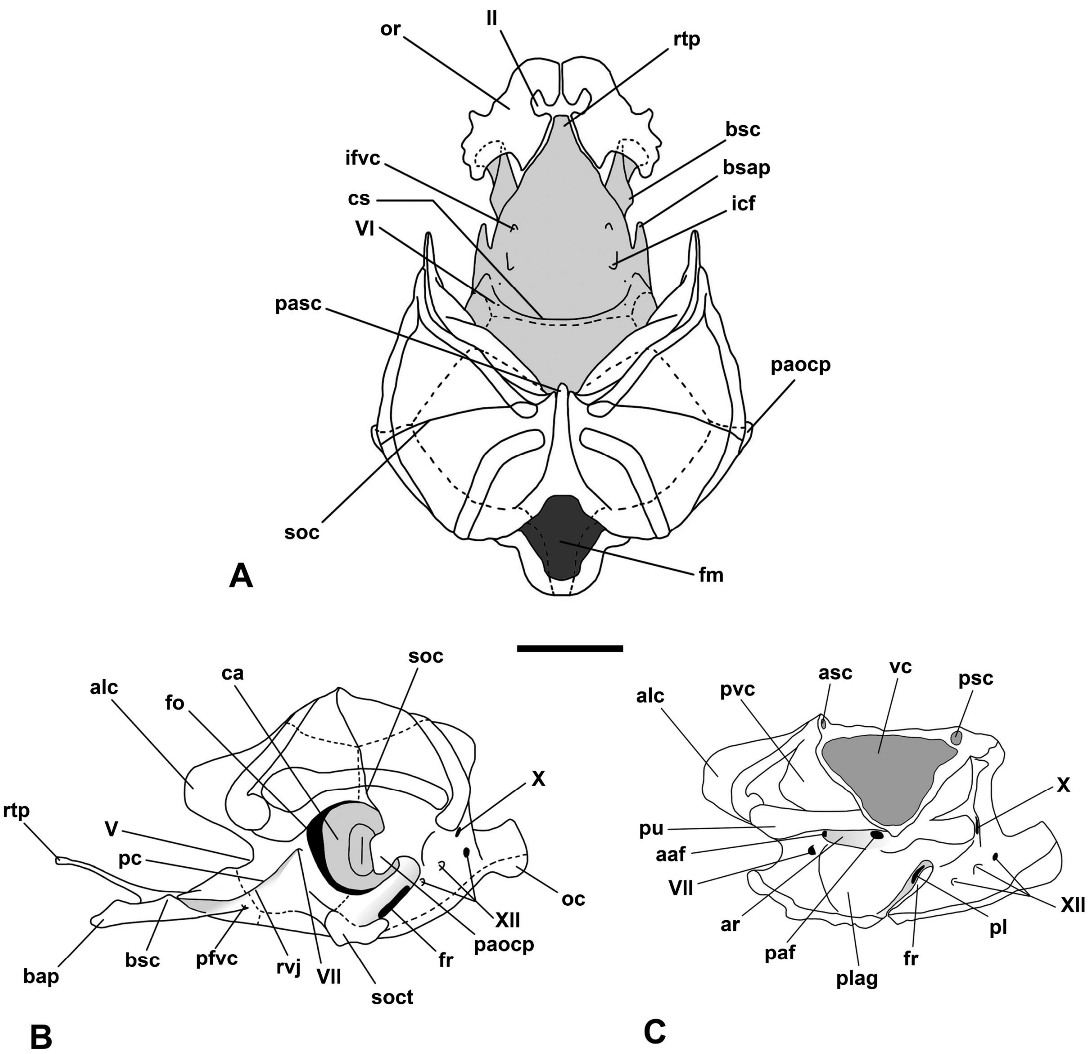
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FIGURE 3.

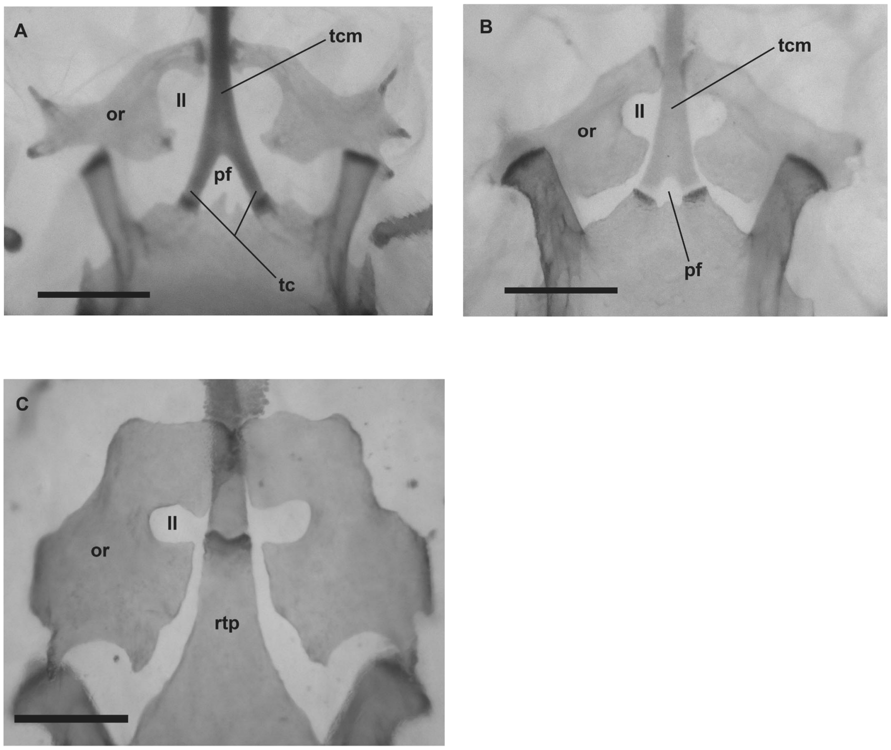

FIGURE 4.

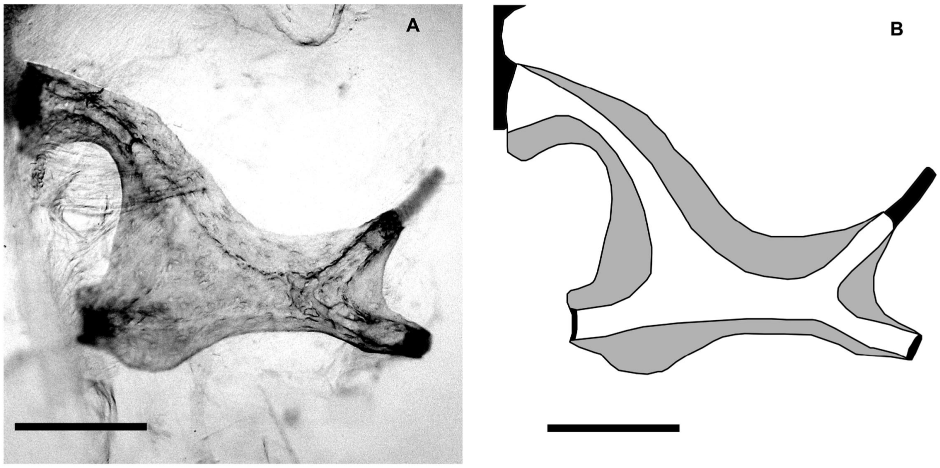

FIGURE LEGENDS.

Figure 1. Adult skull and mandible of *Bachia bicolor* (UIS-R-1459). A, Skull, lateral view. B, skull, platal view. C, skull, dorsal view. D, left mandible, lingual view. E, left mandible, labial view. F, skull, posterior view. Doted lines indicates in F the suture lines betwen neurocranial elements. Scale bar= 1 mm. an angular; ca columella; ci *crista interfenestralis*; cor coronoid; ct *crista tuberalis*; d dentary; ecp ectopterygoid; ep epipterygoid; f frontal; j jugal; l lacrimal; m maxilla; na nasal; oc occipital condyle; or orbitosphenoid; p parietal; pasc supraoccipital *processus ascendens*; pdc postdentary compound bone; pl palatine; pmx premaxilla; pof postfrontal; por postorbital; paocp paraoccipital process; prf prefrontal; pt pterygoid; q quadrate; sa surangular; smx septomaxilla; sp splenial; sq squamosal; st supratemporal; soct spheno-occipital tubercle; tb tympanic bulla; v vomer.

Figure 2. Adult otico-occipital region partially disarticulated of *Bachia bicolor*. (UIS-R-1446) A, dorsal view. B, lateral view. C, internal view (UIS-R-1448), partially disarticulated otico-occipital region, the right prootic and exoccipital are observed. Doted lines indicate the suture lines between neurocranial elements in A and B, and the hidden basipterygoid extremes by the orbitosphenoid in A. Scale bar =1 mm. aaf anterior auditory foramen; alc alar crest; asc anterior semicircular canal; ar acoustic recess; bap basipterygoid process; bsc basiesphenoid dorsal crest; ca columella; cs *crista sellaris*; fm foramen mágnum; fo foramen ovale; fr foramen rotundum; icf internal carotid artery foramen; ifvc internal foramen for the vidian

canal; oc occipital condyle; or orbitosphenoid; paf posterior auditory foramen; paocp paraoccipital proces; pasc supraoccipital *processus ascendens*; pc prootic crest; pfvc posterior foramen for the vidian canal; pl perilymphatic foramen; plag prominence for the lagenar cavity; psc posterior semicircular canal; pu prominence of the utricule; pvc prominence of the vestibular cavity; rtp rostral process; rvj *recessus vena jugularis*; soc supraoccipital transversal crest; soct spheno-occipital tubercle; vc vestibular cavity; *II* optic notch; *V* trigeminal notch; *VI* foramen for abducens; *VII* facial foramen; *X* vagal foramen; *XII* hypoglossal foramina.

Figure 3. Anterior braincase region, the orbitosphenoid and the anterior basiesfenoid region are observed, anterior to the top. A, neonate (ventral view, UIS-R-1452). B, juvenile (ventral view, UIS-R-1438). C, adult (dorsal view, UIS-R-1453). Note the orbitosphenoid growing and the osification of the trabecular cartilages and *trabecula communis*. Scale bars = 0.5 mm. or orbitoesphenoid; pf pituitary fossa; rtp rostral process; tc trabecular cartilages; tcm *trabecula communis*; *ll* optic foramen notch.

Figure 4. Neonate right orbitosphenoid in dorsal view, anterior to the top (UIS-R-1452). A, photograph. B, schematic drawing, cartilage is represented in black, membranous ossifications in gray and endochondral bone in white. Scale bar = 0.25 mm.

Table 1. The most significant events in postnatal development of *Bachia bicolor* skull, according to five stages of snout-vent length.

Elements	Neonate-40 mm	40-50 mm	50-60 mm	60-70 mm
Frontals	Fuses to its opposite. The ventral process arises, and reaches 1/4 of its maximum extension.	The ventral process reaches half of its maximum extension.	The ventral process reaches 3/4 of its maximum extension.	The ventral process reaches its maximum extension.
Parietal	A long slit in the midline is still present.	Ossifies completely	Completely ossified.	Completely ossified.
Prefrontal	The posterior process reaches 1/4 of its maximum extension.	The posterior process reaches the half of its maximum extension.	The posterior process reaches its maximum extension.	Together with the frontal, completes the orbital medial wall.
Quadrate	It shows two apophyses, on the tympanic crest and on the cephalic condyle.	Apophyses growth.	Apophyses growth.	The apophyses fuse.

Epipterygoids	It does not reach the parietal.	Contacts the parietal laterally.	Contacts the parietal laterally.	Contacts the parietal laterally. Dorsal and ventral epiphyses fuse.
Neurocranium	Elements joined by synchondrosis.	Elements joined by synchondrosis.	Elements joined by synchondrosis.	All the elements fuse.
Basisphenoid	The trabecular cartilages ossiffy, reaching half of its length.	The trabecular cartilages ossifiy, reaching 3/4 of its length.	The trabecular cartilages ossifiy completely, and fuse with its opposite medially. The dorsal crest of the basipterigoid process arises.	The *trabecula comunis* ossifies, forming the rostral process. The basipterygoid processes ossifies completely on its tips.
Exoccipital	It shows lateral apophyses on the paraoccipital process.	The lateral apophyses on the paraoccipital process grow.	It shows ventral apophyses on the paraoccipital process.	The apophyses fuses, the paraoccipital process ossifies completely.
Prootic	The alar crest arises, in	The alar crest extends, in	The alar crest reaches the	The alar crest reaches its

	front of the ampullar prominence.	front of the ampullar prominence and above the semicircular canal.	descending process of the parietal, closing the braincase laterally.	maximum extension.
Postdentary compound bone	It shows two apophyses on the articular surface, one dorsomedial and the other dorsolateral.	The articular surface is ossifying.	The articular surface ossifies completely, the apophyses fuse.	The apophyses on the retroarticular process fuses. The surangular and articular bones fuses.

Table 2. Postnatal development of cranial spaces of *Bachia bicolor* according to five stages of snout-vent length.

Craneal spaces	Neonate-40 mm	40-50 mm	50-60 mm	60-70 mm
Postemporal fenestra	Open	Reduced	Closed	Closed
Frontoparietal fontanela				
Basicraneana fenestra				
Pituitaria fosa	Open	Open	Reduced, ossified margins	Closed

APPENDIX 1.

Specimens of *Bachia bicolor* examined. Specimen number is followed by snout-vent length and sex (where known). Neonates: UIS-R-1465, 25.48 mm; UIS-R-1452, 27.52 mm. Juveniles: UIS-R-1252, 28.18 mm; UIS-R-1451, 30.58 mm; UIS-R-1450, 31.62 mm; UIS-R-1253, 32.50 mm; UIS-R-1456, 36.96 mm (female); UIS-R-1245, 40.24 mm; UIS-R-1251, 40.32 mm; UIS-R-1462, 42.84 mm; UIS-R-1438, 45.00 mm; UIS-R-1461, 45.72 mm; UIS-R-1455, 47.69 mm; UIS-R-1443, 48.04 mm. Adults: UIS-R-1458, 49.31 mm (male); UIS-R-1447, 50.46 mm (female); UIS-R-1246, 51.28 mm; UIS-R-1247, 52.35 mm; UIS-R-1464, 54.97 mm (female); UIS-R-1445, 56.73 mm (female); UIS-R-1460, 57.24 mm (male), UIS-R-1248, 58.14 mm; UIS-R-1448, 59.00 mm (male); UIS-R-1437, 61.02 mm; UIS-R-1249, 61.42 mm (female); UIS-R-1250, 62.05 mm (male); UIS-R-1439, 62.21 mm; UIS-R-1444, 62.33 mm (female); UIS-R-1449, 62.40 mm (male); UIS-R-1441, 63.51 mm; UIS-R-1454, 64.16 mm (female); UIS-R-1442, 64.30 mm (male); UIS-R-1440, 64.32 mm; UIS-R-1446, 65.84 mm (male); UIS-R-1453, 66.27 mm (male); UIS-R-1459, 67.69 mm (male); UIS-R-1457, 69.60 (male); UIS-R-1463, 71.39 mm (female).