EMBRYONIC SKULL DEVELOPMENT IN THE NEOTROPICAL VIVIPAROUS SKINK
MABUYA (SQUAMATA: SCINCIDAE)

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RESUMEN. La sistemática del género Mabuya ha sido extensamente estudiada en América y se han propuesto varios arreglos taxonómicos con base en análisis moleculares. Sin embargo, aspectos relacionados con la morfología del esqueleto, su desarrollo y variación ontogenética han sido poco estudiados en este género. En el presente trabajo se describe el desarrollo embrionario del cráneo en tres especies del género Mabuya y se compara con el de la especie africana Trachylepis capensis. Se encontró que el género Mabuya presenta diferencias en el desarrollo del cráneo respecto a la especie africana, incluyendo la pila antótica, el orbitosfenoides, el vómer, y el cierre de la fenestra basicraneal. Estas diferencias en el desarrollo del cráneo son importantes, ya que su presencia en todo el género Mabuya sugiere que se podría tratar de sinapomorfías para este clado.

PALABRAS CLAVE: Desarrollo craneal, condrocráneo, Mabuya, Scincidae, Squamata

INTRODUCTION

The genus Mabuya constitutes a monophyletic unit with a recent diversification, and exhibits a unique combination of reproductive features in Squamata (Blackburn & Vitt 1992; Mausfeld et al. 2002; Carranza & Arnold 2003; Whiting et al. 2006; Miralles & Carranza 2010).

Until recently, the pantropical genus Mabuya included more than a hundred species distributed in America, Africa and Asia (Greer & Nussbaum 2000; Greer et al. 2009). However, on the basis of a molecular phylogenetic analysis this genus was divided into four clades (Mausfeld et al. 2002). In this way, the genus Mabuya actually includes about 53 species, distributed from Mexico to Argentina (Ávila-Pires 1995; Mausfeld et al. 2002; Miralles et al. 2005). The other three clades are Trachylepis (Fitzinger 1843) in Africa, Chioninia (Gray 1845) in Cape Verde, and Eutropis (Fitzinger 1843) in Asia (Mausfeld et al. 2002; Bauer 2003). We follow this taxonomic proposal and all species in this work are regarded to the genus Mabuya.

All Mabuya species present viviparous reproduction, smooth scales, lower eyelid with a semi-transparent disc, pterygoid teeth absent, and 25-31 presacral vertebrae (Mausfeld et al. 2002). This genus inhabits mainly lowland forests and evolved with a group of specializations related to viviparity, which are unique among reptiles and convergent only with placental mammals: a long period of gestation (9 to 12 months) and microlecithal eggs (0.9-2.2 mm) with a highly placental trophic nutritional pattern (Blackburn & Vitt 1992; Blackburn 1993; Jerez & Ramírez 2001, 2003).

Despite the recent phylogenetic and taxonomic interest in the evolution of the genus Mabuya (Mausfeld et al. 2002; Carranza & Arnold 2003; Jesus et al. 2005; Miralles et al. 2005; Whiting et al. 2006; Miralles et al. 2009; Miralles & Carranza 2010; Hedges & Conn 2012), osteological and ontogenetic descriptions in comparative
studies are scarce. Regarding African species, Skinner (1973) described the ontogenetic and adult morphology in *Trachylepis capensis* skull, whereas Rao & Ramaswami (1952) described the fully formed chondrocranium and the adult osteocranium of the Asian *Eutropis carinata*. Concerning American species, Jerez (2012) described the adult skull of Colombian Andean population of *Mabuya* sp., and Caicedo (2012) analyzed the adult skull in different species and populations in Colombia.

Hence, the main purpose of this work is to describe the development of the embryonic skull in *Mabuya* sp., *M. cassaira* and *M. macrorhyncha*. In addition, the chondrocranium of *Mabuya* is compared with the species of the old world *Trachylepis capensis* and *Eutropis carinata*, therefore, these morphological studies could provide additional anatomical characters to support the taxonomic status of this American clade as monophyletic. This is particularly important, given that Hedges & Conn (2012) proposed sixteen genera for America. On the other hand, though many molecular phylogenetic analyses support the monophyly of American clade (Mausfeld et al. 2002; Carranza & Arnold 2003; Jesus et al. 2005; Whiting et al. 2006; Miralles & Carranza 2010), some herpetologists consider that the division of pantropical genus *Mabuya* in four genera has been premature (Jesus et al. 2005; Whiting et al. 2006).

**RESULTS**

*Mabuya* sp. Stage 32-33 (Fig. 1): In this stage, elements of three regions of the chondrocranium are observed: the anterior ethmoidal region, the intermediate orbitotemporal region, and the posterior occipital region (Table 1). In the ethmoidal region, the cartilages of the nasal capsule start being condensed. The interorbital septum is low and contacts the trabecula communis. In the posterior region, the skull consists of the basal plate and the occipital arch. The elements of splanchocranium, the quadrate, the ascending process and the Meckel’s cartilage are observed

**MATERIALS AND METHODS**

We described the skull development in an Andean population of *Mabuya* sp. and compared it with the transandean species *M. caissara* and *M. macrorhyncha*. *Mabuya* is widely distributed in Colombia (Sánchez et al. 1995) and their populations represent a complex of species (Avila-Pires 1995; Miralles et al. 2005; Miralles 2006). According to Miralles (2005) neither *M. mabouya* nor *M. nigropunctata*, nominations for populations in Colombia, are present in the Andean Colombian regions. For this reason, in this work the studied population is referred as *Mabuya* sp. The embryos of *Mabuya* sp. were taken from females of a population collected at the Inspección de Policía Guadualito, in the Municipality of Yacopi, Cundinamarca, Colombia. They are housed in the Colección Herpetológica, Escuela de Biología, Universidad Industrial de Santander.

A series of twelve embryos of *Mabuya* sp. was selected (UIS-R-289, 310, 311, 314, 319, 320, 321, 351, 355, 366, 404, and 415). Stages of development follow Defaure & Hubert (1961), this table starts at stage 1 with the cleavage and ends at stage 40 with the hatching. The series studied include embryos from limb bud stage (stage 32) to preparturition stage (stage 40). The chondrocranium of *Mabuya* sp. was compared with that of *M. cassaira* and *M. macrorhyncha*, two Brazilian species. We described a series of eight embryos of *M. cassaira* from Bertioga, SP Brazil (MZUSP-40720, MZUSP-40771, MZUSP-40777, MZUSP-40779, MZUSP-45703), and five of *M. macrorhyncha* from Guarujá, SP, Brazil (MZUSP-40695, MZUSP-40792, MZUSP 40800) and Ilha dos Búzios, SP, Brazil (MZUSP-11148, MZUSP 11176). In this comparison we described embryos of stages 32, 39 and 40 (D&H) for all species. The stage 34 (D&H) is described just for *Mabuya* sp. The skeletal embryonic development was described using cleared and double-stained specimens, prepared following Wassersug (1976). The description of the chondrocranium follows those of Bellairs & Kamal (1981). In *Mabuya* sp. the first stage is described, while in the subsequent stages only the registered variations are explained. In contrast, with *M. caissara* and *M. macrorhyncha* only the differences relating to *Mabuya* sp. are reported.

![Figure 1](image-url)

**Figure 1.** Chondrocranium of *Mabuya* sp. at stage 32-33 (D&H). Abbreviations: asp, ascending process; atl, atlas; axi, axis; bpl, basal plate; mc, Meckel cartilage; nc, nasal capsule; oca, occipital region; ors, interorbital septum; pt, pterygoid; q, quadrate; tc, trabecula communis. Scale bar: 1 mm.
(Table 1). The Meckel’s cartilages are fused at the symphisis and caudally the retroarticular process is present. Regarding to the dermatocranium, the pterygoid starts to ossify (Table 2).

Differences with *Mabuya macrorhyncha*: in this stage the cartilages of ethmoidal and orbitotemporal regions are not clearly observed in the chondrocranium. However, the trabecula communis, the basal plate, the otic capsule and the occipital arch are totally visible (Table 1). In the dermatocranium, besides the pterygoid, the dentary starts to ossify in the anterior region of Meckel’s cartilage.

Differences to *Mabuya caissara*: There are no differences with this species (Table 1).

**Mabuya sp. Stage 34** (Fig. 2): In this stage the chondrocranium presents further development in orbitotemporal and occipital regions (Table 1). In the orbitotemporal region, the sphenethmoid commissures, a pair of arched slender cartilaginous rods, extends from the nasal capsule to the planum supraseptale. Then it forms a large fenestra olfactoria.

The interorbital septum has increased in height and appears continuously with the trabecula communis and
extends into the ethmoidal region of the chondrocranium shaping of the nasal septum. Furthermore, the interorbital septum begins to develop other cartilages from the orbito-temporal scaffolding. The taenia medialis, the pila metopica and the pila antotica are continuous cartilaginous rods. Further behind, the pila accessoriosa extends between the taenia marginalis and the pila antotica. This last one cartilage doesn’t contact the basal plate. The taenia marginalis extends between the pila accessoriosa and the dor-sal surface of the otic capsule. In the occipital region, the otic capsule is very conspicuous and presents the crista parotica. In this posterior region, the skull roof is formed by growth of the occipital arch and the otic capsule, then the tectum synoticum is observed. In this stage, the basi-cranial fenestra is small and separated from the pituitary fossa by the crista sellaris.

In relation to the dermatocranium, other bony elements start to ossify; these include the prefrontal, the frontal, the parietal, the supratemporal, the palatine, the dentary and the surangular (Table 2).

**Mabuya sp. Stage 39** (Figs. 3, 4): In this stage the chon-drocranium shows the configuration observed in the neo-nate. The principal changes are observed in the ethmoidal region, since the nasal cartilages are completely developed. The nasal capsule exhibits the parietectal and paranasal cartilages (Table 1).

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In the nasal region, the parietotectal cartilage presents de nasal cupola with the foramen apical and the narina. Posteriorly, the fenestra superior is very conspicuous dorsally. The paranasal cartilage exhibits the bifid maxillary process, and the planum antorbitale, which is perpendicular to nasal septum, but they are not in contact.

In the orbitotemporal region, the planum supraseptale is completely formed; rostrally is formed by a cartilaginous rod and caudally by a width cartilaginous shield with a short process in the anterior region. The interorbital septum presents the small anterior and ventral fenestra and the big posterior fenestra below the planum supraseptale. In this stage, the taenia marginalis extends from the planum supraseptale to the otic capsule. So the interobital scaffolding is completely formed with all present cartilages. The epiotic fenestra is closed by the taenia marginalis, the taenia medialis, the pila metoptica and the pila accessorius. On the other hand, the optic fenestra is closed by the pila metoptica and the interorbital septum. Finally, the fenestra prootica and metoptica are continuous because the pila antotica does not have contact with the basal plate.

In the occipital region, the otic capsule presents the fenestra ovalis, and the tectum synoticum exhibits the ascending process. Ventrally, the basipterygoid process is lengthy with the distal portion expanded and contacting...

Figure 2. Chondrocranium of Mabuya sp. at stage 34 (D&H). Abbreviations: ce, sphenethmoid commisure; is, interorbital septum; f, frontal; me, Meckel cartilage; nc, nasal capsule; cp, crista parotica; oc, occipital arch; oca, occipital region; p, parietal; pac, pila accessorius; pia, pila antotica; pm, pila metoptica; pf, prefrontal; pls, planum supraseptale; pt, pterygoid; pof, q, quadrate; pal, palatine; rb, ribs; st, tc, trabecula communis; tma, taenia marginalis; tme, taenia medialis; ver: vertebrae. 1. Fenestra epióptica, 2. Fenestra optica, 3. Fenestra prootica, 4. Fenestra metoptica. Scale bar: 1 mm.

Figure 3. Chondrocranium of Mabuya sp. at stage 39 (D&H). (A) Lateral view, (B) Dorsal view. Abbreviations: afe, anterior fenestra; apr, anterior process; bpl, basal plate; c, nasal cupola; ce, esphenethmoid commisure; ef, foramen ephiphaniale; pm, maxillary process; pac, pila accessorius; pfr, posterior fenestra; pia, pila antotica; pic, parietotectal cartilage; pm, pila metoptica; pla, planum antorbitale; pls, planum supraseptale; pnc, paranasal cartilage; q, quadrate; st, tectum synoticum; t, trabeculae; tma, taenia marginalis; tme, taenia medialis; vfe, ventral fenestra. 1. Fenestra epióptica, 2. Fenestra optica, 3. Fenestra prootica, 4. Fenestra metoptica. Scale bar: 1 mm.
the pterygoid. The crista sellaris is a cartilaginous bar that separates the pituitary fenestra and the basicranial fenestra. This last fenestra is small in this stage. Posteriorly, the fissura metotica is separating the basal plate and the otic capsule. The perilymphatic foramen is present.

In this stage, ossification is beginning in the chondrocranium. The basisphenoid begins to ossify in the proximal region of basipterygoid processes and the crista sellaris (Table 2). Moreover, the parasphenoid is beginning to be observed in the region of the pituitary fenestra.

Regarding splachnocranium, the quadrate is fully differentiated and appears ossified in the medial region. The ascending process has begun to ossify in the middle to form the epitypogyd bone. Meckel’s cartilage has become covered by the membrane bone of the lower jaw.

Regarding dermatocranium, in this stage all dermal bones are present (Table 2). The bony elements of temporal arch, palatine region and lower jaw are fully developed, while the bone elements of nasal and orbital regions are still being developed. This is remarkable in the frontal and parietal bone since only the lateral edges are present.

Differences to *Mabuya caissara*: this species differs to the others species in the nasal capsule, exhibiting a short rostral process and lacking the anterior process of the planum supraspetale in this stage. However, this species is similar to *Mabuya* sp. in the other characteristics of the nasal and orbital region (Table 1). Regarding splachnocranium, the columella is beginning the ossification. In this stage, the ossification of otic capsule, occipital arch and basal plate is more advanced than *Mabuya* sp. and *M. macrorhyncha*.

*Mabuya* sp. Stage 40 (Figs. 7, 8): In this stage the principal change is the advanced ossification of the whole skull. In the chondrocranium this is observed in the occipital and supraoccipital region; the prootico, otoccipital (opisthotic-exoccipital), basioccipital and basisphenoid are present. The parasphenoid is a triradiate bone observed in the anterior region of the pituitary fenestra. The basicranial fenestra is smaller and it is limited by the basisphe-
Figure 5. Chondrocranium of *M. macrorhyncha* at stage 39 (D&H). (A) Lateral view, (B) Dorsal view. Scale bar: 1 mm.

Figure 6. Dermatocranium of *M. macrorhyncha* at stage 39 (D&H). (A) Dorsal View, (B) Ventral view. Scale bar: 1 mm.
Figure 7. Dermatocranium of *Mabuya* sp. at stage 40 (D&H). (A) Dorsal view, (B) Ventral view. Abbreviations: bo, basioccipital; bs, basisphenoid; bfe, basicranial fenestra; ces, quadrate; epi II, epibranchial II; ps, parasphenoid; per, perilymphatic foramen; pro, prootic; otc, otoccipital otc; so, supraoccipital. Scale bar: 1 mm.

Figure 8. Dermatocranium of *Mabuya* sp. at stage 40, close to hatching. (A) Dorsal view, (B) Ventral view. Abbreviations: f, frontal; ffp, frontoparietal fenestra; ore, orbitosphenoid; ps, parabasisphenoid. Scale bar: 1 mm.
noid and basioccipital. The paroccipital process is formed by ossification of the crista parotica. The prootic presents the alar process, which is projecting towards the epityergoids, but does not contact this bone. Regarding dermatoocranium, all bony elements are notably more developed than the stage before except of the frontal and parietal. Consequently, the frontoparietal fenestra is present. In the lower jaw, all bone elements are completely developed.

Embryos in preparturition stage present minimal changes (Fig. 8). In the orbitotemporal region of chondrocranium, the orbitosphenoid is observed (Table 1). This is a semilunar ossification developed on the pila metotica. In the occipital region, the parabasisphenoid is formed by the fusion of basisphenoid and parasphenoid elements. Finally, the basicranial and pituitary fenestrae are closed (Table 1).

In the dermatoocranium, frontal bones are not fully differentiated in its posterior region yet. However, they are fused in the medial region. The parietal is completely differentiated except in the anterior region. Therefore, the frontoparietal suture is not formed and the frontoparietal fenestra is still present. This fenestra is smaller and extends as far out as the parietal foramen.

Differences to *Mabuya macrorhyncha* and *M. casisara* (Fig. 9): the only difference is observed in embryos in preparturition stage, where the basicranial fenestra is not completely closed (Table 1).

**DISCUSSION**

In general, *Mabuya* species included in this morphological study exhibit a complete chondrocranium, with the ethmoidal, orbitotemporal and occipital regions fully developed (Rao & Ramaswami 1952; Skinner 1973; Bellaris & Kamal 1981). In the ethmoidal region, the nasal capsule of the *Mabuya* is broad, very developed, and similar to other lizards such as the scincids *Chalcides ocellatus*, *Eutropis carinata* (= *Mabuya carinata*), *Pleistodon fasciatus* (= *Eumeces quinquelineatus*), *Trachylepis capensis* (= *Mabuya capensis*), *Lygosoma*, the lacertids *Lacerta vivipara*, and *Acanthodactylus boskiana*, the anguid *Anguis fragilis*, and the gymnophthalmid *Ptychoglossus bicolor* (Rice 1920; Pearson 1921; Rao & Ramaswami 1952; El Toubi & Kamal 1961; Skinner 1973; Bellaris & Kamal 1981; Hernandez et al. 2012).

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**Figure 9.** Dermatocranium of *M. macrorhyncha* at stage 40 (D&H). (A) Dorsal View, (B) Ventral view. Scale bar: 1 mm.
The ethmoidal region in *Mabuya* species shares a number of common characteristics with others skinks (Bellaris & Kamal 1981); these species exhibit a large fenestra superior in the nasal capsule (Table 1), and the fenestra lateralis is absent or small. In addition, *Mabuya* species, like other skinks (*C. ocellatus, E. carinata, P. fasciatus, T. capensis, Lygosoma*) present a large fenestra olfactoria (Rice 1920; Pearson 1921; Rao & Ramaswami 1952; Skinner 1973; Bellaris & Kamal 1981). This characteristic is probably related to the olfactory and chemosensory ability, since Hernandez et al. (2012) observed that gimnophthalmids species with a large fenestra olfactoria have the main and accessory olfactory bulbs well developed.

The scaffolding in orbitotemporal region changes with the body-plan, presenting reductions of some cartilages in serpentiniform skinks like *Lygosoma* sp., *Acontias meleagris* and *Chalcides saposoides* (Pearson 1921; Bellaris & Kamal 1981). In lacertiform skinks, the scaffolding is fully developed, like *C. ocellatus, P. fasciatus* and *T. capensis* (Rice 1920; El-Toubi & Kamal 1959; Skinner 1973); this last characteristic is observed in *M. cassaira, M. macrorhyncha* and *Mabuya* sp. On the other hand, the pila antotica is short and has no contact with the basal plate in *Mabuya* species (Table 1). This characteristic is observed in *C. ocellatus, T. capensis* and *Lygosoma* sp., while in *P. fasciatus* is absent (Pearson 1921; El-Toubi & Kamal 1959; Skinner 1973). In *Mabuya* species, the pila antotica is similar to that of *T. capensis*, which is short and only reaches the epiterigoyd position; however, during development *Mabuya* species present differences with African *T. capensis*, since Skinner (1973) observed that the pila antotica is contacting the basal plate in stages 32 to 35 (D&H), this contact being lost in later stages. In *Mabuya* species the pila antotica has not been seen in contact with the basal plate during embryonic development. While we do not have other skink species for further embryonic comparisons, it is nonetheless obvious that *Mabuya* species are different in the development of pila antotica in respect to *T. capensis*, thus indicating a difference between American and African clades in the development of this chondrocranial characteristic.

On the other hand, the differentiation of the orbitosphenoid, a semi-lunar ossification in the pila metoptica of the orbitotemporal region, is observed in the stage 40 (D&H) in *Mabuya* species (Table 1). In *T. capensis* it is developed in postembryonic stages, appearing in adults (Skinner 1973). A similar characteristic is probably present in *Lygosoma* sp., since the orbitosphenoid is not present in the fully formed chondrocranium of the embryo, but it is present in the adult stage (Rao & Ramaswami 1952). Therefore, the development of the orbitosphenoid in *Mabuya* species shows differences in the rate of ossification in respect to African and Asiatic species.

Regarding the ossification of chondrocranium (Table 2), in *Mabuya* species, it starts in stage 39 (D&H); after that, all elements of chondrocranium are ossified and joined by synchondrosis (stage 40 D&H). This condition is observed in general in lizards, e.g. *Trachylepis capensis, Elgaria coerulae, Liolaemus scapularis* and *PsychoGLOSSUS bicolor* (Skinner 1973; Good 1995; Lobo et al. 1995, Hernandez et al. 2012). In *Mabuya* species the basi-cranial fenestra and pituitary fossa are still present in stage 40 D&H. However, in the preparturition stage, the pituitary fossa is closed and the basi-cranial fenestra are closed or almost closed (similar to a slit). This is different from *T. capensis* where the pituitary fossa is closed in the preparturition stage, but the basi-cranial fenestra is still present in the juvenile stage.

In relation to the dermatocranium, the development of bony elements starts in stage 33 with the differentiation of the pterigoyd in *Mabuya* sp. and *M. caissara*, and the pterigoyd and dentary in *M. macrorhyncha* (Table 2). Posteriorly, in stage 34, other bony elements start to ossify (frontal, prefrontal, parietal, supratemporal, palatine, dentary and surangular). Finally, in stage 40 (D&H), all elements are almost completely developed, except for the frontal and the parietal ones, which only show the margins. In the pre-parturition stage, the frontal and parietal bones are almost fully differentiated; therefore, the frontoparietal fenestra is small and remains open. Dermatocranium development in *Mabuya* species is similar to the other lizards and the pterygoids appear early, as in *Elgaria coerulae* (Good 1995), *Trachylepis capensis* (Skinner 1973), and *Liolaemus scapularis* (Lobo et al. 1995). The other bony elements ossify early and correspond to the palatine, orbital and jaw region; this characteristic is observed in *Trachylepis capensis* (Skinner 1973), *Lacerta vivipara* (Rieppel 1992), *L. agilis* (Rieppel 1994) and *Elgaria coerulae* (Good 1995). We found that the entire ossification of parietal and frontal is observed in preparturition stages of *Mabuya* species, while in *T. capensis* it occurs in postnatal development (juvenile stage) (Skinner 1973). On the other hand, the vomer is a paired bony element in *Mabuya* embryos, but in postembryonic stage a distinctive bony element is formed by fusion, this is a characteristic of adult stages of *Mabuya* sp. (Jerez 2012), while in African and Asiatic species the vomer remains a paired bony element through their entire ontogeny.

Therefore, the skull development of the American *Mabuya* presents differences with *Trachylepis capensis* in the development of pila antotica, the differentiation of the orbitosphenoid, the closure of pituitary and basi-cranial fe-
nesteae, the ossification of parietal, and the development of vomer. Our evidences suggest that these characteristics should be regarded as diagnostic for Mabuya. Therefore, these unique developmental patterns of Mabuya sp., Mabuya caissara and M. macrorhyncha add weight to the systematic hypothesis (Mausfeld et al. 2002), splitting the American genus Mabuya from the African genera Trachylepis and Chioninia, and the Asian genus Chioninia.

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