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

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ABSTRACT. The systematics of the Americans skinks of the genus *Mabuya* have been extensively studied, with new arrangements based on molecular analysis. However, the skeletal morphology, their development and ontogenetic variation have been poorly studied in this genus. We described the embryonic skull development of three species of *Mabuya* and compare it with the African species *Trachylepis capensis*. We observed that American genus *Mabuya* presents differences in the skull development, including the pila antotica, orbitosphenoid, vomer, and the basicranial fenestra closure. These morphological differences in *Mabuya* species may be interpreted as putative synapomorphic characters.
Key words: Skull development, chondrocranium, *Mabuya,* skin, Scincidae, Squamata

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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 probremente 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.* 2000). 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 pro-

posal 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 placentotrophic 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).

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. macrorhycha. Mabuya* is widely distributed in Colombia (Sánchez *et al.* 1995) and their populations represent a complex of species (Ávila-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 Yacopí, Cundinamarca, Colombia. They are housed in the Colección Herpetologica, 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.

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 splachnocranium, the quadrate, the ascending process and the Meckel´s cartilage are observed
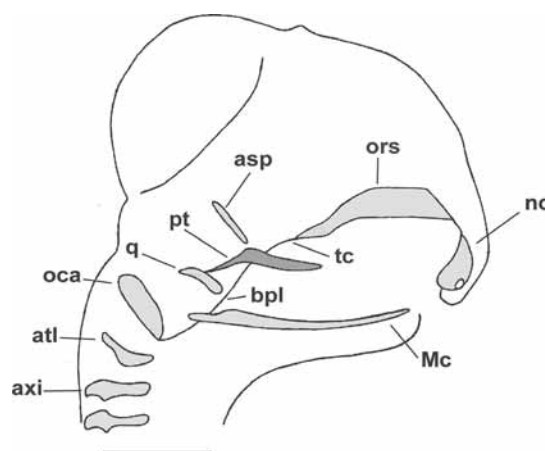
Figure 1. Chondrocranium of *Mabuya* sp. at stage 32-33 (D&H). Abbreviations: asp, ascending process; atl, atlas; axi, axis; bpl, basal plate; mc: Meckel cartilage; nc, nasal capsule; oca, occipital region; ors, interorbital septum; pt, pterygoid; q, quadrate; tc, trabecula communis. Scale bar: 1 mm.

Table 1. Major events of the skull development in three species of the Neotropical genus *Mabuya*. (Ms: *Mabuya* sp., Mm: *M. macrorhyncha*, Mc: *M. caissara*).

Stages	32			34			39			40			Preparturition		
Species	Ms	Mm	Mc	Ms	Mm	Mc	Ms	Mm	Mc	Ms	Mm	Mc	Ms	Mm	Mc
Chondrocranium															
Nasal cartilages	X	X	X												
Interobital septum	X	X	X												
Trabecula comunis	X	X	X												
Basal plate	X	X	X												
Occipital arch	X	X	X												
Capsula otica		X		X					X						
Sphenethmoid commissures				X				X	X						
Fenestra olfactoria				X				X	X						
High interorbital septum				X				X	X						
Nasal septum				X				X	X						
Taenia medialis, pila metoptica, pila accessoria				X				X	X						
Pila antotica does not contact the basal plate				X				X	X						
Basicranial fenestra				X				X	X						
Pariotectal and paranasal cartilages							X	X	X						
Fenestra superior							X	X	X						
Bifid maxillary process							X	X	X						
Planum antorbitale							X	X	X						
Planum supraseptale							X	X	X						
Basicranial fenestra							X	X	X						
Pituitary fenestra							X	X	X						
Basicranial fenestra small										X	X	X			
Pituitary fenestra small										X	X	X			
Orbitosphenoid													X	X	X
Basicranial fenestrae closed or almost closed													X	X	X
Fenestrae pituitary closed													X	X	X

(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

Table 2. Ossification sequence of the skull in three species of the Neotropical genus *Mabuya*.
(Ms: *Mabuya* sp., Mm: *M. macrorhyncha*, Mc: *M. caissara*).

Stages	32			34			39			40			Preparturition		
Species	Ms	Mm	Mc	Ms	Mm	Mc	Ms	Mm	Mc	Ms	Mm	Mc	Ms	Mm	Mc
Ossification sequence															
Pterygoid	X	X	X												
Dentary		X		X											
Prefrontal				X				X	X						
Frontal				X				X	X						
Parietal				X				X	X						
Supratemporal				X				X	X						
Palatine				X				X	X						
Surangular				X				X	X						
Premaxilla							X	X	X						
Maxilla							X	X	X						
Nasal							X	X	X						
Jugal							X	X	X						
Posfrontal							X	X	X						
Postorbital							X	X	X						
Squamosal							X	X	X						
Supratemporal							X	X	X						
Vomer							X	X	X						
Palatine							X	X	X						
Ectopterygoid							X	X	X						
Epipterygoid							X	X	X						
Manbible							X	X	X						
Basisphenoid							X	X	X						
Parasphenoid							X	X	X						
Basioccipital								X	X	X					
Exoccipital								X	X	X					
Prootico										X	X	X			
Ophistotic										X	X	X			
Frontoparietal fenestra small													X	X	X
Orbitosphenoid													X	X	X

extends into the ethmoidal region of the chondrocranium shaping of the nasal septum. Furthermore, the interorbital septum begins to develop other cartilages from the orbitotemporal scaffolding. The taenia medialis, the pila metoptica and the pila antotica are continuous cartilaginous rods. Further behind, the pila accessoria 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 accessoria and the dorsal 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 basicranial 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 chondrocranium shows the configuration observed in the neonate. The principal changes are observed in the ethmoidal region, since the nasal cartilages are completely developed. The nasal capsule exhibits the pariotectal and paranasal cartilages (Table 1).
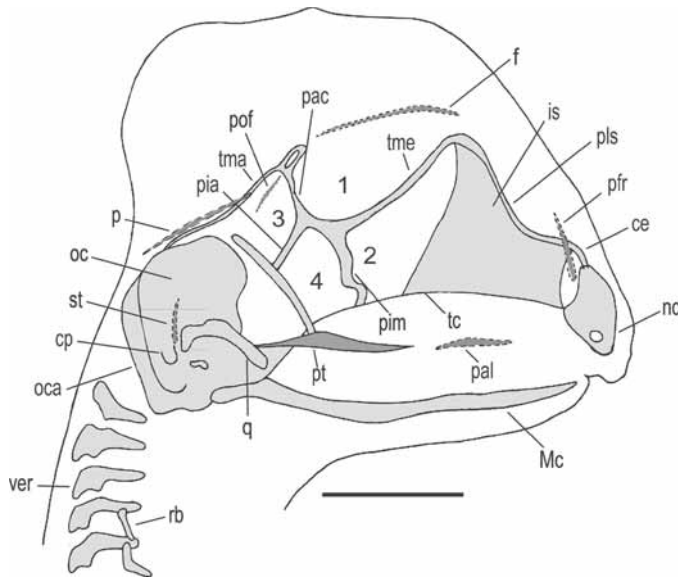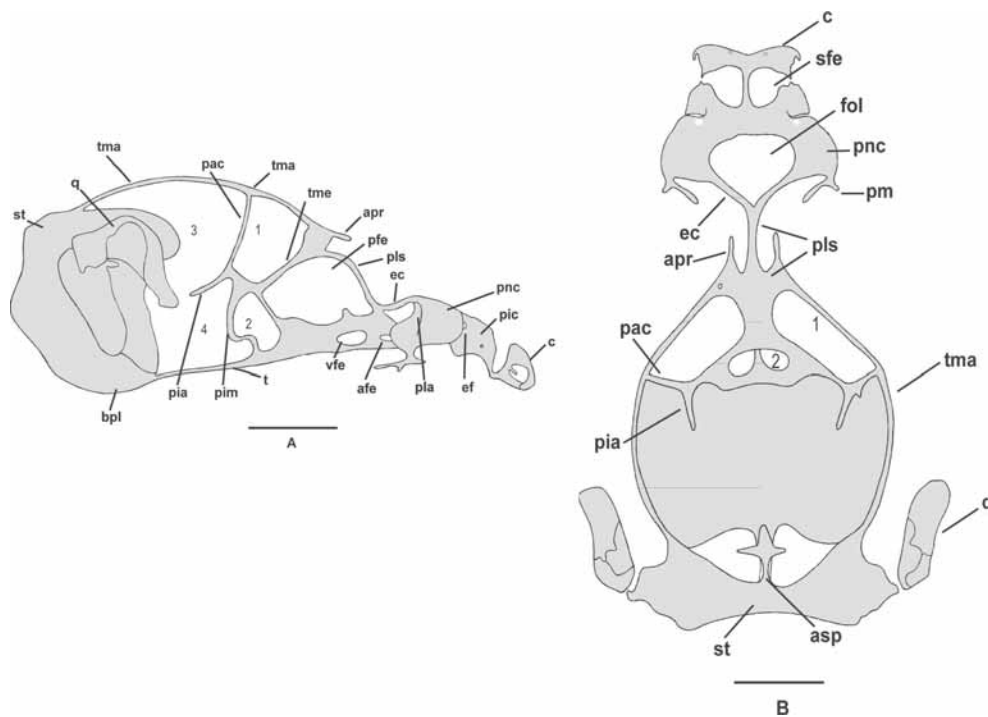
Figure 2. Chondrocranium of *Mabuya* sp. at stage 34 (D&H). Abbreviations: ce, sphenethmoid commisure; is, interorbital septum; f, frontal; mc, Meckel cartilage; nc, nasal capsule; cp, crista parotica; oc, occipital arch; oca, occipital region ; p, parietal; pac, pila accesoria; pia, pila antotica; pim, pila metoptica; pfr, 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.

In the nasal region, the pariotectal 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; rostraly 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 accessoria. 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 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; ec, esphenethomoid commisure; ef, foramen ephiphaniale; pm, maxillary process; pac, pila accessoria ; pfe, posterior fenestra; pia, pila antotica; pic, pariotectal cartilage; pim, pila metoptica; pla, planum antorbitale; pls, planum supraseptale; pnc, paranasal cartilage; q, quadrate; st, tectum synoticum; t, trabeculae; tma, taenis marginalis; tme, taenia medialis; vfe, ventral fenestra. 1. Fenestra epioptica, 2. Fenestra optica, 3. Fenestra prootica, 4. Fenestra metoptica. Scale bar: 1 mm.
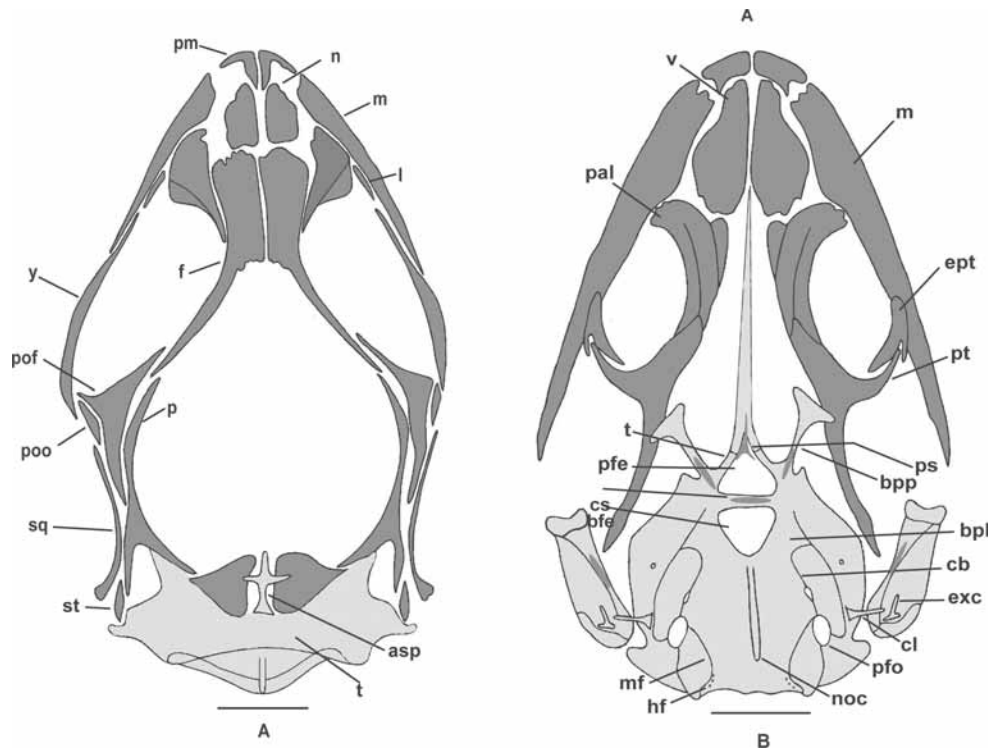
Figure 4. Dermatocranium of *Mabuya* sp. at stage 39 (D&H). (A) Dorsal View, (B) Ventral view. Abbreviations: asp, ascending process; bfe, basicranial fenestra; bpl, basal plate; bpp, basipterygoid process ; cb, basicapsular commisure; cl, columella; cs, crista sellaris; ept, ectopterygoid; exc, extra-columella; f, frontal; hf, hypoglossal foramen; m, maxilla; n, nasal; l, lacrimal; mf, fissura metotica; noc, notochord; p, parietal; pm, premaxilla; ps, parasphenoid; pt, pterygoid; pal, palatine; pfe, pituitary fenestra; pfo, perilymphatic foramen; pof, posfrontal; poo, postorbital; sq, squamosal; st, supratemporal; t, tectum synoticum; v, vomer; y, jugal. 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 epipterygoid 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 macrorhyncha* (Figs. 5, 6): the two species are very similar in their chondrocranium, although there are slight differences between them (Table

1). The fenestra lateralis is present in paranasal cartilage of the nasal capsule, and the anterior process of the planum supraseptale is shorter and thicker. The ossification is observed in the medial and posterior regions of the basal plate, which correspond to basisphenoid, basioccipital and exoccipital.

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 supraseptale 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 prootic, otoccipital (opisthotic-exoccipital), basioccipital and basisphenoid are present. The parasphenoid is a triradial bone observed in the anterior region of the pituitary fenestra. The basicranial fenestra is smaller and it is limited by the basisphe-
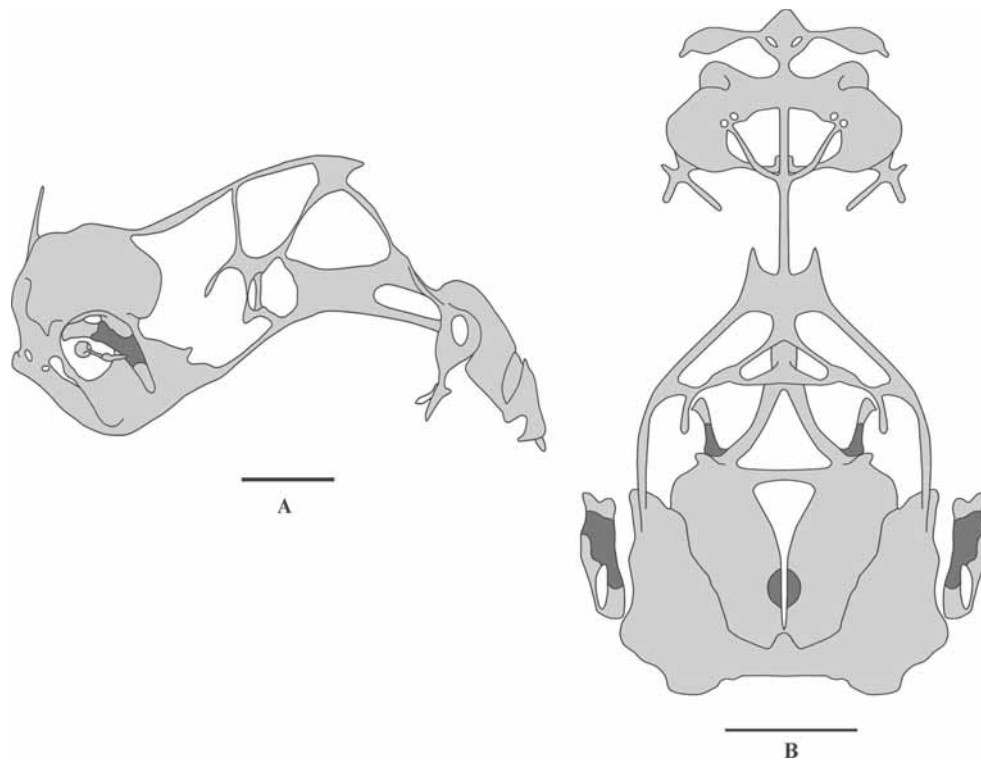
Figure 5. Chondrocranium of *M. macrorhycha at* stage 39 (D&H). (A) Lateral view, (B) Dorsal view. Scale bar: 1 mm.
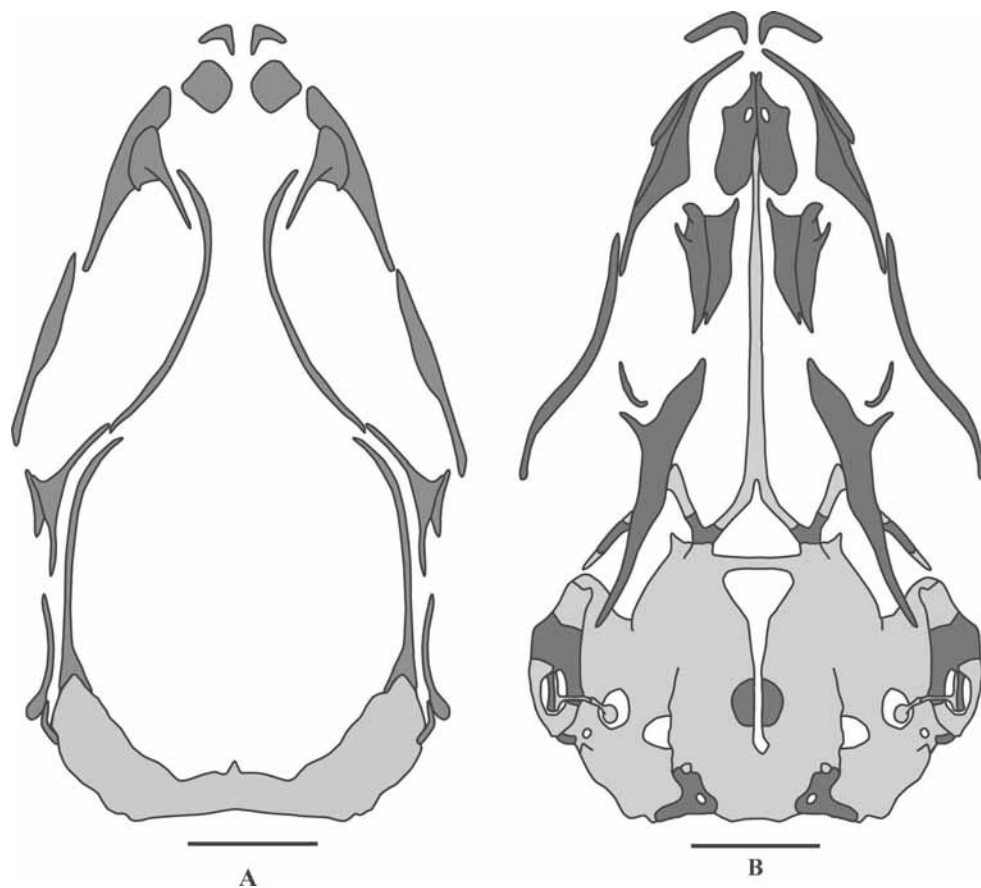
Figure 6. Dermatocranium of *M. macrorhyncha* at stage 39 (D&H). (A) Dorsal View, (B) Ventral view. Scale bar: 1 mm.
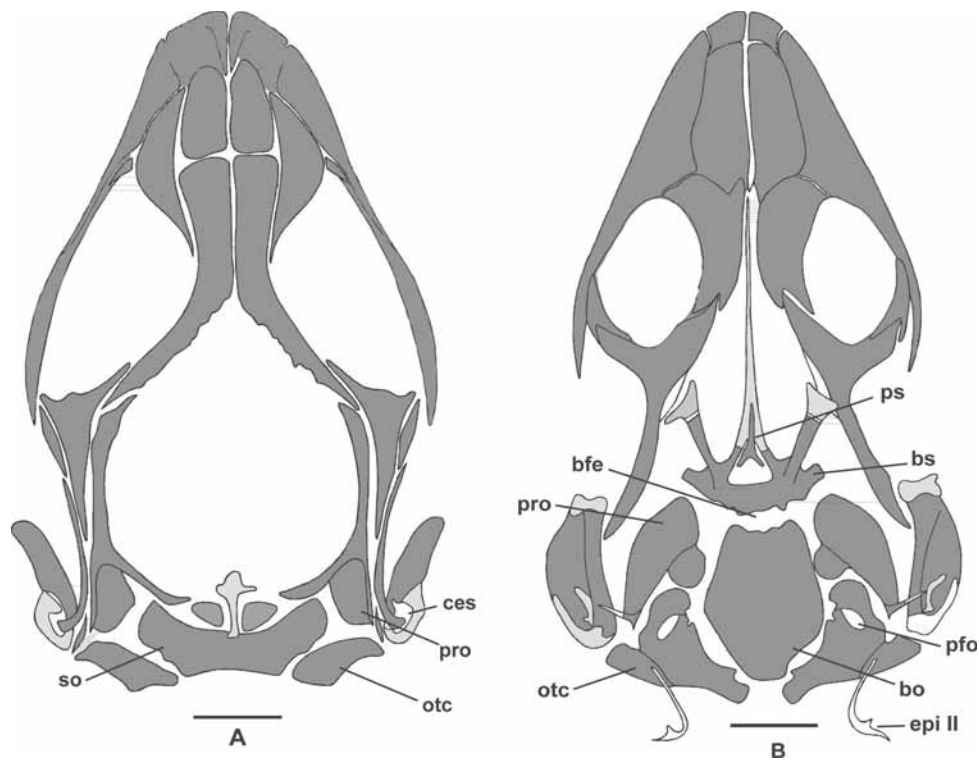
Figure 7. Dermatocranium of *Mabuya* sp. at stage 40 (D&H). (A) Dorsal view, (B) Ventral view. Abbreviations: bo, basioccipital; bs, basisphenoid; bfe, basicranial fenestra; ces, quadrate ; epi II, epibranchial II; ps, parasphenoid; per, perilymphatic foramen; pro, prootico; otc, otoccipital otc; so, supraoccipital. Scale bar: 1 mm.
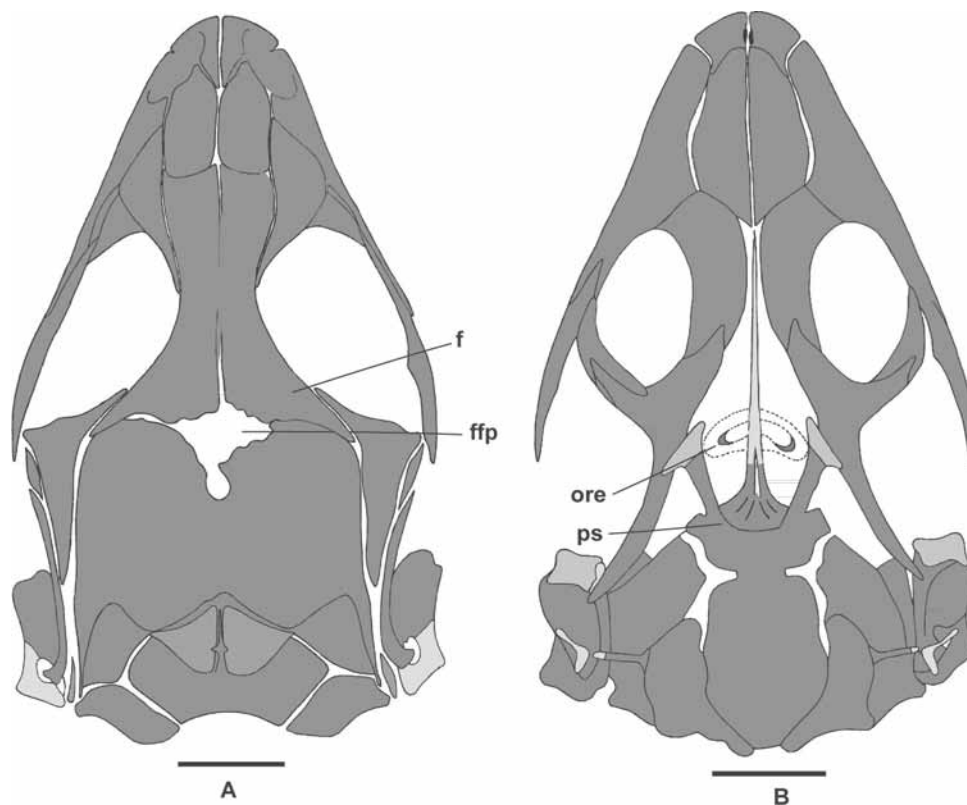
Figure 8. Dermatocranium of *Mabuya* sp. at stage 40, close to hatching. (A) Dorsal view, (B) Ventral view. Abbreviations: f,frontal; ffp, frontoparietal fenestra; ore, orbitosphenoid; ps, parabasisphenoid. Scale bar: 1 mm.

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 epipterygoids, but does not contact this bone. Regarding dermatocranium, 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 dermatocranium, 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. caissara* (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 others lizards such as the scincids *Chalcides ocellatus, Eutropis carinata* (= *Mabuya carinata*), *Plestiodon fasciauts* (= *Eumeces quinquelineatus*), *Trachylepis capensis* (= *Mabuya capensis*), *Lygosoma*, the lacertids *Lacerta vivipara,* and *Acanthodactylus boskiana*, the anguid *Anguis fragilis*, and the gimnophthalmid *Ptychoglossus bicolor* (Rice 1920; Pearson 1921; Rao & Ramaswami 1952; El Toubi & Kamal 1961; Skinner 1973; Bellaris & Kamal 1981; Hernandez *et al.* 2012).
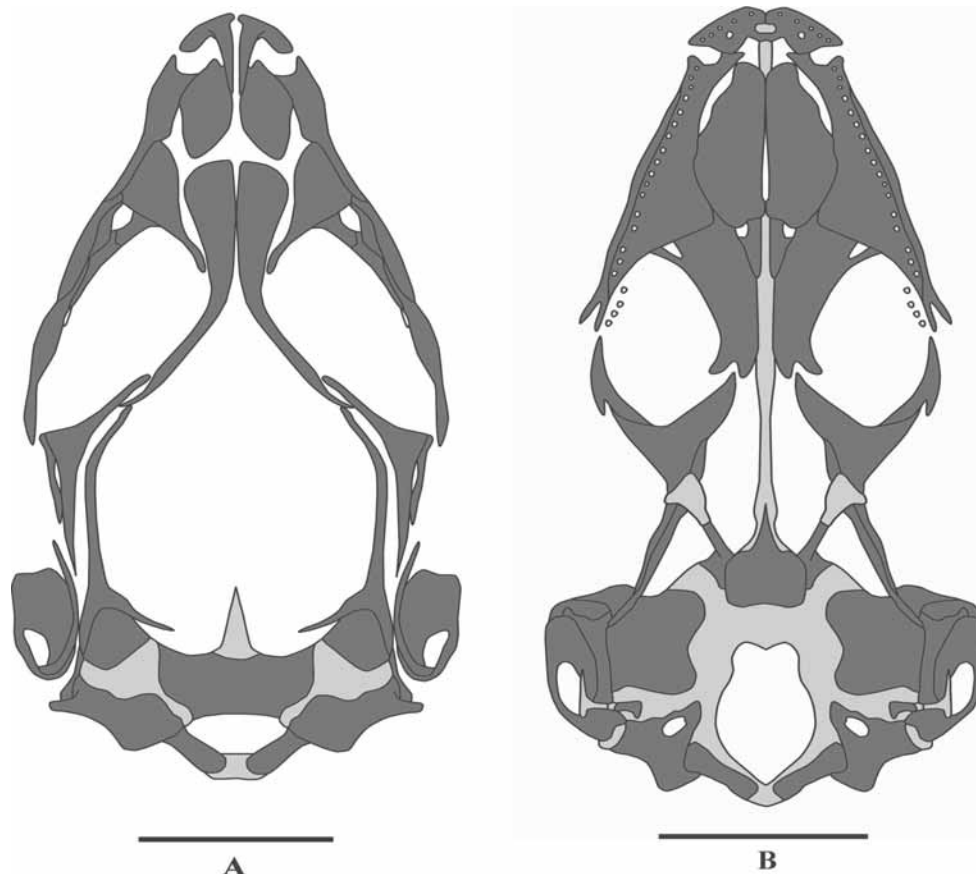
Figure 9. Dermatocranium of *M. macrorhyncha* at stage 40 (D&H). (A) Dorsal View, (B) Ventral view. Scale bar: 1 mm.

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 others skinks (*C. ocellatus, E. carinata, P. fasciauts, 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 serpentiform skinks like *Lygosoma* sp.*, Acontias meleagris* and *Chalcides sepsoides* (Pearson 1921; Bellaris & Kamal 1981). In lacertiform skinks, the scaffolding is fully developed, like *C. ocellatus*, *P. fasciauts* 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. fasciauts* 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 epipterigoyd 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 chondrocraneal 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 coerulea, Liolaemus scapularis* and *Ptychoglossus bicolor* (Skinner 1973; Good 1995; Lobo *et al.* 1995, Hernandez *et al.* 2012). In *Mabuya* species the basicranial fenestra and pituitary fossa are still present in stage 40 D&H. However, in the preparturition stage, the pituitary fossa is closed and the basicranial 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 basicranial 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 coerulea* (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 coerulea* (Good 1995). We found that the entire ossification of parietal and frontal is observed in preparturing 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 postembrionary 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 basicranial fe-

Acta Zool. Mex. (n.s.) 31(3) (2015)

401

nestrae, 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.*

LITERATURE CITED

Avila-Pires, T. C. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zoologische Verhandelingen*, 299: 1-706.

Bauer, A. M. 2003. On the identity of *Lacerta punctata* Linnaeus 1758, the type species of the genus *Euprepis* Wagler 1830, and the generic assignment of Afro-Malagasy skinks. *African Journal of Herpetology*, 52: 1-7.

Bellairs, A. & Kamal, M. A. 1981. The chondrocranium and the development of the skull in recent reptiles. pp 1-263. *In*: Gans, C. & Parson, T. S. (Eds.). *Biology of Reptilia*, Vol 11. Academic Press, London.

Blackburn, D. G. 1993. Choriallantoic placentation in squamate reptiles: structure, function, development, and evolution. *Journal of Experimental Zoology*, 266: 414-430.

Blackburn, D. G. & Vitt, L. J. 1992. Reproduction in viviparous South American lizards of the genus *Mabuya,* pp. 150-154. *In*: Hamlett, W. (Ed.). *Reproductive Biology of South American Vertebrates: Aquatic and Terrestrial.* Springer-Verlag, New York.

Caicedo-Portilla, J. R. 2012. Búsqueda y evaluación de caracteres morfológicos de posible utilidad filogenética y taxonómica del género *Mabuya* (Squamata: Scincidae) con base en especies presentes en Colombia. Tesis de Maestría. Universidad Nacional de Colombia, Bogotá D.C.

Carranza, S. &. Arnold, E. N. 2003. Investigating the origin of transoceanic distributions: mtDNA shows *Mabuya* lizards (Reptilia, Scincidae) crossed the Atlantic twice. *Systematics and Biodiversity*, 1: 275-282.

Dufaure, J. P. & Hubert, J. 1961. Table de developpment de lezard vivipare: *Lacerta* (Zootoca) *vivipara*. Jacquin. *Archives Anatomie Microscopie Morphologie Expérimental,* 50: 309-328.

El-Toubi M. R. & Kamal, A. M. 1959. The development of the skull of *Chalcides ocellatus*. I. The development of the chondrocranium. *Journal of Morphology*, 104:269-306.

El-Toubi M. R. & Kamal, A. M. 1961. The development of the skull of *Ptyodactylus hasselquistii*. I. The development of the chondrocranium. *Journal of Morphology*, 108: 63-93.

Fitzinger, L. J. 1843. *Systema Reptilium. Fasciculus Primus. Amblyglossae.* Vienna: Braumuller et Seidel Biblipolas, Vindobonae.

Good D. A. 1995. Cranial ossification in the northern alligator *Elgaria coerulea* (Squamata, Anguidae). *Amphibia-Reptilia*, 16: 157-166.

Gray, J. E. 1845. *Catalogue of the specimens of lizards in the collection of the British Museum.* London: The Trustees of the British Museum (Natural History).

Greer, A. E., Arnold, C. & Arnold, E. N. 2000. The systematic significance of the number of presacral vertebrae in the scincid lizard genus *Mabuya***.** *Amphibia-Reptilia*, 21: 121-126.

Greer, A. E. & Nussbaum, R. A. 2000. A new character useful in the systematics of the scincid lizard genus *Mabuya*. *Copeia,* 2000: 615-618.

Hedges, S. B. & Conn, C. E. 2012. A new skink fauna from Caribbean islands (Squamata, Mabuyidae, Mabuyinae). *Zootaxa*, 3288: 1-244.

Hernández-Jaimes, C., Jerez, A. & Ramírez, M. P. 2012. Embryonic development of the skull of the Andean lizard *Ptychoglossus bicolor* (Squamata, Gymnophthalmidae). *Journal of Anatomy,* 221: 285-302.

Jerez, A. 2012. Características estructurales del esqueleto en *Mabuya* sp. (Squamata: Scincidae): una comparación con escíncidos africanos. *Actualidades Biológicas*, 34 (97): 207-224.

Jerez, A. & Ramírez-Pinilla, M. P. 2001. The allantoplacenta of *Mabuya mabouya* (Sauria, Scincidae). *Journal of Morphology*, 249: 132-146.

Jerez, A. & Ramírez-Pinilla, M. P. 2003. Morphogenesis of extraembryonic membranes and placentation in *Mabuya mabouya* (Squamata; Scincidae). *Journal of Morphology,* 258: 158-178.

Jesus, J., Brehm, A. & Harris, D. J. 2005. Relationships of scincid lizards (*Mabuya* spp.) from the islands of the Gulf of Guinea based on mtDNA sequence data. *Amphibia-Reptilia* 26, 467-473.

Lobo, F., Abdala, F. & Scrocchi, G. 1995. Desarrollo del esqueleto de *Liolaemus scapularis* (Iguania: Tropiduridae). *Bolletino del Museo Regionale di Scienze Naturali* (Torino), 13: 77-104.

Mausfeld, P., Schmitz, A., Böhme, W., Misof, B., Vrcibradic, D. & Rocha, C. F. D. 2002. Phylogenetic affinities of *Mabuya atlantica* Schmidt, 1945, endemic to the Atlantic Ocean archipelago of Fernando de Noronha (Brazil): necessity of partitioning the genus *Mabuya* Fitzinger, 1826 (Scincidae: Lygosominae). *Zoologischer Anzeiger*, 241: 281-293.

Miralles, A. 2005. The identity of *Lacerta mabouya* Lacepède, 1788, with description of a Neotype: an approach toward the taxonomy of new world Mabuya. *Herpetologica*, 61: 46-53.

Miralles, A. 2006. A new species of *Mabuya* (Reptilia, Squamata, Scincidae) from the Caribbean island of San Andres, with a new interpretation of nuchal scales: a character of taxonomic importance. *Herpetological Journal*, 16: 1-7.

Miralles, A. & Carranza, S. 2010. Systematics and biogeography of the neotropical genus *Mabuya*, with special emphasis on the Amazonian skink *Mabuya nigropunctata* (Reptilia, Scincidae). *Molecular Phylogenetics & Evolution*, 54: 857-869.

Miralles, A., Rivas-Fuenmayor, G. & Barrio-Amorós, C. L. 2005. Taxonomy of the genus *Mabuya* (Reptilia, Squamata, Scincidae) in Venezuela. *Zoosystema*, 27: 825-837.

Miralles, A., Rivas Fuenmayor, G., Bonillo, C., Schargel, W. E., Barros, T., García-Pérez, J. E. & Barrio-Amorós, C. L. 2009. Molecular systematics of Caribbean skinks of the genus *Mabuya*

(Reptilia, Scincidae), with descriptions of two new species from Venezuela. *Zoological Journal of the Linnean Society*, 156: 598-616.

Pearson, H. S. 1921. The skull and some related structures of a late embryo of *Lygosoma. Journal of Anatomy*, 56: 20-43.

Rao, M. K. M. & Ramaswami, L. S. 1952. The fully formed chondrocranium of *Mabuya* with an account of the adult osteocranium. *Acta Zoologica*, 33: 209-275.

Rice, E. L. 1920. The development of the skull in the skink *Eumeces quinquelineatus. Journal of Morphology*, 34: 120-243.

Rieppel, O. 1992. Studies on skeleton formation in reptiles III. Patterns of ossification in the skeleton of *Lacerta vivipara* Jacquin (Reptilia: Squamata). *Fieldiana Zoology*, 68: 1-25.

Rieppel, O. 1994. Studies on skeleton formation in reptiles. Patterns of ossification in the skeleton of *Lacerta agilis exigua* Eichwald (Reptilia, Squamata). *Journal of Herpetology*, 28: 145-153.

Sánchez, H., Castaño, O. V. & Cárdenas, A. G. 1995. Diversidad de los Reptiles en Colombia. pp. 277-324. *In*: Rangel, J. O. (Ed.). *Colombia Diversidad Biotica I.* Convenio Inderena, Universidad Nacional de Colombia, Bogotá.

Skinner, M. M. 1973. Ontogeny and adult morphology of the skull of the south African skink, *Mabuya capensis* (Gray). *Annals of the University of Stellenbosch*, 48: 1-116.

Wassersug, R. J. 1976. A procedure for differential staining of cartilage and bone in whole formalin fixed vertebrates. *Stain* Technology, 51: 131-134.

Whiting, A. S., Sites, J.W., Jr., Pellegrino, K. C. M. & Rodrigues, M. T. 2006. Comparing alignment methods for inferring the history of the new world lizard genus *Mabuya* (Squamata: Scincidae). *Molecular Phylogenetics and Evolution,* 38: 719-730.