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 differential~~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 suprarostral 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 as~~that has characterized the Hylids that~~ ~~have been~~ described in other Hylids ~~species cleared and stained until now~~. Although the hylids comprise a large group (over 700 species), postcranial ossification sequence is only known for 15 species. ~~New~~ Therefore, the descriptions of the skeletal development and ossification sequences ~~of larval stages of these two species~~provided herein ~~, mainlyespecially data concerning the postcranium,~~ should be ~~contribute with~~ useful ~~information~~ for future analyse~~i~~s 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.~~

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Keywords Ossification sequences, ~~rank,~~ skeletal development, tadpoles, morphology

Introduction

Comparative ~~Morphological~~ morphological descriptions have ~~that compare species offerprovide~~provided ~~information that~~ useful ~~systematicians~~ systematic characters ~~have been assessing~~ about ~~anuran relationships from the~~since the ~~-~~1960´s. ~~to the present day, using both molecular and morphological methods.~~ However, most studies of frog morphological characters ~~have widely privileged~~focus on adults, and~~s~~ ~~over~~ tadpoles are often overlooked (Alcalde et al. 2011). ~~(Alcalde et al. 2011).~~ ~~Traditionally,~~Of those comparative studies ~~of~~ that examine ~~frog larvae~~tadpoles, ~~have~~ most consider~~ed~~ external morphological characters and~~,~~ ~~while most~~ skeletal characters ~~(bones and cartilages) have~~are ~~been~~ often ~~been~~ neglected. When~~, and when~~ skeletal features are considered, ~~studies have been concentrated on describing~~ the chondrocranium is most often ~~more~~ described, and the ~~than the~~ postcranium is frequently ignored (e.g., Orton 1953; Starrett 1973; Wassersug 1980; Wassersug and Heyer 1988; Haas 2003). The frog family Hylidae is ~~One of the families of frogs that contribute with~~large and diverse, and frequently the subject of -systematic~~(Orton 1953; Starrett 1973; Wassersug 1980; Wassersug~~ ~~and~~ morphology ~~data is Hylidae~~studies. ~~-~~ However, as with other groups, relatively few detailed comparative morphological studies of hylid tadpole skeletal development have been completed. ~~one of the~~Given the size and ~~most diverse and that has~~ recent~~tly had~~ taxonomic re-arrangements of the hylids (Duellman et al. 2016; Jungfer 2017), ~~.due widely to the diversity and great number of species it 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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~~description of amphibian is important for development studies for such a large group as hylids. Additionally, the order to give comparative characters for anuran morphology and systematics of species belonging to the family Hylidae, ~~about the group as possible. Thus, there continues to be a pressing need to conduct comprehensive comparative studies of hylid developmental morphology.~~one of the most diverse and that has recently had taxonomic arrangements (Duellman et al. 2016; Jungfer 2017).~~~~Heyer 1988; Haas 2003).~~

Interspecific variations in morphology~~The family Hylidae presentsis one of the largest families of frogs with a great number of interspecific variations that have~~ help~~ed~~ to clarify ~~specific~~ taxonomic groups within the Hylidae. ~~It is~~The family is predominantly distributed across the Neotropical region (Frost 2017; Duellman et al. 2016)~~(Frost 2017, Duellman et al. 2016)~~ and comprises 706 species ~~commonly~~ subdivided into seven subfamilies: Acridinae, Cophomantinae, Dendropsophinae, Hylinae, Lophyophylinae, Pseudinae, and Scinaxinae (Faivovich et al. 2005; Wiens et al. 2010; Duellman et al. 2016; Frost 2017).~~(Faivovich et al. 2005; Wiens et al. 2010; Duellman et al., 2016; Frost 2017).~~ ~~Within the Hylidae, the~~ O~~o~~ssification sequences ~~have been studied for~~are known for only15 species, and only ~~of which only~~eight of those ~~in~~ include the postcranial skeleton: ~~eight species,:~~ *Acris blanchardi* (Havens 2010; Maglia et al. 2007),~~(Havens 2010),~~ *Boana lanciformis* (De Sá 1988),~~(De Sá 1988),~~ *Boana pulchella* (Hoyos et al. 2012),~~(Hoyos et al. 2012),~~ *Dryophytes chrysoscelis* (Shearman and Maglia 2014),~~(Sherman and Maglia 2014),~~ *Dryophytes versicolor* (Sheil et al. 2014),~~(Sheil et al., 2014),~~ *Hyla orientalis* (Yıldırım and Kaya 2014),~~(Yıldırım and Kaya, 2014),~~ *Osteopilus*

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septentrionalis (Sheil et al. 2014),~~(Sheil et al., 2014),~~ *Pseudacris crucifer* (Havens 2010).~~ were(Havens, 2010), have included the postcranial skeleton.~~

~~Taking into account~~Because identifying ~~that~~ variations in developmental moprphology and ~~the~~ ossification sequence ~~, placed in a phylogenetic context, will help~~can ~~to recognize~~ lead to ~~potential~~ informative phylogenetic characters ~~and evolutionary relationships among species~~ (Weisbecker and Mitgutsch 2010; Harrington et al. 2013), herein we~~. The(Weisbecker and Mitgutsch 2010; Harrington et al. 2013), the goal of the present study is to~~ provide ~~a~~ detailed anatomical comparisons ~~on~~ of the ~~larval morphology (~~cranial and~~um and~~ postcranial development~~um development)~~ ~~and~~ (including the sequence of onset of ~~the~~ ossification) ~~sequence information~~ between two species of ~~frogs~~ Andean hylids, *Dendropsophus labialis* and *Scinax ruber*. ~~These species were chosen to givewith the aim of giving a contribution to the knowledge on the timing and sequences of ossification, this baseline information to be used later in comparisons of heterochrony within a phylogenetic context. Additionally, in order to provide comparative characters for anuran morphology and systematics of species belonging to the family Hylidae, one of the most diverse and that has recently had taxonomic arrangements (Duellman et al., 2016; Jungfer, 2017).~~

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Materials and methods

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

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

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

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

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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 shgowed stain? Please add a line here to clarify.

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Results

~~Individual~~ Skeletal d~~d~~evelopment and sequence of onset of ossification of the cranial and poscranial elements ~~in~~ of *Dendropsophus labialis* and *Scinax ruber* are showed in T~~t~~able 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 mustelement so touched use more specimens than in *D.* copies. In~~*~~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 differentiate~~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 [AMM7]: What stage did you use to compare the "typical" larval morphology? Please indicate that here.

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ruber we could not see the oculomotor foramen. ~~these foramina.~~ The cartilaginous region~~area~~ of the taenia tecti medialis and tectum sinoticum ~~(ts)~~ both represent~~s~~ a quarter of ~~that~~ the basis cranii, extending from the frontoparietal fontanelle~~a~~ in both species. The ectum~~The tectum~~ nasi ~~is a~~ roofs ~~structure located anteriorly in~~ the nasal region ~~,~~ and the ethmoid~~al~~ plate ~~is a~~forms the floor ~~structure~~. The tectum nasi is separated from the orbit by a wall, the lamina orbitonasalis (= planum antorbitale sensu XXX?). Because ~~of~~ these regions ~~remain~~ are ~~only~~ weakly chondrified, the lamina orbitonasalis is not observable~~ed~~ in the tadpole stages, and the nasal capsules ~~are~~ becomes visible ~~in~~ on after metamorphic climax ~~later stages~~ (~~posterior~~ Stage ~~to the GS~~42 and beyond). The taenia tecti marginalis is evident and clearly differentiated ~~at~~ by GS37 in *D. labialis* and ~~at~~ by GS35 in *S. ruber*. In n~~N~~either species ~~we~~ did we observe~~d~~ a frontoparietal fenestra, nor ~~the~~ was a taenia tecti transversalis ~~was perceivedobserved~~visible ~~directly~~ on the edge of the frontoparietal fontanelle~~a~~ (Fig. 1A).

Suprarostral cartilage. ~~(cs).~~ In both species, the suprarostral cartilage is composed of a discontinuous cartilaginous plate divided into a corpus suprarostralis and ~~a~~ pars alaris; ~~, while~~ posterolaterally we observed a distal syndesmotic junction between the corpus and the ala. ~~(a).~~ The ala has three processes: two rounded anterolateral processes that join syndesmotically with the cornu trabecula, ~~(ct),~~ and one process posterolaterally (Fig. 1C). ~~The~~ F~~f~~enestrations were not observed in the suprarostral cartilage nor ~~, and~~ in the 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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posterior~~,~~ *sensu* Bowatte and~~&~~ Meegaskumbura 2011). ~~and.Bowatte & Meegaskumbura, 2011) and.~~ In *D. labialis* the corpus suprarostral is curved, while in *S. ruber* it is straighter and wider distally, articulating proximally with the cornu trabecula (= trabecular horn, *sensu* Cannatella 1999)~~etrabecula~~. The cornua trabeculae are~~trabecula is~~ approximately 35% of the total length of chondrocranium (lateral view) in both species; they are ~~, and this is~~ shorter and narrower in *D. labialis* than in *S. ruber*. The cornua trabeculae articulate ~~(trabecular horn, *sensu* Cannatella 1999)Cannatella, 1999)~~ anteriorly with the corpus rostrale and laterally with the pars alaris of the suprarostral cartilage.

Cartilago Meckeli.~~ (cm).~~ The cartilago Meckeli (= Meckel's cartilage, *sensu* Cannatella, 1999)~~Cannatella, 1999)~~ has three processes**:** the retroarticular (short and blunt), the dorsomedial, and the ventromedial. These processes articulate with ~~both~~ the infrarostral cartilage(= commissura intramandibularis *sensu* Cannatella, 1999)~~, (ci)~~ which is ~~,~~ composed of two syndesmotically-joined flat plates ~~(commissura intramandibularis, *sensu* Cannatella, 1999),Cannatella, 1999),~~ and the processus muscularis quadrati;~~ (pmq);~~ the shape of the processus dorsomedialis and the processus ventromedialis are the same in both species. The palatoquadrate cartilage and the commissura quadratocranialis ~~(cqc)~~ are ~~joining~~ joined anteriorly to the base cranii. Laterally, the palatoquadrate cartilage ~~(pq)~~ forms the arcus subocularis. The process muscularis quadrati is joined to the processus antorbitalis (= pars plana *sensu* Parker 1876;~~Parker, 1876;~~ = lamina externa *sensu* Higgins 1921;~~Higgins, 1921;~~ = processus antorbitalis *sensu* Roček 1981;~~Roček, 1981;~~ = *triangular plane sensu* Hall and Larsen 1998~~Hall & Larsen,~~

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~~1998~~ = cartilaginous planum triangulare *sensu* Púgener and Maglia 2007)~~Púgener 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~~ T~~t~~his 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 ~~occupying~~ 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 anteriolateralis hyalis~~third, 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 (= ~~b~~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 Púgener 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~~ ~~(cb I-IV)~~ and the planum hypobranchiale is syndesmotic. The ceratobranchia~~lia~~ ~~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,~~ (c),~~ coracoid,~~ (co)~~ and scapula appears at GS36 (Fig. 3A). The clavicle and the cleithrum are distinct, and ~~the~~ an epicoracoid~~s~~ cartilage ~~(ps)~~ is prominent between the clavicle and the coracoid. The epicoracoids are not mineralized~~ in tadpoles~~. I~~T~~n *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~~sternun~~ ~~are~~ is formed by the epicoracoids~~s~~ and the ~~sternum element~~ ~~(~~mesosternum,~~)~~ ~~joining~~ which joins the medial junction of the epicoracoids (Fig. 2B).

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

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

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

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

Axial skeleton

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

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

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vertebral ~~centrum ~~centra begin~~s~~ 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 transverse 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 earlie~~r~~st~~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 ~~I-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 perceivedobserved that the ~~M~~m~~etamorphic 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~~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 hylid species on the planet, ~~there are very few~~few previous studi~~es~~ies ~~about~~ have considered developmental ossification ~~sequences~~of Colombian hylids. ~~The species of the~~The family Hylidae ~~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 hylids may help to support or refute these hypotheses.

~~3106998803~~ ~~The~~ Previous studies ~~about~~of the cranial morphology in hylid 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 Candioti et al. 2004Vera Candioti et al. 2004); *Hyla orientalis* (Yıldırım 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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aromothyella and *O. berthae* (Rodrigues et al. 2017; ~~(~~Alcalde et al. 2011; Faivovich 2002); *O. skuki* (Rodrigues et al. 2017);~~);~~ *Scinax* species: *Scinax granulatus* and *S. squalirostris* (Rodrigues et al. 2017; Alcalde and Rosset 2003~~Alcalde and Rosset 2003~~); *S. boulengeri* (Rodrigues et al. 2017; Vera Candioti 2007~~Vera Candioti 2007~~); *S. fuscovarius* (Rodrigues et al. 2017; Fabrezi and Vera 1997~~Fabrezi and Vera 1997~~); *S. nasicus* (Rodrigues et al. 2017; Vera Candioti 2007~~Fabrezi and Vera 1997~~; Vera Candioti et al. 2004; Fabrezi and Vera 1997); *S. ruber* (Haas 1996) For a complete overview of the findings of these studies, please ~~(S~~see Appendix 1~~)~~.~~ Vera Candioti 2007).~~

~~The studies about cranial morphology in hylid tadpoles being known in *Acris crepitans* (Maglia et al., 2007); *Boana raniceps* (Alcalde and Rosset, 2003); *Dendropsophus nanus* (Fabrezi & Lavilla 1992; Vera Candioti et al., 2004); *Hyla orientalis* (Yıldırım and Kaya, 2014); *Boana pulchella* (Hoyos et al., 2012); *Julianus* species: *J. acuminatus* (Fabrezi and Lavilla, 1992; Alcalde et al., 2011; Faivovich, 2002), *J. uruguayus, J. aff. pinimus* (Alcalde et al., 2011); *Ololygon* species: *Ololygon aromothyella* and *O. berthae* (Alcalde et al., 2011; Faivovich, 2002); *O. skuki* (Rodrigues et al., 2017); *Scinax* species: *Scinax granulatus* and *S. squalirostris* (Alcalde and Rosset, 2003); *S. boulengeri* (Vera Candioti 2007); S. fuscovarius (Fabrezi and Vera 1997); *S. nasicus* (Fabrezi and Vera, 1997; Vera Candioti et al., 2004; Vera Candioti, 2007).~~

The c~~C~~hondrocranial morphology and hyobranchial apparatus ~~development~~ is generally similar between ~~both~~ the species examined herein and those previously studied, but we did ~~. We found~~identify 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 similitudes observed between between taxa not closely related: Dendropsophus labials (Dendropsophinae) and Scinax ruber (Scinaxinae) c ... [91]

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in: 1) the shape of the suprarostral, 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) ~~(opf) (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) t~~t~~he development of the branchial apparatus ~~(xii)~~, 12) the presence of ~~copula~~ Copula I, ~~(xiii),~~ and 13) the type of junction between the ceratobranchia~~lia~~ 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)(2012) in *Boana pulchella*.~~

~~The~~The overall similariti~~r~~es ~~of~~in the skeletal development~~al~~ ~~skeleton in tadpoles~~ of *Scinax ruber* (Scinaxinae) and *Dendropsophus labialis* (Dendropsophinae) relative to other hylids for which similar data are available ~~could be~~may 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

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quadrate in *S. ruber* is wide, and it is not clearly distinct from the processus articularis, ~~while~~ whereas in *D. labialis*, the processes are easily distinguishable, and similar to that described by Alcalde and Rosset (2003),~~(2003),~~ who ~~also~~ found ~~the same~~similar features in *Hyla raniceps* ~~comparing~~ compared ~~with~~ to the *Scinax* ~~species~~ group (*S. squalirostris* and *S. granulatus, Scinax ruber* group). The palatoquadrate is similar between the species but the processus ascendens of the palatoquadrate in *D. labialis* is wider than in *S. ruber*, ~~while~~ and the distal side of the cornu trabecula~~e~~ extends posteriorly toward the otic capsule. ~~and~~ T~~t~~he anterior region of the palatoquadrate is distinctively broader in *S. ruber* than in *D. labialis*, and i~~. I~~n *S. ruber* the dorsomedial process is wider than the ventromedial process in *D. labialis*. The lateral development of the crista parotica is more prominent in *S. ruber* than in *D. labialis*. It is possible that some of the variation in the ~~outstanding~~ anatomical structures of the otic capsule are functionally ~~(oc) allow~~related to ~~to~~ perce~~iv~~eption of vocalizations ~~of their own~~(i.e., same species recognition) ~~species~~ in adult~~ ~~s~~stages~~, but experiments must be conducted to check the relationship of these anatomical structures with hearing physiological functions (Ruggero and Temchin 2002; Boistel et al. 2013).~~(Ruggero and Temchin 2002; Boistel et al. 2013).~~

The chondrification of skull in *S. ruber* ~~was~~ is faint when ~~it is~~ viewed laterally, and foramina are not clearly visualized. By contrast, in *D. labialis*, much more blue coloration was observed. This could ~~, may~~ be due to ~~the~~ abundant chondrification of these parts or to the early developmental stages of this anatomical area ~~the~~ in ~~larvae in this region~~, which allowed differentiation of craniopalatine carotid

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~~(2006).~~ Although the sample size for the *D. labialis* is very small in comparison with *S. ruber*,~~.~~ *Dendropsophus*~~, D.~~ *labialis* exhibited more ossified elements with stronger chondrification and less intraspecific variation, while ~~in~~ *S. ruber*~~,~~ showed more intraspecific variation and less overall chondrification in the samples (Fig 1). *D.* ~~*Scinax ruber* showed ossification variations in various elements relative to total individuals ossified regarding. *D.*~~ *labialis* presented uniform~~e~~ly stained (~~ossification ossified~~) elements in all individuals ~~stainedstaining and clearedclearing~~ (Table 3).

~~The~~This variation between *S. ruber* and *D. labialis*~~Table 3). This variation suggests that may be~~could be caused by ~~the~~ intrinsic factors that determines the timing of development or ~~because~~ extrinsic factors ~~may affect the~~affecting osteogenesis (Vera and Ponssa 2014). It may not be a coincidence that ~~On the other~~another~~ hand,~~ *S. ruber* is a generalist species and *D. labialis* is an endemic one~~species~~ (Frost 2017).~~(Vera and Ponssa, 2014).~~

Haas (1996) ~~identified(1996) observed~~reported that ~~the c~~Ceratohyalia II-IV are fused in *Scinax ruber* and *Megophrys montana nasuta*, characteristics that ~~separating~~ separate them from other species. ~~; this character has to be taken into account when taxonomic studies based on morphology are carried on. This~~Herein, this ~~character~~ state was ~~found~~ confirmed in *S. ruber* but not in *D. labialis*. The ceratohyal in *D. labialis* ~~presents~~ has a process on the articular condyle that is not present in *S. ruber*. Alcalde and Rosset (2003)~~(2003)~~ found this process in both *S. granulatus* and *S. squalirostris.* Spicules I-III on the posterior margin of the

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

C~~The c~~opula II ~~cp (II)~~ is present in both species; ~~, but the c~~Copula 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*~~*HylaHyla*~~ *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 ~~found~~identified.

~~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 a~~forms a bicondylar articulation with the sacral vertebra ~~with~~ and the condyles are widely separated. The shoulder girdle of both ~~tadpoles~~ species present~~s~~ 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 art{iculo está como Hyla microcephala

Comment [AMM22]: Reword this

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

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

Regarding ~~the~~ ossification sequence, the first bones ossified in the cranium were the exoccipital, the frontoparietal and the parasphenoid after~~atat~~by GS 36. Haas (1999)~~(1999)~~ found that in *S. ruber*, and in other species of *Hyla* ~~(some species named after as *Dendropsophus*)~~, this occurred one stage later, by~~at~~ GS37. Similar to those that Haas (1999) described for other species of Hylidae, ~~The~~ the ossification of the ~~the~~ vertebrae begins from the centra of the presacral vertebrae and ~~continuing~~ contines ventrally along the notochord, forming osseous rings around the notochord in both species. We found that the ossification of the centra in both species we studied begins ventrally and proceeds dorsally, as Haas (2003) recorded for *Litoria nannotis*. ~~similar to those that Haas (1999)(1999) described for other species of Hylidae.~~ Haas (1999)~~Haas (1999)~~ ~~also~~ recorded the ~~the time of the first~~ ossification ~~timing of the~~ transverse processes ~~of~~ of ~~the presacral~~ Presacral ~~vertebrae~~ Vertebrae II-~~-~~III as the first to ossify---~~;~~ we found that it was the

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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 exocippital 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. labilis* (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. labilis* (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 ~~D~~d~~ifferences between the ossification sequences of these two species are also ~~seen ~~evident ~~with regard to the~~when examining the ossification ranks and number of ossified bones; in particular, *D. labialis* ~~presented the~~has ~~highest number of~~more ranks in the sequence and more elements that begin ossification prior to metamorphosis~~gan 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, we~~The ~~ 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 the~~by examining the order of ~~begining of~~

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

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

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

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

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

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

~~The characters these researchers suggest is~~ ~~to deep in~~additional comprehensive descriptions of ~~the changes occurying in the appearance of ~~skeletal development and ossifications~~,be employed all this include both cranium and post-cranium, relating them to contribute to the~~are needed to truly understand patterns of ~~ingtype~~ ~~of ~~heterochrony in the group~~ies~~. ~~development, including sequences of fossils,~~

Some of the biological implications of ~~the ~~heterochrony~~ies, ~~---which are well known in amphibians (Alberch 1985; Reilly et al. 1991)~~,(Alberch 1985; Reilly et al. 1991)~~---~~, are to observe~~include changes ~~of ~~in the shape and size of anatomical structures~~ in shape and size,~~ and ~~the evolution of~~changes in the ~~relative ~~rate~~s~~ of growth of ~~developmental events among taxa~~entire organisms (Raff 1996; Smith 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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Formatted: Underline, Font color: Blue recognized thet heterochrony may work as modules of ~~these~~ developmental events ~~as modules~~ with evolutionary implications that ~~, which~~ can ~~can~~ promote or ~~reveal interactions or~~ restrict~~ions~~ ~~on~~ the development ~~with individual events~~of individual morphologies (Wagner 1996).~~(Wagner 1996).~~

Studies that have used statistical methods (e.g., Parsimov) to aAnaly~~sis~~ze ~~of 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~~O~~ssify in ~~ication 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~~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~~i~~ntraspecific 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.~~

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~~in 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.~~

~~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~~

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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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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~~ herein ~~is supported by the~~provides futher information 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~~ o~~ssification sequence~~s~~ 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. A~~a~~s 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 maxilas 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.

The authors declare that they lack~~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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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 between taxa not closely related: Dendropsophus labials

(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 labials (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

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