

**Comparative description and ossification patterns of *Dendropsophus labialis* (Peters, 1863) and *Scinax ruber* (Laurenti, 1758)(Anura: Hylidae)**  
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**Short Title:** Skeletal development of two hylids

**Abstract** Although comparative studies of anuran ontogeny have provided

new data on heterochrony in the life cycles of frogs, most of them have not

included ossification sequences of ~~Neotropical frogs.Colombian species.~~ Using

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different~~nt~~ staining techniques, we observe and describe the cranial and

poscranial ~~elements~~ development in two hylid species, *Scinax ruber* and

*Dendropsophus labialis*, providing new data for more comprehensive ontogenetic

studies ~~in-of Colombian species.Neotropical frogs.~~ We examined specimens

tadpoles ranging from Gosner ~~stages~~ Stages 25 to 45. We found differences

between the species in the infrarostral and suprarostal cartilages, optic foramen,

planum ethmoidale, and ~~the~~ gill apparatus. In ~~the ossification sequence~~both

species, ~~one-of~~ the first elements to ossify were the atlas and transverse processes

of spinal vertebral column ~~and atlas in both species,~~ and the parasphenoid ~~in the~~

skull. ~~These two~~Both species ~~showed exhibited the~~ suprascapular processes

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~~as that has characterized the Hylids that~~ have been described in other Hylids

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~~species cleared and stained until now.~~ Although the hylids comprise a large group

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(over 700 species), postcranial ossification sequence is only known for 15 species.

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~~New~~ Therefore, the descriptions of the skeletal development and ossification

sequences ~~of larval stages of these two species~~provided herein, ~~mainly~~especially

data concerning the posteranium, ~~should be~~ contribute with useful information for

future analysis of ~~sequential~~ heterochrony in the group, ~~because although the~~

hylids are widely known, there are few works (15 of 700 species) about ossification

sequence that include the whole skeleton.

32 **Keywords** Ossification sequences, [rank](#), skeletal development, tadpoles,  
33 [morphology](#)

## 34 Introduction

35 ~~Comparative Morphological~~ morphological descriptions have that compare species  
36 ~~offerprovideprovided~~ information that useful systematians systematic characters  
37 ~~have been assessing about anuran relationships from the~~ since the 1960's to the  
38 present day, using both molecular and morphological methods. However, most  
39 studies of ~~frog~~ morphological characters ~~have widely privileged~~ focus on adults,  
40 ~~ands over~~ tadpoles are often overlooked (Alcalde et al. 2011). (Alcalde et al. 2011).  
41 ~~Traditionally~~ Of those comparative studies of that examine frog-larvaetadpoles,  
42 ~~have most~~ considered external morphological characters and, while most skeletal  
43 characters ~~(bones and cartilages)~~ haveare been often been neglected. When, and  
44 when, skeletal features are considered, ~~studies have been concentrated on~~  
45 describing the chondrocranium is most often more described, and the than the  
46 postcranium is frequently ignored (e.g., Orton 1953; Starrett 1973; Wassersug  
47 1980; Wassersug and Heyer 1988; Haas 2003). The frog family Hylidae is One of  
48 the families of frogs that contribute withlarge and diverse, and frequently the  
49 subject of ,systematic(Orton 1953; Starrett 1973; Wassersug 1980; Wassersug and  
50 morphology data is Hylidaestudies. However, as with other groups, relatively few  
51 detailed comparative morphological studies of hylid tadpole skeletal development  
52 have been completed. one of theGiven the size and most diverse and that has  
53 recent tly had taxonomic re-arrangements of the hylids (Duellman et al. 2016;  
54 Jungfer 2017). due widely to the diversity and great number of species it  
55 ~~represents~~ it is important to amass as much comparative information Each

**Comment [F1]:** If the main goal (as described in the introduction and conclusions) is to provide baseline information to be used later in comparisons of heterochrony within phylogenetic context and/or for phylogenetic character, why not just describe each species individually? What new information does comparing the two species provide? Do the developmental differences relate to adult morphological differences? Providing more justification for the comparative approach in the introduction would make the paper more interesting, and the significance and new knowledge gained by comparing them should be discussed in the conclusions.

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**Comment [AMM2]:** Maybe include a few of the classic citations here---Duellman, Cannatella, etc.

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56 description of amphibian is important for development studies for such a large  
 57 group as hylids. Additionally, the order to give comparative characters for anuran  
 58 morphology and systematics of species belonging to the family Hylidae, about the  
 59 group as possible. Thus, there continues to be a pressing need to conduct  
 60 comprehensive comparative studies of hylid developmental morphology, one of the  
 61 most diverse and that has recently had taxonomic arrangements (Duellman et al.  
 62 2016; Jungfer 2017; Heyer 1988; Haas 2003).  
 63 Interspecific variations in morphology. The family Hylidae presents one of the  
 64 largest families of frogs with a great number of interspecific variations that have  
 65 helped to clarify specific taxonomic groups within the Hylidae. It is The family is  
 66 predominantly distributed across the Neotropical region (Frost 2017; Duellman et  
 67 al. 2016) (Frost 2017; Duellman et al. 2016) and comprises 706 species commonly  
 68 subdivided into seven subfamilies: Acridinae, Cophomantinae, Dendropsophinae,  
 69 Hylinae, Lophyophylinae, Pseudinae, and Scinaxinae (Faivovich et al. 2005; Wiens  
 70 et al. 2010; Duellman et al. 2016; Frost 2017) (Faivovich et al. 2005; Wiens et al.  
 71 2010; Duellman et al., 2016; Frost 2017). Within the Hylidae, the Ossification  
 72 sequences have been studied for are known for only 15 species, and only of which  
 73 only eight of those include the postcranial skeleton: eight species: *Acris*  
 74 *blanchardi* (Havens 2010; Maglia et al. 2007) (Havens 2010), *Boana lanciformis*  
 75 (De Sá 1988) (De Sá 1988), *Boana pulchella* (Hoyos et al. 2012) (Hoyos et al.  
 76 2012), *Dryophytes chrysoscelis* (Shearman and Maglia 2014) (Sherman and  
 77 Maglia 2014), *Dryophytes versicolor* (Sheil et al. 2014) (Sheil et al., 2014), *Hyla*  
 78 *orientalis* (Yıldırım and Kaya 2014) (Yıldırım and Kaya, 2014), *Osteopilus*

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79 *septentrionalis* (Sheil et al. 2014), (Sheil et al., 2014), *Pseudacris crucifer* (Havens  
80 2010), were (Havens, 2010), have included the postcranial skeleton.  
81 Taking into account Because identifying that variations in developmental  
82 morphology and the ossification sequence, placed in a phylogenetic context, will  
83 help can to recognize lead to potential informative phylogenetic characters and  
84 evolutionary relationships among species (Weisbecker and Mitgutsch 2010;  
85 Harrington et al. 2013), herein we, The (Weisbecker and Mitgutsch 2010;  
86 Harrington et al. 2013), the goal of the present study is to provide a detailed  
87 anatomical comparisons on of the larval morphology (cranial andum and  
88 postcranial developmentum development) and (including the sequence of onset of  
89 the ossification) sequence information between two species of frogs Andean hylids,  
90 *Dendropsophus labialis* and *Scinax ruber*. These species were chosen to givewith  
91 the aim of giving a contribution to the knowledge on the timing and sequences of  
92 ossification, this baseline information to be used later in comparisons of  
93 heterochrony within a phylogenetic context. Additionally, in order to provide  
94 comparative characters for anuran morphology and systematics of species  
95 belonging to the family Hylidae, one of the most diverse and that has recently had  
96 taxonomic arrangements (Duellman et al., 2016; Jungfer, 2017).

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## 98 Materials and methods

99 ~~According to the availability of biological material, the~~ We cleared and double-  
100 stained for cartilage and bone (Dingerkus and Uhler 1977) tadpoles and  
101 metamorphs of *Dendropsophus labialis* (N= 32), and *Scinax ruber* (N=114); the  
102 number in each series correspondes to the availability of specimens in the Museo  
103 de Historia Natural “Lorenzo Uribe” at the Universidad Javeriana (MUJ) and the  
104 Instituto de Ciencias Naturales at the Universidad Nacional in Bogotá – Colombia  
105 (ICN). ~~The larval stages of *D. labialis* were collected from the Municipio Tenjo,~~  
106 ~~Cundinamarca Departament, 3200 m (MUJ 9250). The larval stages of *S. ruber*~~  
107 ~~were collected from the Mun. Neiva, Huila Dep., 570 m; Mun. Granada, Meta Dep.,~~  
108 ~~470 m (MUJ 3727, MUJ 6178, ICN 46015-46017). Tadpoles and metaphorphs~~  
109 ~~were staged according to Gosner (1960).The larval stages of *D. labialis* were~~  
110 ~~collected from the Municipio Tenjo, Cundinamarca Departament, 3200 m (MUJ~~  
111 ~~9250),) and adult stages from the Mun. Fomeque, Cundinamarca Dep., 3150 m~~  
112 ~~(MUJ 497). The larval stages of *S. ruber* were collected from the Mun. Neiva, Huila~~  
113 ~~Dep., 570 m; Mun. Granada, Meta Dep., 470 m (MUJ 3727, MUJ 6178, ICN~~  
114 ~~46015-46017). Tadpoles and metaphorphs) and adult stages from the Mun. La~~  
115 ~~Dorada, Caldas Dep., 490 m (MUJ 9037). All of these were staged according to~~  
116 ~~Gosner (1960)(1960).~~

117 Observations and photographs were made with a stereomicroscope (Advanced  
118 optical) equipped with a digital camera (Infinity 1 Lumenera Corporation) with white  
119 LED light and Image Pro Insight software (version 8.0.3). Drawings were made

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Comment [AMM3]: Isn't this protocol mainly for cartilage? Was it modified from their protoicol?

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120 using a digitizing tablet (~~Wacom Bamboo Connect Pen~~)(Wacom Bamboo Connect  
121 Pen) -and edited using Adobe Illustrator 5. Anatomical nomenclature for tadpoles  
122 follows ~~Parker 1876; Higgins 1921; Jolie 1962; Roček 1981; Duellman and Trueb~~  
123 ~~1986; Haas 1995; Haas 1997; Hall and Larsen 1998; Maglia and Púgener 1998;~~  
124 ~~Cannatella 1999; Haas 1999; Sheil and Alamillo 2005; Púgener and Maglia 2007;~~  
125 ~~Bowatte and Meegaskumbura 2011; Hoyos et al. 2012;~~ adult nomenclature is  
126 based on Avilán ~~and~~ Hoyos (~~2006~~),(2006); using Latin names given by the  
127 ICVAN (~~1973~~),(1973); and taking into account that a Nomina Anatomica  
128 Batrachologica does not exist.

129 We refer to metamorphic climax (MC) *sensu* Banbury and Maglia (2006) as the  
130 Gosner stages at which major modifications and fundamental structural changes  
131 occur, resulting in the loss of most larval characters. We also use the term "rank" to  
132 refer to the ordinal number within an ossification sequence at which an element  
133 begins to ossify. If two or more elements begin ossifying at the same Gosner  
134 stage, they were assigned the same rank (i.e., a tie) as per Nunn and Smith  
135 1998).~~We refer to metamorphic climax (MC) *sensu* Banbury and Maglia (2006) as~~  
136 ~~the Gosner stages at which (2006)major modifications and fundamental structural~~  
137 ~~changes-occur, resulting in the loss of most larval characters. We also use the term~~  
138 ~~"rank" to refer to the ordinal number within an ossification sequence at which an~~  
139 ~~element begins to ossify. If two or more elements begin ossifying at the same~~  
140 ~~Gosner stage, they were assigned the same rank (i.e., a tie) as per Nunn and~~  
141 ~~Smith 1998).~~(Nunn and Smith 1998).

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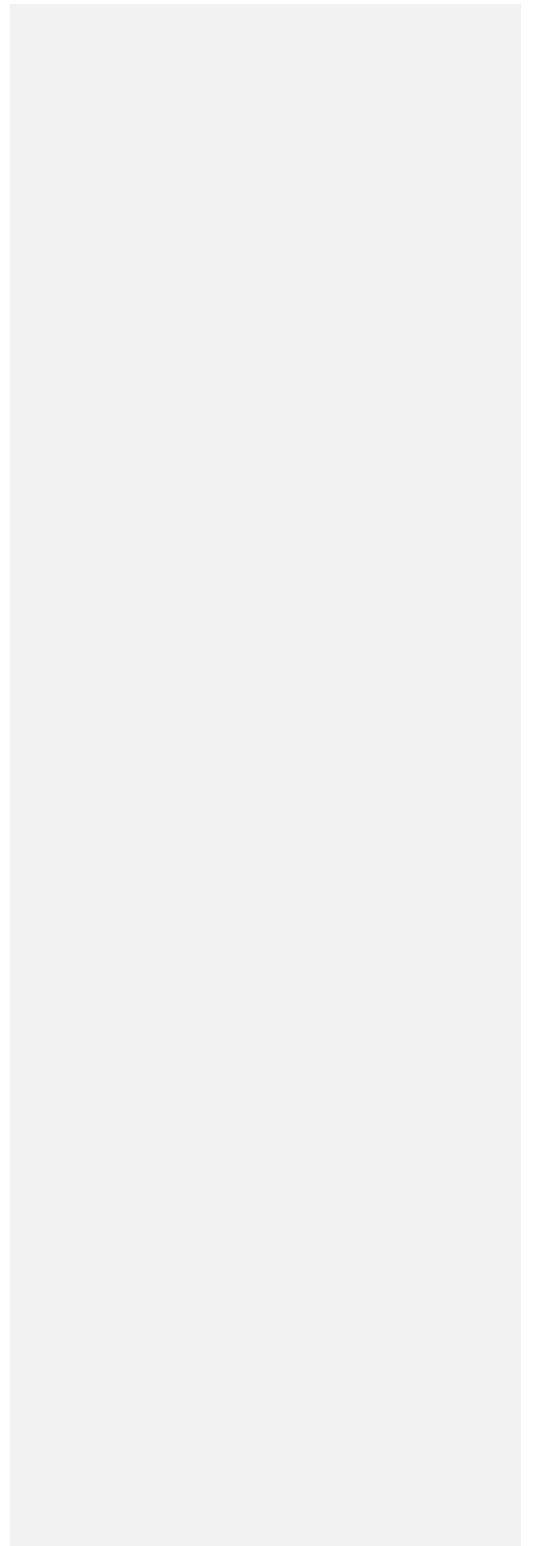
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**Comment [AMM4]:** Did you decide this based on the first time any specimen at that stage showed stain or when more than 50% of the specimens at that stage showed stain? Please add a line here to clarify.

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## Results

Individual Skeletal development and sequence of onset of ossification of the cranial and poscranial elements in *Dendropsophus labialis* and *Scinax ruber* are showed in Table 1 and 2, each one showing ossification sequences. Because a number of specimens in our original series of *Scinax ruber* did not show marked clear staining ossified elements, thus we increased our sample size. Most of the poorly stained specimens we must element so touched use more specimens than in *D. labialis*. Besides, the were between largest stages 26 to 35, the total number of individuals that did not show ossification (GS stages 26 and -35); after Stage 35, specimens stained more clearly specimens with red coloration reduced, was 67 in *S. ruber* while in *D. labialis* it was and 16 individuals in *D. labialis*, which allowed to compare these two species stages from 36 onwards.

### Chondrocranium

We observed similar the changes in the shape, size, and increase absorption modification of structures in the development of chondrocranium in between the two species. The overall width of the chondrocranium in *Dendropsophus labialis* and *Scinax ruber* is roughly approximately 80-90% of this total length (Fig 1). The chondrocranium in *D. labialis* is wider (dorsal view) and lower (lateral view) than *S. ruber* (Fig 1A, 1B, 1C). Basicranial The basicranial fenestrae did not differentiated differentiated with Alcian Blue in both either species. We perceived observed a stronger blue coloration in *D. labialis*, and the jugular (jf), prootic (pof) and oculomotor (of) foramen were clearly differentiated, whereas in *S.*

**Comment [F5]:** 2) I suggest to present the results in a comparative way, and that the idea of the development of the described structures be clearly reflected:

Results:

The data of the tables 1 and 2 would be useful to see in a comparative way

- The authors study the development of the skeletal system of two species of anurans, but in the description is not recorded in which stages / moments of development the structures, ossifications, etc., appear. This is a serious problem since the main objective of the work is to describe the development, and such as the results are presented, this is not reflected. In the section "ossification sequence" there is a summary on this subject, but it is not useful to transmit to the reader what are the elements (each one) that appear before or later, and what would be the difference between both species studied in this aspect.

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**Comment [AMM6]:** Not sure you need this sentence

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**Comment [AMM7]:** What stage did you use to compare the "typical" larval morphology? Please indicate that here.

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165 *ruber* we could not see the oculomotor foramen.

166 ~~these foramina~~ The cartilaginous ~~region~~area of the taenia tecti medialis and

167 tectum sinoticum (~~ts~~) both represents a quarter of ~~that the~~ basis cranii, extending

168 from the frontoparietal fontanellea in both species. ~~The ectum~~The tectum nasi is a

169 roof's structure located anteriorly in the nasal region, and the ethmoidal plate is

170 aforms the floor structure. The tectum nasi is separated from the orbit by a wall, the

171 lamina orbitonasalis (= planum antorbitale sensu XXX?). Because of these regions

172 ~~remain are only~~ weakly chondrified, the lamina orbitonasalis is not observabled in

173 the tadpole stages, and the nasal capsules are becomes visible in on after

174 metamorphic climax later stages (~~posterior Stage to the GS42 and beyond~~). The

175 taenia tecti marginalis is evident and clearly differentiated at by GS37 in *D. labialis*

176 and at by GS35 in *S. ruber*. In nNeither species we did we observed a

177 frontoparietal fenestra, nor ~~the was a~~ taenia tecti transversalis was

178 ~~perceived~~observedvisible directly on the edge of the frontoparietal fontanellea (Fig.

179 1A).

180 Suprarostril cartilage (cs). In both species, the suprarostril cartilage is

181 composed of a discontinuous cartilaginous plate divided into a corpus

182 suprarostralis and a pars alaris, while posterolaterally we observed a distal

183 syndesmotic junction between the corpus and the ala (a). The ala has three

184 processes: two rounded anterolateral processes that join syndesmotically with the

185 cornu trabecula (ct), and one process posterolaterally (Fig. 1C). The

186 Fenestrations were not observed in the suprarostril cartilage nor, and in the

187 adrostral cartilage near the processus posterodorsalis (= processus dorsalis

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Comment [F8]: But in the figure 1 are indicated the foramina pof and jf in *Scinax ruber*

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Comment [F9]: in some parts of the text, the abbreviations of the structure are placed in parentheses and in others not, the authors should standardize the edition

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188 posterior, *sensu* Bowatte and Meegaskumbura 2011) and Bowatte &  
189 Meegaskumbura, 2011) and. In *D. labialis* the corpus suprarostal is curved, while  
190 in *S. ruber* it is straighter and wider distally, articulating proximally with the cornu  
191 trabecula (= trabecular horn, sensu Cannatella 1999) trabecula. The cornua  
192 trabeculae are trabeculae is approximately 35% of the total length of chondrocranium  
193 (lateral view) in both species; they are, and this is shorter and narrower in *D.*  
194 *labialis* than in *S. ruber*. The cornua trabeculae articulate (trabecular horn, sensu  
195 Cannatella 1999) Cannatella, 1999) anteriorly with the corpus rostrale and laterally  
196 with the pars alaris of the suprarostal cartilage.

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197 *Cartilago Meckeli* (em). The cartilago Meckeli (= Meckel's cartilage, *sensu*  
198 Cannatella, 1999) Cannatella, 1999) has three processes: the retroarticular (short  
199 and blunt), the dorsomedial, and the ventromedial. These processes articulate with  
200 both the infrarostral cartilage (= commissura intramandibularis sensu Cannatella,  
201 1999), (ei) which is, composed of two syndesmotically joined flat plates  
202 (commissura intramandibularis, sensu Cannatella, 1999), Cannatella, 1999), and  
203 the processus muscularis quadrati: (pmq); the shape of the processus  
204 dorsomedialis and the processus ventromedialis are the same in both species. The  
205 palatoquadrate cartilage and the commissura quadratocranialis (eqe) are joining  
206 joined anteriorly to the base cranii. Laterally, the palatoquadrate cartilage (pq)  
207 forms the arcus subocularis. The process muscularis quadrati is joined to the  
208 processus antorbitalis (= pars plana sensu Parker 1876; Parker, 1876; = lamina  
209 externa *sensu* Higgins 1921; Higgins, 1921; = processus antorbitalis *sensu* Roček  
210 1981; Roček, 1981; = *triangular plane sensu* Hall and Larsen 1998; Hall & Larsen,

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1998 = cartilaginous planum triangulare *sensu* Pügener and Maglia 2007) Pügener  
and Maglia, 2007) and is placed anterolaterally, projecting above the cornu  
trabecula. The processus hyoquadrati of the palatoquadrate cartilage articulates  
ventrally with the ceratohyalia of the hyobranchial apparatus (Fig. 1D).

*Otic capsule.* In the tadpoles this structure is longer and higher than wide,  
occupying about one-a fifth of the total length of the skull. The crista parotica  
exhibits a more pronounced lateral projection in *D. labialis* than in *S. ruber*. The  
crista parotica is laterally developed, forming a small processus posterolateralis (=  
processus lateralis posterior *sensu* Bowatte and Meegaskumbura 2011) Bowatte  
& Meegaskumbura, 2011) and a small processus anterolateralis (pal) (more  
developed in *D. labialis*). The processus anterolateralis projects vertically,  
descending obliquely and overlapping the ventral posterolateral margin of the  
palatoquadrate cartilage. The otic capsule is perforated by the fenestra ovalis, (fo),  
which occupies about 20% of the otic capsule.

*Hyobranchial apparatus.* The large ceratohyal has a processus anterioris hyalis,  
(pah), a processus posterioris hyalis (pph) and a processus anterolateralis hyalis  
(palh). The first two processes are longer than the processus anterolateralis  
hyalisthird, which extends to meet the transverse crease of the processus lateralis  
hyalis. (plh).

The basihyal plate is oval and extends proximally to the copula anterior (=  
Basibranchial I *sensu* Duellman and Trueb 1986; Duellman & Trueb, 1986; =  
basihyale *sensu* Haas 1995; Haas, 1995 and *sensu* Haas 1997; Haas, 1997; =  
copula Copula I *sensu* Maglia and Pügener 1998; Sheil and Alamillo 2005) Maglia

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and Púgener, 1998; Sheil and Alamillo, 2005) in *D. labialis*, but ~~in~~ is absent in *S. ruber* ~~is absent~~. The basibranchial plate is semi-oval ~~and~~ placed ~~located~~ between the two hypobranchial plates (~~planum hypobranchiale, phb~~) (= planum hypobranchiale *sensu* Haas 1999; Haas, 1999; = plate hyoid *sensu* Maglia and Púgener 1998; Maglia & Púgener, 1998; = hyobranchial plate *sensu* Sheil and Alamillo 2005; Sheil and Alamillo, 2005); ~~the~~ a branchial bridge is present in both species, being wider in *S. ruber* than in *D. labialis*. The junction between each ceratobranchium ~~al~~ (~~eb I-IV~~) and the planum hypobranchiale is syndesmotic. The ceratobranchialia ~~is~~ are united posteriorly by the commissura terminalis ~~and~~ (~~ct~~) bear ~~ing~~ three spicules anteriorly (~~sp~~) (Fig. 1D).

#### Appendicular skeleton

*Shoulder girdle.* The pectoral girdle is arciferal in both species. The earliest ossification of clavicle ~~is~~ (~~c~~), coracoid ~~is~~ (~~co~~) and scapula appears at GS36 (Fig. 3A). The clavicle and the cleithrum are distinct, and ~~the~~ an epicoracoids cartilage (~~ps~~) is prominent between the clavicle and the coracoid. The epicoracoids are not mineralized ~~in tadpoles~~. ~~In~~ *D. labialis*, ~~the~~ omosternum (~~o~~) ~~in~~ *D. labialis* is elongated and the sternum has two projections; the omosternum and the sternum (~~st~~) are oval in *S. ruber*. The clavicle ~~articulates~~ articulated with the coracoid, ~~it is~~ being which is ossified in *D. labialis* at GS41 and in *S. ruber* at GS46. The ~~sternum~~ sternum ~~are~~ is formed by the epicoracoid ~~ss~~ and the ~~sternum~~ element (~~mesosternum~~) ~~joining which joins~~ the medial junction of the epicoracoids (Fig. 2B).

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256 Pelvic girdle. ~~In both species, the~~The primordium of the ilium ~~(il)~~ appears at GS34  
 257 and is fully developed ~~at by~~ GS41 ~~in both species~~. The ilium ~~is~~ begins to ossified  
 258 ~~ossify during development in~~ ~~in~~ by GS41 *D. labialis* ~~at GS41~~ and ~~by GS39/40~~ in *S.*  
 259 *ruber* ~~at GS39/40~~, ~~and articulating articulates~~ anteriorly with the ventral surface of  
 260 the lateral margin of the sacral diapophyses ~~at by~~ GS42. The iliac crest appears  
 261 dorsally prominent; the primordia of the pubis ~~(pu)~~ and the ischium ~~(is)~~ appear at  
 262 GS36, ~~and are~~ synchondrotically fused ~~at by~~ GS38 ~~in both species~~. The sacral  
 263 diapophysis is wider in *D. labialis* than in *S. ruber*. The pubis is ~~totally completely~~  
 264 fused ~~at by~~ GS40. The pelvic girdle is completely ossified with the halves fused at  
 265 the midline, extending anterodorsally forming an angle of 55° with the head of the  
 266 femur ~~at by~~ GS45 (Fig. 3B).

267 Forelimb and hindlimb. The first cartilaginous elements of the forelimbs (radius,  
 268 ulna, and humerus) appear at GS32, and those of the hindlimbs at GS33 (femur,  
 269 tibia, and fibula). The tibia and fibula are fused ~~at in~~ *D. labialis* ~~by (GS41)~~ and ~~in~~ *S.*  
 270 *ruber* ~~by (GS38)~~. We observed ossification of the radius and ulna in *D. labialis* ~~by~~  
 271 ~~(GS41)~~ and *S. ruber* ~~(postafter metamorphosisie)~~; these elements are fused in both  
 272 species. Primordia of the four carpal and five tarsal elements appear ~~at by~~ GS33  
 273 and complete development ~~at by~~ GS41.

274 The phalangeal carpal formula is 3-3-4-4 and the phalangeal tarsal formula is 3-3-  
 275 4-5-4 in both species. Metacarpals ~~(me)~~ are curved and phalanges are cylindrical,  
 276 having a conical shape at the tip of the terminal phalanges. Digits IV (manus and  
 277 pes) and V (pes) begin to ossify ~~at by~~ GS42 ~~only~~ in *D. labialis*, although all  
 278 phalanges are ossified at GS45 ~~in~~ both species (Fig. 3). The carpal~~sia~~

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279 ~~stayremainwere~~ cartilaginous in ~~the all~~ specimens and stages examined, and the  
280 distal tarsals ~~remain-were~~ cartilaginous in *S. ruber*. The relative size of carpal  
281 elements (~~me~~) is  $3 < 4 < 2 < 1$  prehallux (~~ph~~) and the tarsal elements (~~mt~~) is  $4 < 5$   
282  $< 3 < 2 < 1$  prepollex (~~pr~~). Sesamoids are absent from GS25 to GS45. ~~In the~~  
283 Figure 3A ~~shows the limb elements (showed elements as~~ central (~~ce~~), fibulare  
284 (~~fi~~), radiale (~~rd~~), tibiale (~~ti~~), ulnare, and intermedium) ~~at Stage XXX.-(ul).~~

## 285 Axial skeleton

286 The vertebral column is composed of eight procoelous presacral vertebrae, the  
287 sacrum, and the urostyle. The notochord ~~length~~ diminishes as the tadpoles grow,  
288 ~~reaching a total and is complete resorption-resorbed at by~~ GS44 in both species  
289 (Fig. 4). We found that the axial skeleton was more chondrified in *D. labialis* than in  
290 *S. ruber*. The first postcranial skeletal elements to develop in both species were the  
291 nine pairs of semicircular cartilaginous primordia of neural arches, included eight  
292 presacral vertebrae, the sacrum, the urostyle (~~u~~) and the hypochord (~~hy~~). The  
293 sacral diapophyseal (~~sd~~) primordia are cylindrical. The last postsacral vertebra (first  
294 coccygeal or ~~vertebra-Vertebra~~ X *sensu* Haas 1999) and the second coccygeal  
295 vertebra ~~ossified-ossify~~ only in *D. labialis* ~~at by~~ GS45. Simultaneous ~~to they~~ ~~with~~  
296 ~~the absorption of the ossification of presacral vertebrae, there is~~ notochord  
297 ~~absorption,~~ the coccygeal elements ~~fusionfuse~~ and ~~form the~~ urostyle ~~formation~~.  
298 The urostyle has a bicondylar articulation with the sacral vertebra and the condyles  
299 are widely separated (~~Haas 1999~~)(~~Haas 1999~~) in both species (Fig. 4).

300 The atlas (~~a~~) is concave at its point of articulation with the convex occipital  
301 condyles at the base of the skull. Semicircular, ~~procoelous~~ (*sensu* Jolie 1962)

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vertebral ~~centrum centra~~ begins to develop ~~as procoelous (sensu Jolie 1962) Jolie~~  
~~1962) vertebra from as early as~~ GS31 in *D. labialis* and ~~at~~ GS32 in *S. ruber*,  
increasing the thickness of both the neural arches and the transverse process. The  
neural arches appear ~~as cartilaginous cartilage~~ at GS33 in both species; these are  
complete at GS34 in *D. labialis* and at GS38 in *S. ruber*. The arches are fused  
dorsally at the midline at GS38 in *S. ruber* and at GS38 in *D. labialis*. ~~The~~  
~~t~~ransverse processes are the first elements to ossify in both species (Tables 1 and  
2). ~~Both p~~Postzygapophyses and prezygapophyses are conspicuous in presacral  
vertebrae II, III, and IV in both species. Sesamoids are absent from GS25 to GS45.

### Ossification sequence

The ~~earlier~~~~earliest~~ stage ~~examined of the two in both~~ species was ~~the~~ GS25.  
~~The o~~Ossification ~~timing~~ in *D. labialis* ~~begins appears at by~~ GS34 and in *S. ruber* ~~at~~  
~~by~~ GS35 (Fig. 1A). Ossification in *D. labialis* begins with the atlas and the  
transverse processes, whereas in *S. ruber* it begins with the parasphenoid, the ~~+~~  
~~VII-t~~Transverse ~~processes~~~~Processes I-VII~~ and ~~neural-Neural arches-Arches~~ I-III.  
The ossification sequence was constructed with the first appereance of ~~bone~~.  
~~We perceived~~~~observed that the M~~metamorphic climax (MC) begins at GS41 in *D.*  
*labialis*, and ~~GS39-40~~ in *S. ruber*. ~~at GS39-40~~. We identified seven ranks (I–VII) in  
*D. labialis* and five ranks (I–V) in *S. ruber* (Tables 1 and 2). ~~The GS wherein which~~  
~~we found O~~ssified elements ~~(or bones) in were perceptible in D. labialis were~~ from  
GS35 to GS45, with 46 ~~ossified~~ elements, and ~~from GS36 to GS43~~ in *S. ruber* ~~from~~  
~~GS36 to GS43~~, with 26 ~~ossified~~ elements. ~~S. ruber showed the number of ossified~~  
~~elements of each specimen according to the Gosner stage was more variable~~

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(Table 3). The MC Metamorphix climax in *D. labialis* was at GS45 with 14 ossified elements, and in *S. ruber* at GS39-40 with seven ossified elements. Of these, the structures in common were are the femur, tibia, fibula, humerus, ilium, and radioulna. (rad). The two species present both differences and similarities with respect to the ossification of the chondrocranium and postcranium.

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## Discussion

Notwithstanding the fact that Despite Colombia is housing the the second richest country in the planet, after Brazil, concerning the largest number of hyliid species on the planet, there are very few previous studies about have considered developmental ossification sequences of Colombian hyliids. The species of the The family Hyliidae show variation in the has gone through a number of taxonomic re-arrangements, as it was showed by the variety of elucidated by various phylogenetic hypotheses based on molecular, chromosomal, and morphological data from both larvae and adults (Faivovich 2002; Faivovich et al. 2005; Wiens et al. 2010; Pyron and Wiens 2011; Duellman et al. 2016). (Faivovich 2002; Faivovich et al. 2005; Wiens et al. 2010; Pyron and Wiens 2011; Duellman et al., 2016). Data from additional morphological studies of Colombia hyliids may help to support or refute these hypotheses.

The Previous studies about of the cranial morphology in hyliid tadpoles include being known in *Acris crepitans* (Maglia et al. 2007); *Boana pulchella* (Hoyos et al. 2012); *Boana raniceps* and *Boana lanciformis* (Alcalde and Rosset 2003); *Dendropsophus nanus* (Fabrezi and Lavilla 1992; Alcalde and Rosset 2003; Vera Candiotti et al. 2004 Vera Candiotti et al. 2004); *Hyla orientalis* (Yildirim and Kaya 2014); *Boana pulchella* (Hoyos et al. 2012); *Julianus* species: *J. acuminatus* (Fabrezi and Lavilla 1992; Faivovich 2002; Alcalde and Rosset 2003; Alcalde et al. 2011 Alcalde et al. 2011; Faivovich 2002); *J. uruguayus*, *J. aff. pinimus* (Alcalde et al. 2011; Rodrigues et al. 2017); *Ololygon* species: *Ololygon*

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| Comment [F12]: The discussion section should  | ... [46] |
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353 *aromothyella* and *O. berthae* (Rodrigues et al. 2017; Alcalde et al. 2011; Faivovich  
 354 2002); *O. skuki* (Rodrigues et al. 2017); *Scinax* species: *Scinax granulatus* and *S.*  
 355 *squalirostris* (Rodrigues et al. 2017; Alcalde and Rosset 2003; Alcalde and Rosset  
 356 2003); *S. boulengeri* (Rodrigues et al. 2017; Vera Candiotti 2007; Vera Candiotti  
 357 2007); *S. fuscovarius* (Rodrigues et al. 2017; Fabrezi and Vera 1997; Fabrezi and  
 358 Vera 1997); *S. nasicus* (Rodrigues et al. 2017; Vera Candiotti 2007; Fabrezi and  
 359 Vera 1997; Vera Candiotti et al. 2004; Fabrezi and Vera 1997); *S. ruber* (Haas  
 360 1996). For a complete overview of the findings of these studies, please (See  
 361 Appendix 1). Vera Candiotti 2007).  
 362 The studies about cranial morphology in hylid tadpoles being known in *Aeris*  
 363 *crepitans* (Maglia et al., 2007); *Boana raniceps* (Alcalde and Rosset, 2003);  
 364 *Dendropsophus nanus* (Fabrezi & Lavilla 1992; Vera Candiotti et al., 2004); *Hyla*  
 365 *orientalis* (Yıldırım and Kaya, 2014); *Boana pulchella* (Hoyos et al., 2012); *Julianus*  
 366 species: *J. acuminatus* (Fabrezi and Lavilla, 1992; Alcalde et al., 2011; Faivovich,  
 367 2002); *J. uruguayus*, *J. aff. pinimus* (Alcalde et al., 2011); *Ololygon* species:  
 368 *Ololygon aromothyella* and *O. berthae* (Alcalde et al., 2011; Faivovich, 2002); *O.*  
 369 *skuki* (Rodrigues et al., 2017); *Scinax* species: *Scinax granulatus* and *S.*  
 370 *squalirostris* (Alcalde and Rosset, 2003); *S. boulengeri* (Vera Candiotti 2007); *S.*  
 371 *fuscovarius* (Fabrezi and Vera 1997); *S. nasicus* (Fabrezi and Vera, 1997; Vera  
 372 Candiotti et al., 2004; Vera Candiotti, 2007).  
 373 The chondrocranial morphology and hyobranchial apparatus development is  
 374 generally similar between both the species examined herein and those previously  
 375 studied, but we did not find several differences between the two species.

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**Comment [F15]:** If the main goal (as described in the introduction and conclusions) is to provide baseline information to be used later in comparisons of heterochrony within phylogenetic context and/or for phylogenetic character, why not just describe each species individually? What new information does comparing the two species provide? Do the developmental differences relate to adult morphological differences? Providing more justification for the comparative approach in the introduction would make the paper more interesting, and the significance and new knowledge gained by comparing them should be discussed in the conclusions.

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**Comment [F16]:** which more relevant differences the authors found in relationship with these previous works?

**Comment [F17]:** Validity of the findings  
The discussion section should be focused to compare related species. In this sense, *S. ruber* should be compared with the information available for *Scinax* species (i.e. Alcalde and Rosset, 2003; Alcalde et al., 2011), and inferences (with caution by the absence of data in most taxa) with *Julianus* and other *Scinaxinae* (like *Ololygon*), in the framework of *Hylidae*. In *Dendropsophus*, the authors omitted references useful to make comparisons (see above) and the result obtained should be discussed considering the complete framework of *Hylidae*. The similarities observed between taxa not closely related: *Dendropsophus labialis* (*Dendropsophinae*) and *Scinax ruber* (*Scinaxinae*) c (... [91]

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in: 1) the shape of the suprarostrum, 2) ~~(i)~~, the size and width of infrarostral  
 cartilages, 3) ~~(ii)~~, the length of processus articularis, 4) ~~(iii)~~, the thickness of  
 palatoquadrate, 5) ~~(iv)~~, the size of optic foramen, 6) ~~(v)~~, the presence of an  
 operculum ~~(vi)~~ and processus posterolateralis of the ~~auditive-otic~~ capsule ~~(vii)~~, 7)  
 the thickness of the processus muscularis quadrati ~~(viii)~~, 8) the presence of a  
 quadratoethmoid and pseudopterygoid ~~(ix)~~, 9) the attachment of the ascending  
 process to the braincase, 10) the ~~(x)~~, thickness of the planum ethmoidale ~~(xi)~~, 11)  
 the development of the branchial apparatus ~~(xii)~~, 12) the presence of ~~copula~~  
 Copula I ~~(xiii)~~, and 13) the type of junction between the ceratobranchialia and  
 planum hypobranchiale ~~(xiv)~~ (Fig. 1 and 2). These differences likely represent  
 species-specific differences among the taxa examined. There are no admandibular  
 cartilages attached to the anteroventral margin of the cartilago Meckeli as  
 described by Hoyos et al. (2012) in *Boana pulchella*.  
 The overall similarities of the skeletal developmental skeleton in tadpoles  
 of *Scinax ruber* (Scinaxinae) and *Dendropsophus labialis* (Dendropsophinae)  
 relative to other hylids for which similar data are available could be an  
 indication of a recent consequence of common origin, or, but also could be a  
 consequence of homoplasy with independent origins. However, the absence  
 of Without additional morphologic data in combination with and molecular data on  
 other species, it is not possible to answer this question does not allow a clear  
 comparison.  
 Several of the differences between the two species examined present interesting  
 avenues for future examination. For example, the The processus ethmoidalis of the

**Comment [AMM18]:** Not discussed anywhere else—  
maybe elaborate here?

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399 quadrate in *S. ruber* is wide, and it is not clearly distinct from the processus  
400 articularis, ~~while-whereas~~ in *D. labialis*, the processes are easily distinguishable,  
401 ~~and~~ similar to that described by Alcalde and Rosset ~~(2003), (2003)~~, who ~~also~~ found  
402 ~~the-same~~ similar features in *Hyla raniceps* ~~comparing-compared with-to~~ the *Scinax*  
403 ~~species~~ group (*S. squalirostris* and *S. granulatus*, *Scinax ruber* group). The  
404 palatoquadrate is similar between ~~the~~ species but the processus ascendens of the  
405 palatoquadrate in *D. labialis* is wider than in *S. ruber*, ~~while-and~~ the distal side of  
406 the cornu trabeculae extends posteriorly toward the otic capsule, ~~and-I~~ the anterior  
407 region of the palatoquadrate is distinctively broader in *S. ruber* than in *D. labialis*,  
408 ~~and i-~~ In *S. ruber* the dorsomedial process is wider than the ventromedial process  
409 in *D. labialis*. The lateral development of the crista parotica is more prominent in *S.*  
410 *ruber* than in *D. labialis*. It is possible that some ~~of the variation in the outstanding~~  
411 anatomical structures of the otic capsule ~~are functionally (cc)-allow~~ related to ~~the~~  
412 perception of vocalizations ~~of their own (i.e., same species recognition) -species~~  
413 in adult ~~sstages~~, but experiments must be conducted to check the relationship of  
414 ~~these~~ anatomical structures with hearing physiological functions ~~(Ruggero and~~  
415 ~~Temchin 2002; Boistel et al. 2013), (Ruggero and Temchin 2002; Boistel et al.~~  
416 ~~2013)~~.  
417 The chondrification of skull in *S. ruber* ~~was-is~~ faint when ~~it is~~ viewed laterally, and  
418 foramina are not clearly visualized. By contrast, in *D. labialis*, ~~much~~ more blue  
419 coloration was observed. ~~This could ,may~~ be due to ~~the~~ abundant chondrification  
420 of these parts or to the early developmental stages of ~~this anatomical area the-in~~  
421 ~~larvae in this region~~, which allowed differentiation of craniopalatine carotid

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422 foramina, contrary to what was found by Alcalde and Blotto (2006).  
 423 (2006). Although the sample size for the *D. labialis* is very small in comparison  
 424 with *S. ruber*, ~~*Dendropsophus*~~ *D. labialis* exhibited more ossified elements with  
 425 stronger chondrification and less intraspecific variation, while ~~in~~ *S. ruber* showed  
 426 more intraspecific variation and less overall chondrification in the samples (Fig 1).  
 427 ~~*D. Scinax ruber* showed ossification variations in various elements relative to total~~  
 428 ~~individuals ossified regarding~~ *D. labialis* presented uniformly stained (ossification  
 429 ossified) elements in all individuals stainedstaining and clearedclearing (Table 3).  
 430 ~~The~~This variation between *S. ruber* and *D. labialis*Table 3). This variation  
 431 suggests that ~~may be~~could be caused by the intrinsic factors that determines the  
 432 timing of development or ~~because~~ extrinsic factors may affect theaffecting  
 433 osteogenesis (Vera and Ponssa 2014). ~~It may not be a coincidence that~~ On the  
 434 ~~otheranother~~ hand, *S. ruber* is a generalist species and *D. labialis* is an endemic  
 435 ~~onespecies~~ (Frost 2017). ~~(Vera and Ponssa, 2014)~~.  
 436 Haas (1996) ~~identified(1996)-observedreported~~ that the ~~c~~Ceratohyalia II-IV are  
 437 fused in *Scinax ruber* and *Megophrys montana nasuta*, characteristics that  
 438 separating ~~separate~~ them from other species; ~~this character has to be taken into~~  
 439 ~~account when taxonomic studies based on morphology are carried on~~. ~~This~~Herein,  
 440 ~~this character state~~ was ~~found-confirmed~~ in *S. ruber* but not in *D. labialis*. The  
 441 ceratohyal in *D. labialis* ~~presents~~ ~~has~~ a process on the articular condyle that is not  
 442 present in *S. ruber*. Alcalde and Rosset (2003)(2003) found this process in both *S.*  
 443 *granulatus* and *S. squalirostris*. Spicules I-III on the posterior margin of the

Comment [AMM19]: Not really sure what point you are trying to make here. Could you rework this paragraph to better explain?

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Comment [AMM20]: If you keep this sentence, you should explain the connection between chondrification and dietary habits

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hypobranchial plate are present in *D. labialis* and *S. ruber*, but the sSpicule IV is not.

The copula II ep (II) is present in both species, but the cCopula I ca (I) is present in *D. labialis*---absent in *S. ruber* and it is present in *D. labialis*, just as in *S. squalirostris*---but absent in *S. ruber*, as in but in *S. granulatus*, *Boana**Hyla**Hyla**raniceps* (Alcalde and Rosset 2003)(Alcalde and Rosset 2003) and *Tlalocohyla smithii* (Vera and Haas 2004)*Dendropsophus nanus* (Vera and Haas 2004) is absent. Although the presence of copula Copula I is extremely variable in hylids, and is shared by all non-hylid macrophages (Vera and Haas 2004),(Vera and Haas 2004), a relationship between of this structure with and the ecological function that it can performs (e.g., prey utilization), for example in relation to the type of food, has not been foundidentified.

The Additional characteristics of the developmental morphology of these species align them with other hylids that have been studies previously. For example, the urostyle in of *D. labialis* and *S. ruber* presents aforms a bicondylar articulation with the sacral vertebra with and the condyles are widely separated. The shoulder girdle of both tadpoles species presents differences in the shape of the omosternum and sternum at GS 45. *Dendropsophus labialis* and *S. ruber* present suprascapular processes in tadpoles and adults similar to those in other species of the family Hylidae~~hylids~~: *Hypsiboas lanciformis* (De Sá 1988),(De Sá 1988), *Boana pulchella* (Hoyos et al. 2012),(Hoyos et al. 2012), *Pseudacris crucifer*, *Acris blanchardi*

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Comment [F21]: En el artículo está como Hyla microcephala

Comment [AMM22]: Reword this

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465 (~~Havens 2010~~)(~~Havens 2010~~) and *A. crepitans* (~~Maglia et al. 2007~~)(~~Maglia et al.~~  
466 ~~2007~~).

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467 The ~~v~~Variation of larval characters ~~has been evaluated in the genera~~between  
468 *Scinax* and *Dendropsophus* ~~in have been included in~~ several phylogenetic studies  
469 (~~Fabrezi and Vera 1997; Haas 1996; 1999; 2003; Alcalde and Rosset 2003; Vera~~  
470 ~~2007~~)(~~Fabrezi and Vera 1997; Haas 1996; 1999; 2003; Alcalde and Rosset 2003;~~  
471 ~~Vera 2007~~). In our study, the skeleton shows significant differences between the  
472 species *Scinax ruber* and *Dendropsophus labialis*, beginning with fact that  
473 elements ossified in *S. ruber* exhibit more intraspecific variability than in *D. labialis*  
474 (see Table 3).

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475 Regarding ~~the~~ ossification sequence, the first bones ossified in the cranium were  
476 the exoccipital, the frontoparietal and the parasphenoid ~~after at~~by GS 36. Haas  
477 (~~1999~~)(~~1999~~) found that in *S. ruber*, and in other species of *Hyla* ~~(some species~~  
478 ~~named after as Dendropsophus)~~, this occurred ~~one stage later, by at~~ GS37.

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479 ~~Similar to those that Haas (1999) described for other species of Hylidae. The the~~  
480 ossification of ~~the the~~ vertebrae begins from ~~the~~ centra of the presacral vertebrae  
481 and ~~continuing contains~~ ventrally along the notochord, forming osseous rings  
482 around the notochord in both species. ~~We found that the ossification of the centra~~  
483 ~~in both species we studied begins ventrally and proceeds dorsally, as Haas (2003)~~  
484 ~~recorded for Litoria nannotis. similar to those that Haas (1999)(1999) described for~~  
485 ~~other species of Hylidae. Haas (1999)Haas (1999) also recorded the the time of~~  
486 ~~the first ossification timing of the transverse processes of of the presacral Presacral~~  
487 ~~vertebrae Vertebrae II-III as the first to ossify---~~; we found that it was the

**Comment [F23]:** Line 317: Regarding the ossification sequence, the first bones ossified in the cranium were the exoccipital, the frontoparietal and the parasphenoid at GS 36. I'm a bit confused---this doesn't seem consistent with the tables. In fact, in Table 2, shouldn't exoccipital be listed at GS38?

There is little in terms of conclusion beyond the fact that the data might be useful in future studies. I think the paper might be more interesting if you used the conclusions to comment/speculate on why you think there might be differences among these two species. Just a thought.

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ossification of Neural Arches I through IX in *D. labialis* (GS37) and I through III in *S. ruber* (GS36). identifiedobserved these elements beginning at GS36 in both species. The ossification of the neural arches I to IX was in *D. labialis* (GS37) whereas in *S. ruber* (GS36) was I to III; the ossification of the arcs in these species is completed in the GS37. Interestingly, the first elements to ossify were those from the postcranium: the transverse process of the vertebral column and the atlas in *D. labialis* (Figure 4). The ossification process of the vertebra in the two species started ventrally from the centrum of each vertebra, and followed dorsally to close the vertebrae in advanced stages, as Haas (2003)(2003) recorded for *Litoria nannotis*.

The Differences between the ossification sequences of these two species are also seen evident with regard to thewhen examining the ossification ranks and number of ossified bones; in particular, *D. labialis* presented thehas highest number ofmore ranks in the sequence and more elements that begin ossification prior to metamorphosisgan the process of ossification. With respect to the postcranium, the number of elements ossified appears earlier in *D. labialis* than in *S. ruber*. Because Gosner stages are base don external characteristics that rely on underlying skeletal changes, it is only a relative measure of timing and should not be used as a way to compare between species. Instead, weThe compared the occurrence of events in the development of each species is the relative timing of of each events in the ossification sequence; allowing us to compare the relative timing of developmental events across different taxa. For this reason we did not take the developmental GS and we take theby examining the order of begining of

**Comment [AMM24]:** Not sure if this is what you were trying to say in this paragraph---if not, please change back.

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**Comment [AMM25]:** Not sure what the point of this is---reword to make the point more clearly.

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511 the onset of ossification of each element, because these are based on the  
512 appearance of external morphological structures that are the same in both species  
513 studied. However, as Moreover, Nunn and Smith (1998:1998-86) considered  
514 "that ontogeny may be ordered by age, size, or stage"; none of these measures are  
515 useful for comparing ontogeny across significantly divergent taxa".

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516 Analysis of the ossification sequences with different methodologies, for example  
517 Parsimov, could be found that the heterochronic cranium elements, or ossification  
518 timing appearing at different times, were the parasphenoid and prootic when we  
519 compared *S. ruber* with *H. pulchellus* (Hoyos et al. 2012), (Hoyos et al. 2012), but in  
520 *Dendropsophus labialis* and *Pseudis platensis* were the frontoparietal, dentary and  
521 maxilla (Fabrezi and Goldberg 2009). (Fabrezi and Goldberg 2009). Ossification  
522 sequences of *D. labialis* and *S. ruber* showed that the ossification timing of the  
523 parasphenoid was at the first rank. Meanwhile, the timing of ossification of the  
524 exoccipital, frontoparietal and prootic was at the second rank in both species.

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Comment [F26]: not exclude of what?  
This does not seem a justification to exclude or not the postcranial study

525 Cranial and postcranial characters described (Table 4 outlines the ossification  
526 sequences of different species of the family Hylidae. A) show that among these  
527 Hylid species, the number of ranks that includes elements of the skull and  
528 postcranium vary from one to five. The number of ranks increase when postcranial  
529 elements are included; the information lost in the ossification sequences, when the  
530 postcranial elements they are excluded, showed postcranial elements.  
531 demonstrating the importance of these structures including not excluding them.  
532 Weisbecker and Mitgutsch (2010), (2010), Harrington et al. (2013), (2013), and Sheil  
533 et al. (2014), (2014) used these similar ranked ossification sequence data for to

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534 reconstruct ~~ing~~ phylogenetic trees of amphibians ~~with in the families~~ ossification  
535 ~~sequences of cranial and postcranial elements~~ of Leptodactylidae, Ranidae and  
536 Bufonidae. ~~These researchers suggested to~~ advocated for using cranium and  
537 post-cranium data, relating ~~them~~ the data to the type of development exhibited by  
538 the species, and ~~to including~~ ossification sequence informations ~~effrom~~ fossils  
539 ~~too, as far as possible~~ when available.

540 Although the morphology and systematics of amphibians are organisms that  
541 have been extensively studied (Canatella and Trueb 1988; de Sá and Hillis 1990;  
542 Baez and Pugener 2003; Roelants and Bossuyt 2005; Faivovich et al. 2005, Frost  
543 et al. 2006; Pyron and Wiens 2011; Duellman et al. 2016), ~~we need~~ UTILIZAR  
544 ~~TODOS LOS CARACTERES PARA PARSIMOV~~

545 ~~The characters these researchers suggest is to deep in~~ additional comprehensive  
546 descriptions of the changes occurring in the appearance of skeletal development  
547 and ossifications, ~~be employed~~ all this  
548 include both cranium and post-cranium, relating them to contribute to the are needed to  
549 truly understand patterns of ~~ing~~ type of heterochrony in the groupies. development,  
550 including sequences of fossils.

551 Some of the biological implications of the heterochronyies, --- which are well  
552 known in amphibians (Alberch 1985; Reilly et al. 1991), (Alberch 1985; Reilly et al.  
553 1991) ---, are to observe include changes of in the shape and size of anatomical  
554 structures in shape and size, and the evolution of changes in the relative rates of  
555 growth of developmental events among taxa entire organisms (Raff 1996; Smith  
556 2001; 2002; 2003). (Raff 1996; Smith 2001; 2002; 2003). Some scholars have

Comment [F28]: Which characters of this study would recommend to include in a phylogeny

Comment [F29]: Which characters of this study would recommend to include in a phylogeny

Comment [AMM27]: Direct developing vs. Metamorphosing? what do you mean here

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recognized ~~that heterochrony may work as modules of these~~ developmental events  
as modules with evolutionary implications ~~that, which can can promote or reveal~~  
~~interactions or restrictions on the~~ development with individual events of individual  
morphologies (Wagner 1996). (Wagner 1996).

Studies that have used statistical methods (e.g., Parsimov) to ~~a~~ analyze the  
ossification sequences with different methodologies, for example Parsimov, could  
~~be found that the~~ have revealed heterochrony in the timing of onset of ossification in  
some cranial elements, such as the heterochronic cranium elements, or  
ossification timing appearing at different times, were the parasphenoid and prootic  
when we compared in *S. ruber* with *vs. H. pulchellus* (Hoyos et al. 2012) or the  
frontoparietal, dentary and maxilla, but in *Dendropsophus labialis* and *vs. Pseudis*  
*platensis* were the frontoparietal, dentary and maxilla (Fabrezi and Goldberg 2009).

In our study, we found that the parasphenoid was the first element to ~~o~~ ossify in  
ossification sequences of both *D. labialis* and *S. ruber* showed that the ossification  
timing of the parasphenoid was at the first rank. Meanwhile, the ~~and~~ timing of  
ossification of the exoccipital, frontoparietal and prootic was at the ~~the~~ were the second  
second rank in elements to ossify in both species.

It is possible that the difference in cartilage formation between the two species  
examined herein is due to paracrine factors induced in cells that express  
mesodermal transcription factors involved in the activation of genes specific to  
cartilage (Gilbert 2000; Kozhemyakina et al. 2015); however, we did not account  
for these factors. Additionally, The ~~i~~ intraspecific variation in the ~~of the~~ ossified  
elements between these species could be linked with the ~~to~~ specific genes involved

**Comment [F30]:** A discussion about sequence variation or heterochrony might make a more compelling argument.

**Comment [F31]:** A discussion about sequence variation or heterochrony might make a more compelling argument.

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in these variations (Raff 1996). (Raff 1996). We should note that it is possible that the difference in cartilage formation between the two species is due to paracrine factors induced in cells that express mesodermal transcription factors involved in the activation of gene specific to cartilage (Gilbert 2000; Kozhemyakina et al. 2015); (Gilbert 2000; Kozhemyakina et al. 2015); the present study did not account for these factors.

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The detection of more intraspecific variability in *Scinax ruber* than in *Dendropsophus labialis* could also be due to the presence of the more great intra-generic diversity within the *Scinax ruber* clade. e *Scinax ruber*, this issue has been poorly studied, then it could be studied in greater detail when comparing the adults of these species. (Fig. 5). Although amphibians are organisms that have been extensively studied (Canatella and Trueb 1988; de Sá and Hillis 1990; (Canatella and Trueb 1988; de Sá and Hillis 1990; Haas 2001; Baez and Pugener 2003; Roelants and Bossuyt 2005; Faivovich et al. 2005, Frost et al. 2006; Pyron and Wiens 2011; Duellman et al. 2016) Baez and Pugener 2003; Roelants and Bossuyt 2005; Faivovich et al. 2005, Frost et al. 2006; Pyron and Wiens 2011; Duellman et al. 2016) would solve taxonomic and morphology voids.

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Comment [F32]: but why this would explain the variability within od *D. labialis*

Comment [AMM33]: I think this whole paragraph needs to be explained a little more. Not sure where you are trying to go with this.

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PERO NO DEL DESARROLLO DEL CRANEO Y MENOS POSCRANEO  
SEPARAR LO DEL ADULTO  
NOS INTERESA EL DESARROLLO DEL CRANEO Y QUE TENGAN LAS  
SECUENCIAS DE OSIFICACION CUALES EN CADA ESTADIO  
NO HAY TRABAJOS DE SECUENCIAS DE OSIFICACION EN SCINAX Y  
DENDROPSOPHUS

Comment [F34]: the generality of this sentence makes it empty and the relationship with the previous sentence is not followed

## Conclusions

**Comment [F35]:** and new knowledge gained by comparing them should be discussed in the conclusions.

The contribution of ~~the~~ ontogenetic data (~~development and ossification sequences of skeletal structures of skeleton and ossification sequences~~) provided here ~~in is supported by the~~ provides further information to help knowledge that affords opportunity to understand the interactions between ontogeny and phylogeny in morphological and ecological diversity of frog ~~s~~genera. Likewise, ~~O~~ ossification sequences data ~~for the skeletal elements~~, combined with evolutionary hypotheses, may shed light ~~about on~~ patterns of development to support ~~be used in~~ future phylogenetic hypotheses. ~~Aas~~ Larson ~~et al. (2003)~~(2003) ~~claimed: suggested~~, “~~the~~ variation in chondrocranial morphology in larval anurans can be phylogenetically informative, even among closely related taxa”.

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~~The great diversity that exists among tadpoles, especially for the type of food, are closely related to the type of maxillas they have, in addition larval forms could help predict characters in adults.~~

## Acknowledgements

We thank to the Pontificia Universidad Javeriana and the Paläontologisches Institut und Museum, Universität Zürich, for partial funding of this work. We want to thank Timothy Sosa for ~~help~~assistance with the English translation.

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The authors declare that they ~~jack~~have no conflicts of interest of any kind.

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**Comment [F36]:** The figures could be much more detailed—for example, are the craniopalatine and carotid foramina in D. labialis visible? They aren't shown in Figure 1. You describe them in text but do not show them in the illustration.

**Comment [F37]:** The figures could be much more detailed—for example, are the craniopalatine and carotid foramina in D. labialis visible? They aren't shown in Figure 1. You describe them in text but do not show them in the illustration. Also, Figure 5. Really doesn't provide much information and should probably be deleted (or given more treatment in text).

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(Dendropsophinae) and *Scinax ruber* (Scinaxinae) could be consequence of common origin, but also could be consequence of homoplasy with independent origin. So the absence of data not allow a clear comparison, and result obtained should be discussed considering the complete framework of Hylidae. The similitudes observed between between taxa not closely related: *Dendropsophus labialis* (Dendropsophinae) and *Scinax ruber* (Scinaxinae) could be consequence of common origin, but also could be consequence of homoplasy with independent origin. So the absence of data not allow a clear comparison, and the authors should be caution with such issue.

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which more relevant differences the authors found in relationship with these previous works?

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Validity of the findings

The discussion section should be focused to compare related species. In this sense, *S. ruber* should be compared with the information available for *Scinax* species (i.e. Alcalde and Rosset, 2003; Alcalde et al., 2011), and inferences (with caution by the absence of data in most taxa) with *julianus* and other *Scinaxinae* (like *Ololygon*), in the framework of *Hylidae*. In *Dendropsophus*, the authors omitted references useful to make comparisons (see above) and the result obtained should be discussed considering the complete framework of *Hylidae*. The

similitudes observed between taxa not closely related: *Dendropsophus labialis* (*Dendropsophinae*) and *Scinax ruber* (*Scinaxinae*) could be consequence of common origin, but also could be consequence of homoplasy with independent origin. So the absence of data not allow a clear comparison, and the authors should be caution with such issue.