

## Evidence for heterochrony in the cranial evolution of fossil crocodyliforms

Lorena Godoy, Pedro; Ferreira, Gabriel; Montefeltro, Felipe; Vila Nova, Bruno; Butler, Richard; Langer, Max C.

DOI:

[10.1111/pala.12354](https://doi.org/10.1111/pala.12354)

License:

Other (please specify with Rights Statement)

*Document Version*

Peer reviewed version

*Citation for published version (Harvard):*

Lorena Godoy, P, Ferreira, G, Montefeltro, F, Vila Nova, B, Butler, R & Langer, MC 2018, 'Evidence for heterochrony in the cranial evolution of fossil crocodyliforms', *Palaeontology*, vol. 61, no. 4, pp. 543-558. <https://doi.org/10.1111/pala.12354>

[Link to publication on Research at Birmingham portal](#)

### **Publisher Rights Statement:**

Checked for eligibility: 26/7/2018

This is the peer reviewed version of the following article:

Godoy, P. L., Ferreira, G. S., Montefeltro, F. C., Vila Nova, B. C., Butler, R. J., Langer, M. C. and Benson, R. (2018), Evidence for heterochrony in the cranial evolution of fossil crocodyliforms. *Palaeontology*, 61 (4), 2018, 543-558, which has been published in final form at doi:10.1111/pala.12354. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

### **General rights**

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

### **Take down policy**

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact [UBIRA@lists.bham.ac.uk](mailto:UBIRA@lists.bham.ac.uk) providing details and we will remove access to the work immediately and investigate.

Evidence for heterochrony in the cranial evolution of fossil crocodyliforms

PEDRO L. GODOY<sup>1</sup>, GABRIEL S. FERREIRA<sup>2,3,4\*</sup>, FELIPE C. MONTEFELTRO<sup>5</sup>,  
BRUNO C. VILA NOVA<sup>2</sup>, RICHARD J. BUTLER<sup>1</sup> *and* MAX C. LANGER<sup>2</sup>

<sup>1</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham,  
Birmingham, United Kingdom; emails: pedrolorenagodoy@gmail.com,  
r.butler.1@bham.ac.uk  
<sup>2</sup>Laboratório de Paleontologia de Ribeirão Preto, FFCLRP, Universidade de São Paulo,  
Ribeirão Preto, Brazil; emails: gsferreirabio@gmail.com, bruno.vilanova@gmail.com,  
mclanger@ffclrp.usp.br  
<sup>3</sup>Senckenberg Center for Human Evolution and Palaeoenvironment (HEP), Eberhard Karls  
Universität, Tübingen, Germany  
<sup>4</sup>Fachbereich Geowissenschaften, Eberhard Karls Universität, Tübingen, Germany  
<sup>5</sup>Departamento de Biologia e Zootecnia, Universidade Estadual Paulista, FEIS, Ilha Solteira,  
Brazil; email: fcmontefeltro@bio.feis.unesp.br

\*Corresponding author

**Abstract:** The southern supercontinent of Gondwana was home to an extraordinary diversity  
of stem-crocodylians (Crocodyliformes) during the Late Cretaceous. The remarkable  
morphological disparity of notosuchian crocodyliforms indicates that this group filled a wide  
range of ecological roles more frequently occupied by other vertebrates. Among

notosuchians, the distinctive cranial morphology and large body sizes of Baurusuchidae suggest a role as apex predators in ecosystems in which the otherwise dominant predatory theropod dinosaurs were scarce. Large-bodied crocodyliforms, modern and extinct, are known to have reached large sizes by extending their growth period. In a similar way, peramorphic heterochronic processes may have driven the evolution of the similarly large baurusuchids. To assess the presence of peramorphic process in the cranial evolution of baurusuchids, we applied a geometric morphometric approach to investigate ontogenetic cranial shape variation in a comprehensive sample of notosuchians. Our results provide quantitative morphological evidence that peramorphic processes influenced the cranial evolution of baurusuchids. After applying size and ancestral ontogenetic allometry corrections to our data, we found no support for the action of either hypermorphosis or acceleration, indicating that these two processes alone cannot explain the shape variation observed in Notosuchia. Nevertheless, the strong link between cranial shape variation and size increase in baurusuchids suggests that peramorphic processes were involved in the emergence of hypercarnivory in these animals. Our findings illustrate the role of heterochrony as a macroevolutionary driver, and stress, once more, the usefulness of geometric morphometric techniques for identifying heterochronic processes behind evolutionary trends.

**Key words:** heterochrony, peramorphosis, ontogenetic scaling, geometric morphometrics, Crocodyliformes, Baurusuchidae.

HETEROCHRONY, the shifts in timing and rate of development, has been hypothesized to drive major phenotypic modifications in many groups (Gould 1977; McKinney 1988; McNamara and McKinney 2005; Bhullar *et al.* 2012; Koyabu *et al.* 2014). The identification of heterochronic processes requires information about the ancestral condition and the

ontogenetic stage (age) of the studied organisms (Alberch *et al.* 1979; Shea 1983; Klingenberg 1998). However, as well-preserved ontogenetic series and precise information on absolute ages of individuals are rare for fossil vertebrates, palaeontologists have often used relative size as a proxy for ontogenetic stage (Erickson *et al.* 2004; Schoch 2010; Ezcurra and Butler 2015; Foth *et al.* 2016a). In this context, the recent discovery of a beautifully preserved new specimen of the baurusuchid crocodyliiform *Pissarrachampsia sera* (Fig. 1), noticeably smaller than the other specimens previously reported (Montefeltro *et al.* 2011), provides the opportunity to investigate the role of ontogenetic changes in the evolution of one of the most remarkable crocodyliiform groups, the notosuchians.

Notosuchia is the most diverse crocodyliiform group in the Cretaceous of Gondwana (Turner and Sertich 2010; Godoy *et al.* 2014; Pol *et al.* 2014; Pol and Leardi 2015), showing an extraordinary taxonomical and ecological diversity (Bronzati *et al.* 2015; Mannion *et al.* 2015; Stubbs *et al.* 2013). Among the notosuchian subclades, baurusuchids are distinguished by their peculiar anatomy, including a high and laterally compressed skull and blade-like ziphodont teeth. These features have been used to infer an ecological role as land-dwelling hypercarnivores, acting as apex predators in specific Gondwanan ecosystems in which theropod dinosaurs, the dominant terrestrial predators throughout most of the Mesozoic, were scarce (Montefeltro *et al.* 2011; Riff and Kellner 2011; Godoy *et al.* 2014, 2016). Despite the long history of research on baurusuchids (Price 1945; Gasparini 1971), few studies have examined aspects of their ontogeny, as juvenile specimens have been rarely reported and their preserved fossils are mostly fragmentary (e.g. Carvalho *et al.* 2011). Likewise, although Crocodyliformes is a highly diverse and fossil-rich clade, studies identifying the role of heterochronic processes in their evolutionary history are relatively rare and usually focused on extant crocodylians (e.g. Gignac and O'Brien 2016).

When compared to adult baurusuchids, the juvenile individual reported here bears a general cranial morphology more typically seen in adults of non-baurusuchid notosuchians, such as *Mariliasuchus amarali*, *Comahuesuchus brachybuccalis*, and the various species of *Araripesuchus*. Based on these differences, we hypothesized that the ancestral notosuchian cranial morphology was modified by peramorphic heterochronic processes, leading to the adult baurusuchid skull. Peramorphosis (“shape beyond”) is identified when the descendant development (size or shape) extends beyond that of the ancestor, producing exaggerated adult traits (Alberch *et al.* 1979; Klingenberg 1998). Ancestral adult characters are therefore seen in juveniles of the descendent. The opposite process is known as paedomorphosis, in which the descendant retains at adult size the shape (or the characteristics) of the ancestral juvenile (Alberch *et al.* 1979; Klingenberg 1998).

As previously documented (Erickson and Brochu 1999), large extant and extinct crocodyliforms have achieved larger bodies by extending the growth period, suggesting the action of time hypermorphosis, a peramorphic process that leads to an increase in size. Accordingly, the evolution of larger body sizes in baurusuchids may have been the result of similar processes, but this hypothesis has not been previously examined. In this work, we use the new specimen of *Pissarrachampsa sera* to document heterochronic changes and assess the action of peramorphic processes in the cranial evolution of Baurusuchidae.

*Institutional abbreviations.* LPRP/USP, Laboratório de Paleontologia, Universidade de São Paulo, Ribeirão Preto, Brazil.

## SYSTEMATIC PALAEOLOGY

CROCODYLIFORMES Benton and Clark 1988

MESOEUCROCODYLIA Whetstone and Whybrow 1983

BAURUSUCHIDAE Price 1945

PISSARRACHAMPSINAE Montefeltro *et al.* 2011

*Pissarrachampsa sera* Montefeltro *et al.* 2011

*Holotype.* LPRP/USP 0019; nearly complete skull and mandibles lacking the rostralmost portion of the rostrum, seven dorsal vertebrae, partial forelimb, pelvic girdle, and hindlimbs (Montefeltro *et al.* 2011; Godoy *et al.* 2016).

*Newly referred specimen.* LPRP/USP 0049; a juvenile individual comprised of a complete skull with lower jaws, articulated neck/trunk vertebrae and partial right scapula and forelimb (Fig. 1).

*Locality.* Inhaúmas-Arantes Farm, Gurinhatã, Minas Gerais state, Brazil (Martinelli and Teixeira 2105).

*Age and horizon.* Adamantina Formation, Bauru Group, Bauru Basin; Late Cretaceous, Campanian–Maastrichtian (Marsola *et al.* 2016; Batezelli 2017).

*Diagnosis.* The new specimen LPRP/USP 0049 was identified as *Pissarrachampsa sera* based on the presence of the following combination of features, unique to that taxon (Montefeltro *et al.* 2011; Godoy *et al.* 2016): a longitudinal depression on the rostral portion of frontal; frontal longitudinal ridge extending rostrally beyond the frontal midlength; supratemporal fenestra with equally developed medial and rostral rims; lacrimal duct positioned at the

angular junction between the dorsal and lateral surfaces of the lacrimal; well-developed rounded foramen between the anterior and posterior palpebrals; quadratojugal and jugal do not form a continuous ventral border (a notch is present due to the ventral displacement of the quadratojugal); four subtympenic foramina (*sensu* Montefeltro *et al.* 2016) visible laterally; a single ventral parachoanal fenestra and one ventral parachoanal fossa (divided into medial and lateral parachoanal subfossae); lateral Eustachian foramina larger than the medial one; a deep depression on the caudodorsal surface of the pterygoid wings; complete absence of postcranial osteoderms.

## METHODS

### *Heterochronic terminology*

It is important to clearly define the peramorphic processes used in the context of this work, as distinct heterochronic processes have been defined using different formalisms (evolutionary *versus* developmental concepts, for example) in the past (Klingenberg 1998). The definitions of the peramorphic processes used herein (Fig. 2) follow mainly the works of Gould (1977), Alberch *et al.* (1979), Shea (1983), and Klingenberg (1988). Accordingly, we recognize that the effects of heterochrony on the phenotype may be realized on three different and independent dimensions – shape of a given structure, body size, and age (Klingenberg 1998). The variation of three parameters – rate of change (either of a structure or the entire body), and times of onset and offset of growth (either of a structure or the entire body) – can be used to describe the processes (Alberch *et al.* 1979; Klingenberg 1998).

Acceleration is identified when anatomical structures of the descendant develop faster (increased rate) than the rest of the body, when compared to the ancestor. There is a break of

the ancestral allometry (size-shape relations), so these changes are not ontogenetically scaled (i.e., heterochronic changes do not maintain the ancestral allometric relationships). There is no change of the times of onset and offset of growth. The outcome is a peramorphic structure, in an individual with the same body size and an equivalent period of development as the ancestor (Fig. 2).

Hypermorphosis can be divided in two subtypes (Shea 1983). Time hypermorphosis, is when the entire body of the descendant (including the studied part) develops for a longer period than in the ancestor. The ancestral allometry is maintained, so the changes are ontogenetically scaled. There is no change in the time of growth onset, but the offset is delayed. The outcome is a peramorphic structure, in an individual with larger body size and a longer period of development than the ancestor (Fig. 2). By contrast, in rate hypermorphosis the entire body of the descendant (including the studied part) develops faster than in the ancestor. The ancestral allometry is maintained, so the changes are ontogenetically scaled. There is no change in the times of onset and offset of growth. The outcome is a peramorphic structure, in an individual with a larger body size and the same period of development as in the ancestor (Fig. 2). The distinction between rate and time hypermorphosis, introduced by Shea (1983), was not part of the original classification of Alberch *et al.* (1979), and the use of the term rate hypermorphosis has been criticized by some authors (e.g. Gould 2000). In any case, the resulting morphology (i.e. the descendant's morphology) is ontogenetically scaled in both time and rate hypermorphosis.

Finally, predisplacement is when a structure of the descendant starts to develop earlier than in the ancestor. This often leads to a break of the ancestral allometry, but not if the entire body also starts developing earlier. The onset of growth is anticipated (at least that of the structure), but the offset is maintained. The outcome is a peramorphic structure, in an individual with the same body size and the same period of development as the ancestor or



with a larger body size and a longer period of development than the ancestor if the earlier onset also affected the entire body (Fig. 2).

### *Data collection*

To test if the cranial modifications seen in Baurusuchidae were generated by heterochronic processes, we assessed the cranial disparity of Notosuchia using 2D geometric morphometric analyses of general skull shape. The specimens/species sampling took into account the phylogenetic positions within Notosuchia of the species and the preservation of the specimens. Only fairly complete skulls, for which most of the landmarks could be readily identified and digitized, were sampled. Specimens too deformed or lacking important parts of the skull were not included. However, to maximise the sample size, we also included specimens in which only a small portion of the skull was missing (e.g. the rostralmost tip of the snout) or specimens that were slightly deformed. In these cases, we used closely related taxa to project the landmark positions during the digitization.

As a result, we sampled 38 specimens, from a total of 27 taxa across Notosuchia, including four juvenile specimens: the baurusuchids *Pissarrachampsa sera* and *Campinasuchus dinizi*, as well as *Anatosuchus minor* and *Mariliasuchus amarali* (for the complete list, see Supporting Information, Table S1). To obtain more detailed interpretations of skull shape variation, we used both lateral and dorsal views for the analyses (Openshaw *et al.* 2016), with 19 and 17 landmarks respectively (see Supporting Information for the position and description of landmarks, Fig. S1; Table S3). Landmarks were digitized using the software tpsDig 2.22 (Rohlf 2015). We used both right and left sides of the skulls, choosing the side that offered the best conditions for digitization (considering either preservation or quality of photographs). Then, we extract the reflected shape of the specimens that were

digitized on the right side while performing the Procrustes fit in MorphoJ. To minimize error, landmarks were collected twice for each specimen (by a single person), and the subsequent analyses employed the average coordinates from the two digitizations of each specimen.

*Phylogenetic framework*

Notosuchia is a group of mesoeucrocodylians that has been consistently supported as monophyletic, even though its exact taxonomic content may vary in different phylogenetic hypotheses (e.g. Turner and Sertich 2010; Andrade *et al.* 2011; Bronzati *et al.* 2012; Montefeltro *et al.* 2013; Pol *et al.* 2014; Sertich and O'Connor 2014; Turner 2015; Wilberg 2015). The placement of Baurusuchidae deeply nested within Notosuchia is supported even by studies that have highly distinct taxonomic and character samples (Montefeltro *et al.* 2013; Pol *et al.* 2014; Turner 2015; Martin and Lapparent de Broin 2016; Meunier and Larsson 2016), but uncertainties remain regarding the nearest relatives of baurusuchids. The morphological similarities with Sebecidae, a group of Cenozoic terrestrial crocodyliforms, have led many phylogenetic studies to cluster Baurusuchidae and Sebecidae into Sebecosuchia (Turner and Sertich 2010; Kellner *et al.* 2014; Pol *et al.* 2014). Alternative positions placed Baurusuchidae closer to other Cretaceous notosuchians, such as Sphagesauridae, with Sebecidae placed closer to other groups such as Peirosauridae and Mahajangasuchidae (Serenio and Larson 2009; Montefeltro *et al.* 2013; Wilberg 2015; Meunier and Larsson 2016). It is almost universally agreed, however, that baurusuchids are not very closely related to a set of mostly small-bodied notosuchians, such as *Mariliasuchus*, *Araripesuchus*, *Notosuchus*, and *Uruguaysuchus* (Kellner *et al.* 2014; Pol *et al.* 2014; Leardi *et al.* 2015a, b; Martin and Lapparent de Broin 2016).

The phylogenetic hypothesis proposed by Montefeltro *et al.* (2013) was selected as the primary phylogenetic framework for our geometric morphometric analyses (Fig. 3A). We added four taxa to the original topology of Montefeltro *et al.* (2013), for which we had morphometric data available: *Aplestosuchus sordidus*, *Campinasuchus dinizi*, *Candidodon itapecuruensis*, and *Pakasuchus kapilimai*. We employed information from Godoy *et al.* (2014) to define the phylogenetic position of the first two taxa, and from Pol *et al.* (2014) for the latter two. Following this phylogenetic framework, we divided the sampled specimens into four different taxonomic groups, which was necessary to test our hypothesis of peramorphosis in baurusuchid evolution: “Baurusuchidae”, “Sphagesauridae”, “Peirosauridae + Sebecidae”, and the remaining notosuchians falling outside of these groups (clustered here as “other notosuchians”). As *Sebecus icaeorhinus* was the only representative of Sebecidae included, it was combined with peirosaurids into a single group for the analyses.

In order to test the robustness of our results to changes in phylogenetic hypotheses, we also divided the sampled specimens to fit an alternative phylogenetic framework. We selected the topology of Pol *et al.* (2014), as the data matrix presented in this work has formed the basis of many subsequent phylogenetic analyses of notosuchians (e.g. Leardi *et al.* 2015a, b; Godoy *et al.* 2016). As a result, we reallocated the specimens within three alternative taxonomic groups: “Sebecosuchia” (baurusuchids + *Sebecus icaeorhinus*), “Uruguaysuchidae + Peirosauridae” (*Araripesuchus* species, *Uruguaysuchus* and *Anatosuchus* in Uruguaysuchidae + peirosaurids) and “other notosuchians” (all remaining species, including sphagesaurids).

#### *Geometric morphometrics analyses*

To extract shape information from both lateral and dorsal view datasets, we first applied a Procrustes fit with reflection, using the software MorphoJ 1.06e (Klingenberg 2011), and also obtained centroid size, to be used in subsequent analyses as a proxy for size. Next, to visualize the skull shape transformations during the postnatal ontogeny of *Pissarrachampsa sera*, we performed a thin plate spline (Bookstein 1991), using the lateral view dataset of both the juvenile and adult specimens of this taxon. This procedure was conducted using ‘geomorph’ package (Adams and Otárola-Castillo 2013) in R (R Core Team 2017), and shape variation (the position of the Procrustes coordinates) of the adult against the juvenile was plotted in a deformation grid. We then conducted principal component analyses (PCA) in MorphoJ to investigate the morphospace occupied by the sampled taxa. For these comparisons, we divided the specimens into taxonomic groups using both phylogenetic frameworks outlined above. The position of individual specimens within the morphospace will not change using alternative phylogenetic frameworks – the only difference should be in the morphospace occupation by the different taxonomic groups. We also mapped the topology of Montefeltro *et al.* (2013) onto centroid size (using only the lateral view dataset) to explore the size differences among the sampled taxa.

Subsequently, we performed a set of analyses to assess which specific heterochronic processes could be driving baurusuchid cranial evolution. Peramorphic changes in the shape of structures can be decoupled from (acceleration) or accompanied by (hypermorphosis and predisplacement) changes in size (Gould 1977; Alberch *et al.* 1979; Shea 1983; Klingenberg 1998). To explore this relation, we employed a size-correction to our datasets to test whether the shape differences remained after removing the effect of allometric changes (Gould 1966; Revell 2009; Klingenberg 2016). Using MorphoJ, we obtained the residuals of a multivariate regression of the Procrustes coordinates against centroid size (Monteiro 1999; Klingenberg *et al.* 2012; Klingenberg 2016). For this, we used a subset restricted to adult specimens, as we

1  
2  
3 were interested only in interspecific size variation. The residuals from this regression were  
4  
5 then used as the input for a second PCA to explore the occupied morphospace after removing  
6  
7 the effect of size on the observed variation. As for the first PCA, the specimens were also  
8  
9 divided into taxonomic groups using both the primary and alternative phylogenetic  
10  
11 frameworks. To test the significance of the differences in the distributions of groups in the  
12  
13 morphospace, we used a non-parametric multivariate analysis of variance, npMANOVA,  
14  
15 which, in contrast to a parametric MANOVA, does not require the data to be normally  
16  
17 distributed, and tests for significant differences on the basis of permutations (Anderson 2001;  
18  
19 Foth *et al.* 2016b). These tests were performed in PAST (Hammer *et al.* 2001), and we used  
20  
21 the PC scores that represent at least 95 per cent of shape variation. These scores were then  
22  
23 transformed into a Euclidean distance matrix (Euclidean similarity index), and permuted with  
24  
25 10,000 replications. Comparisons were made using the Bonferroni correction, to reduce the  
26  
27 likelihood of type 1 statistical errors (Rice 1989). Additionally, we projected the topology  
28  
29 based on the hypothesis of Montefeltro *et al.* (2013) onto the PC scores (using both dorsal and  
30  
31 lateral view datasets), creating a phylomorphospace to explore the evolutionary history of  
32  
33 shape changes in the sampled taxa.  
34  
35

36  
37 To evaluate the specific action of time hypermorphosis, we applied the methodology  
38  
39 described by Strelin *et al.* (2016), to test whether the shape modifications seen in the  
40  
41 baurusuchid skull evolved by ontogenetic scaling. Time hypermorphosis corresponds to an  
42  
43 extension of the ancestral ontogenetic trajectory, a pattern previously detected in other  
44  
45 crocodyliforms known to extend the growth period and attain larger body sizes (e.g. Erickson  
46  
47 and Brochu 1999). As such, based on whether the differences among taxa remain or not after  
48  
49 this procedure, we can reject or confirm hypermorphosis as the sole peramorphic process  
50  
51 acting on baurusuchid skull evolution, as this is the only process that extends the ontogenetic  
52  
53 trajectory in time.  
54  
55  
56  
57  
58  
59  
60

For this, we compared skull size and shape variation from juvenile to adult baurusuchids to those changes seen along the ontogenetic trajectory of a hypothetical ancestral notosuchian. The ancestral ontogenetic trajectory was inferred via a phylogenetic approach based on outgroup taxa to Baurusuchidae. Ideally, this approach would incorporate information from as many non-baurusuchid notosuchians as possible. However, only two non-baurusuchid notosuchians have juvenile specimens reported with well-preserved skulls. Those two species are *Mariliasuchus amarali*, with one juvenile and five adult specimens included in our sample, and *Anatosuchus minor*, with one juvenile and one adult specimen sampled. Although using only two taxa is not ideal, the phylogenetic positions of these two species relative to baurusuchids support their use as the best available proxies for the ancestral condition of baurusuchids (see Supporting Information for further discussion).

Accordingly, we created an ontogenetic regression model for both *Mariliasuchus amarali* and *Anatosuchus minor*, using all sampled specimens (including juveniles), by regressing the Procrustes coordinates against the log-transformed centroid size in MorphoJ (Klingenberg 2011; Strelin *et al.* 2016). This ontogenetic regression model was used to perform an allometric size-correction (which we refer to here as the “ancestral ontogenetic allometry correction”) for all other taxa in our sample (Strelin *et al.* 2016). Regression residuals were calculated in MorphoJ, by using the vector of regression coefficients for the ontogenetic allometry estimated for the two taxa and applying them to our shape data. This process removes the potential effect of ontogenetic scaling from the variation among taxa. These residuals were then used as the input data for a third PCA, again including only adults, to explore the morphospace occupied after removing the effect of the ancestral ontogenetic allometry trajectory from our data. As for the first and second PCA, we investigated morphospace occupation using both primary and alternative phylogenetic frameworks. As also done following the size-correction, we used npMANOVA to test the significance of the

differences between groups and created phylomorphospaces, by projecting the topology of Montefeltro *et al.* (2013) onto the PC scores.

Finally, we note that the use of *Anatosuchus minor* as a proxy for the ancestral ontogenetic trajectory should be treated with caution. The holotype specimen of *Anatosuchus minor*, which has been interpreted as a juvenile, is not much smaller than the only other known specimen of this taxon, which has been interpreted as an adult. Moreover, this taxon also exhibits a cranial morphology notably distinct from those of other notosuchians (Serenó *et al.* 2003; Sereno and Larsson 2009). Accordingly, as a sensitivity test, we also estimate the ancestral ontogenetic trajectory without including *Anatosuchus minor*, instead performing the ancestral ontogenetic allometry correction using only the *Mariliasuchus amarali* specimens.

## RESULTS

The thin plate spline shows that the cranial changes observed during the ontogeny of *Pissarrachampsa sera* include an expansion of the rostrum (both rostrocaudally and dorsoventrally), a rostrocaudal shortening of the skull roof (orbitotemporal region), and the reduction of the relative size of the orbits and the lower temporal fenestrae (Fig. 3B). Furthermore, based on the primary phylogenetic framework (Montefeltro *et al.* 2013), the first PCA shows that juvenile and adult baurusuchids occupy different regions of the morphospace. In both the lateral (PC1 accounting for 60.6 per cent of the variation, PC2 = 9.9 per cent) and dorsal views (PC1 = 57.9 per cent, PC2 = 11.3 per cent), juvenile baurusuchids fall outside the morphospace of adult baurusuchids, but within the morphospace occupied by non-baurusuchid notosuchians. By contrast, when compared to juveniles, adult baurusuchids occupy a distinct part of the morphospace, mainly displaced along the PC1 axis for the lateral view dataset (Fig. 3A), and along both PC1 and PC2 axes for the dorsal view dataset

(Supporting Information, Fig. S2). A similar pattern of morphospace occupation was found when we used the alternative phylogenetic framework (Pol *et al.* 2014), with the sampled taxa rearranged into different groups. In both lateral and dorsal views (Supporting Information, Fig. S3, S4) juvenile sebecosuchians (the group that includes baurusuchids) are displaced in relation to the morphospace occupied by adults.

The allometric regression of the Procrustes coordinates against log-transformed centroid size shows that changes related to size differences accounted for 36.4 and 40.5 per cent of the variation in the dorsal and lateral view datasets, respectively (see Supporting Information for more about this allometric regression, Table S4, S5; Fig. S5). The second PCA, with size-corrected data, shows that size variation strongly influences morphospace occupation of the different lineages, in both lateral and dorsal views (Fig. 5A, B). For the primary phylogenetic framework (Montefeltro *et al.* 2013), the confidence ellipses (90 per cent) for baurusuchids, sphagesaurids, and even peirosaurids/sebecids overlapped with the confidence ellipse of other notosuchians (see Supporting Information for the phylomorphospaces, Fig. S6). The absence of significant differences in the distribution of these groups was supported by the npMANOVA test (Table 1), showing that changes in size can explain the apparent separation of groups found in our previous analyses (first PC plots). Additionally, when the alternative phylogenetic framework (Pol *et al.* 2014) was taken into account through rearranging the specimens into different taxonomic groups (see Methods above), we found very similar results. The npMANOVA results also indicate that the morphospaces of sebecosuchians (i.e. baurusuchids) and other notosuchians are not significantly different, in both dorsal and lateral views (Supporting Information, Fig. S7, S8).

Finally, the ancestral ontogenetic trajectory was estimated by using the ontogenetic trajectories of *Mariliasuchus amarali* and *Anatosuchus minor* as proxies. First, to assure that the ontogenetic trajectories of these two species (representing the ancestral condition) differ



from that of *Pissarrachampsa sera* (representing the baurusuchid trajectory), we compared the reconstructed trajectories of these three taxa with a regression analysis. As expected, the trajectories of these three species are clearly displaced in relation to one another (Fig. 6). However, in dorsal view, whereas the trajectories of *Mariliasuchus amarali* and *Pissarrachampsa sera* exhibit a similar slope, that of *Anatosuchus minor* is clearly different. This might indicate that the use of *Anatosuchus minor* for reconstructing the ancestral ontogenetic trajectory should be treated with caution, given its unique cranial morphology among Notosuchia (see Methods above).

The distinction between those ontogenetic trajectories (that of the hypothetical ancestor, represented by *Mariliasuchus* and *Anatosuchus*, and that of baurusuchids, represented by *Pissarrachampsa*) allowed us to progress further with the ancestral ontogenetic allometry correction (i.e. removing the effect of ontogenetic scaling from our data). The results of the third PCA, after this correction, employing the primary phylogenetic framework (Montefeltro *et al.* 2013), are apparently conflicting. Using the lateral view dataset, the morphospaces occupied by adult baurusuchids and other notosuchians overlap and are not significantly separated (Fig. 5D; Table 1), suggesting that the shape variation observed in baurusuchids could be ontogenetically scaled. However, the dorsal dataset shows a different result, with baurusuchid and other notosuchian morphospaces significantly separated (Fig. 5C, Table1). Furthermore, when using the alternative phylogenetic framework (Pol *et al.* 2014), we found the morphospaces of sebecosuchians (i.e. baurusuchids) and other notosuchians to be significantly separated, in both dorsal and lateral views (Supporting Information, Fig. S10, S11; Table S10, S11). Finally, to test the influence of the ontogenetic trajectory of *Anatosuchus minor* on our results (given its unique morphology, see Methods above), we applied an ancestral ontogenetic allometry correction using only *Mariliasuchus amarali* for estimating the ancestral trajectory. The results, in both dorsal and lateral views,

show the morphospaces of baurusuchids and other notosuchians to be significantly separated (Supporting Information, Fig. S13, S14; Table S14, S15).

**DISCUSSION**

*Peramorphosis in Baurusuchidae*

The results of the initial analyses (first PCA and thin plate spline) indicate that juvenile baurusuchids bear a more generalized notosuchian morphotype, whereas adults diverge from this morphotype in later ontogenetic stages. This supports our hypothesis of peramorphic processes operating in the evolution of notosuchians, even when considering different phylogenetic frameworks (Supporting Information, Fig. S3, S4). During their ontogeny, baurusuchids seem to expand their rostrum (both rostrocaudally and dorsoventrally), shorten their skull roof rostrocaudally, and reduce the relative sizes of the orbits and the lower temporal fenestrae, differences that can be observed on the deformation grid of the thin plate spline (Fig. 3B). The first PCA corroborates these ontogenetic transformations. In lateral view (Fig. 4A), the PC1 axis, from negative to positive values, represents relative rostrocaudal shortening of the rostrum as well as relative enlargement of the orbit, and the PC2 axis displays changes in skull height (higher skulls represented by more negative values). Adult baurusuchids are all located on the negative side of the PC1 axis, whereas the juvenile *Pissarrachampsia sera* is positioned in a positive region along this axis, illustrating the rostrocaudal expansion of the rostrum during the ontogeny of this taxon. Other modifications can be observed in the dorsal view morphospace (Supporting Information, Fig. S2), in which the PC1 axis also represents rostrocaudal shortening of the rostrum (as in lateral view). The PC2 axis accounts for the mediolateral compression of the skull (from negative to positive

values), and illustrates the mediolateral compression of the skull that occurs during the ontogeny of *Pissarrachampsa*.

Studies using geometric morphometric methods to investigate the ontogenetic trajectories of extant crocodylians (e.g. Piras *et al.* 2010; Watanabe and Slice 2014; Foth *et al.* 2017) allowed us to identify similarities between the morphological modifications during the ontogeny of *Pissarrachampsa sera* and the ontogenies of living taxa. For example, the best documented transformation is the relative reduction of the orbits, also found in living representatives of the three main lineages of Crocodylia: Gavialoidea, Crocodyloidea and Alligatoroidea (e.g. Piras *et al.* 2010; Foth *et al.* 2015, 2017). Other common modifications previously reported include the mediolateral compression of the rostrum, although in *Caiman latirostris* the opposite process is observed (i.e. snouts relatively broader later in ontogeny; Bona and Desojo 2011; Foth *et al.* 2017). Nevertheless, quantitative investigations of possible heterochronic processes acting on the evolution of Crocodyliformes are rare (e.g. Gignac and O'Brien 2016), and our work represents the first attempt to verify the action of heterochrony in fossil lineages of the group using geometric morphometric methods.

However, given the lack of juveniles of other baurusuchids with complete skulls, further assumptions cannot be quantitatively tested. For example, we can only hypothesize the phylogenetic distribution of cranial peramorphism within Baurusuchidae (i.e. determining whether the action of peramorphic processes started at the base of Baurusuchidae or later within the lineage). The size and phylogenetic positions of *Cynodontosuchus rothi* and *Gondwanasuchus scabrosus* suggest that the peramorphic changes occurred just prior or within the clade composed of Pissarrachampsinae + Baurusuchinae (Godoy *et al.* 2014). These two early-diverging species, known from fragmentary remains, have been suggested to be adults, but are substantially smaller than other baurusuchids (estimated as approximately

50 per cent the size of an adult *Pissarrachampsa sera*; Montefeltro *et al.* 2011; Godoy *et al.* 2014).

*Acceleration, predisplacement or hypermorphosis?*

Among the known peramorphic processes (i.e. acceleration, predisplacement, and hypermorphosis; Fig. 2; Gould 1977; Alberch *et al.* 1979; Shea 1983; Klingenberg 1998), acceleration is the only one that does not affect total body size (i.e. based on the definition used here, shape and size are not coupled; Fig. 2A) (Klingenberg 1998). Our results show that the apparent separation between baurusuchids and other notosuchians seen in the first PCA disappears after applying the size-correction (Fig. 5A, B), suggesting a strong correlation between cranial shape and size (centroid size) variation in baurusuchids. Therefore, according to our results, acceleration cannot, as a sole process, explain the shape changes observed in the baurusuchid skull.

We further examined if hypermorphosis could explain the shape variation seen in baurusuchid cranial morphology, by testing the ontogenetic scaling hypothesis. The ontogenetic scaling hypothesis predicts that heterochronic changes can occur by maintaining the ancestral allometric relationships, generating a descendant morphology via proportional changes in size and shape that follow the same ancestral ontogenetic pathway (Fig. 2B) (Shea 1983; Klingenberg 1998; Strelin *et al.* 2016). Based on the definitions used here, hypermorphosis is the peramorphic process that incorporates the concept of ontogenetic scaling, either by increasing the duration of ontogeny (time hypermorphosis) or by increasing the rate of size and shape changes during the same period of growth (rate hypermorphosis) (Fig. 2A, C; Shea 1983). Accordingly, in both time and rate hypermorphosis the shape variation is ontogenetically scaled.

As such, if our data fit the predictions of the ontogenetic scaling model, after removing the effects of the ancestral ontogenetic allometry the confidence ellipses of baurusuchids should collapse to the same morphospace as other notosuchians. This should be true for all shape variation observed in our sample, in both lateral and dorsal views. Accordingly, our results do not corroborate the ontogenetic scaling hypothesis, since the apparently ontogenetically scaled shape variation seen in lateral view (Fig. 5D) is not congruent with the results for the dorsal view or for the other analyses performed. In dorsal view (Fig. 5D), the morphospaces of baurusuchids and other notosuchians remain separate after the ancestral ontogenetic allometry correction (significantly separated, as confirmed by the npMANOVA tests; Table 1), which indicates that the shape variation is not ontogenetically scaled (see Supporting Information for further information and results, Table S4, S5, S8, S9, S12, S11; Fig. S6, S9, S12). This also highlights the importance of using different views when studying skull shape and interpreting their evolutionary patterns (Openshaw *et al.* 2016). Furthermore, when we used a different phylogenetic framework, which essentially rearranged the sampled species into different taxonomic groups (see Methods), the morphospaces of sebecosuchians (which includes baurusuchids) and other notosuchians remain significantly separated (Supporting Information, Fig. S10, S11; Table S10, S11). The same is observed when we removed the *Anatosuchus minor* specimens from the ancestral ontogenetic trajectory estimation (Supporting Information, Fig. S13, S14; Table S14, S15). These complementary results corroborate the idea that the cranial shape variation observed in baurusuchids is not ontogenetically scaled.

The lack of support for the ontogenetic scaling hypothesis demonstrates that neither time nor rate hypermorphosis can be considered as the single, isolated driver of baurusuchid peramorphism (Shea 1983; Strelin *et al.* 2016). Accordingly, the only process that acting alone could possibly explain the peramorphism observed in baurusuchids is predisplacement,

in which the onset age of growth of a structure occurs earlier than in the ancestor (Alberch *et al.* 1979; McNamara 1986) (Fig. 2C). However, changes in the time of onset can only be comprehensively assessed by comparing changes in traits (shape) as a function of ontogenetic stages (age) (Klingenberg 1998). As such, we cannot, at present, confirm the role of predisplacement in the evolution of the baurusuchid skull. Indeed, information such as growth rates and time of onset and offset would be necessary to precisely identify the action of any specific heterochronic process, not only predisplacement. Histological studies comparing growth patterns among different notosuchians have the potential to test whether the onset of baurusuchid traits occurred earlier than in their close relatives (e.g. Cubo *et al.* 2017), which would allow further investigation on the action of peramorphic processes on the evolution of this group. Moreover, the action of a single evolutionary process on morphological structures is expected to be rare (Alberch *et al.* 1979; Klingenberg 1998) and one should expect a combination of two (or more) heterochronic processes acting in the evolution of such complex traits (Klingenberg 1998). Accordingly, as our results are derived from indirect investigation of the action of heterochrony, they only allow us to discard acceleration and hypermorphosis acting in isolation in the cranial evolution of baurusuchids.

*Heterochrony explains hypercarnivory*

Hypercarnivores, as defined by Van Valkenburgh (1991), are taxa that consume at least 70 per cent of vertebrate flesh. They frequently have a specialized dentition, such as the ziphodont teeth of baurusuchids (Riff and Kellner 2011), in which the primary function is slicing. Our documentation of peramorphosis in the evolution of the baurusuchid skull provides important palaeoecological insights, as it supports a strong relation between the reported cranial modifications and size, changes that might have occurred together with the

1  
2 shift to a hypercarnivorous habit. A link between size increase and the evolution of  
3 hypercarnivory has been previously documented in other vertebrate lineages, such as  
4 carnivoran and creodont mammals (Werdelin 1996; Van Valkenburgh 1999; Van  
5 Valkenburgh *et al.* 2004; Wesley-Hunt 2005). Furthermore, heterochrony is commonly  
6 associated with evolutionary trends leading to size increase (McNamara 1982, 1990), and one  
7 of the possible triggers of these trends is the positive pressure caused by competition (Van  
8 Valkenburgh *et al.* 2004; McKinney 1990).

9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
Theropod dinosaurs, the top predators of most terrestrial environments in the  
Mesozoic, are scarce in the Adamantina Formation, from which the greatest diversity of  
baurusuchids has been recovered (Méndez *et al.* 2012; Godoy *et al.* 2014). Thus, the large  
size of baurusuchids, coupled with their cranial specializations, could have granted access to  
new feeding resources (Erickson *et al.* 2012), efficiently occupying the niches more  
commonly filled by theropods elsewhere. Baurusuchids coexisted and interacted with other  
crocodyliform taxa in Gondwanan palaeoecosystems during the Late Cretaceous, including  
carnivorous forms such as peirosaurids (Carvalho *et al.* 2007; Barrios *et al.* 2016).  
Interestingly, the coeval notosuchians (including baurusuchids) are inferred to have filled a  
broad range of feeding habits (herbivorous, omnivorous, and carnivorous), with a high degree  
of niche/resource partitioning (O'Connor *et al.* 2010; Stubbs *et al.* 2013; Ősi 2014). In this  
context, the peramorphic size increase of baurusuchids may have played a key role in this  
niche partitioning, and may also have influenced other aspects of their unique palaeobiology.  
The life history strategy hypothesized for baurusuchids, and notosuchians in general, includes  
a shift to the *K*-selected end of the *r/K* selection spectrum. The shift is suggested by the  
consistently smaller egg clutches present in notosuchians, including *Pissarrachampsa sera*  
(2–5 eggs per clutch; Marsola *et al.* 2016) when compared to fossil neosuchians, such as  
atoposaurids and dyrosaurids (approximately 12 eggs per clutch; Russo *et al.* 2014; Srivastava

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

*et al.* 2015). The smaller egg clutches of notosuchians (and baurusuchids) is also dissimilar to those of extant crocodylians, in which the number of eggs varies from a lower limit of 10 and reaches up to 80 eggs (Brazatis and Watanabe 2011; Marsola *et al.* 2016). The features of *K*-selected organisms are commonly associated with hypermorphosis, primarily because this process is classically related to size increase. Even though our results do not support the action of hypermorphosis as the single process in the cranial evolution of baurusuchids, predisplacement can also lead to size increase (Fig. 2C), and it may similarly be linked to the evolution of *K*-selection strategies.

Here we demonstrate that changes in the skull shape of baurusuchids, likely accompanied by highly specialized cranial modifications, were strongly linked to size increase in the lineage. As these shape changes occurred through their ontogeny, they provide evidence for the action of heterochronic processes in the shift to a hypercarnivorous diet during baurusuchid evolutionary history. These are interesting advances in the knowledge of the underlying processes that drove notosuchian evolution, and provide important clues for understanding the exceptional diversity displayed by this peculiar group of crocodyliforms.



*Acknowledgments.* We thank the excavation crew from the Laboratório de Paleontologia de Ribeirão Preto (Universidade de São Paulo). We also thank Christian P. Klingenberg for insightful comments on the research design, and Hans Larsson for comments on an earlier version of the manuscript. Access to fossil collections was possible thanks to Carl Mehling, Mark Norell, Alan Turner, Tayler Keillor, Paul Sereno, William Simpson, David Evans, Kevin Seymour, Oliver Rauhut, Mario Bronzati, Thiago Marinho, Sandra Tavares, Fabiano Iori, Rodrigo da Rocha Machado, Stella Alvarez, and Alejandro Kramarz. We thank Sally Thomas, Christian Foth, and one anonymous reviewer for their helpful comments. This research was supported by the University of Birmingham (funding to P.L.G. and R.J.B.); CAPES (grant numbers 3581-14-4 to P.L.G.; and 20131696 to B.C.V.N.); FAPESP (grant numbers 2014/25379-5 and 2016/03934-2 to G.S.F.; 2014/03825-3 to M.C.L.); and UNESP (grant “Primeiros Projetos PROPe UNESP”, number 730, to F.C.M.).

*Author contributions.* G.S.F. and M.C.L. designed the research. G.S.F., P.L.G., F.C.M. and B.C.V.L. collected the data. F.C.M., R.J.B., and M.C.L. provided evolutionary expertise for the project. G.S.F. and P.L.G. performed the analyses, jointly wrote the manuscript and created the figures and tables. G.S.F., P.L.G., F.C.M., B.C.V.L., R.J.B. and M.C.L. discussed the results and contributed to manuscript revisions.

## DATA ARCHIVING STATEMENT

Data for this study, including the Supporting Information (with supplementary text, tables, and figures) as well as the TPS files with digitized landmarks (of both lateral and dorsal views), and the R and MorphoJ scripts for conducting the geometric morphometrics analyses described here, are available in the Dryad Digital Repository:

<http://datadryad.org/review?doi=doi:10.5061/dryad.7m48r> [please note that the

data for this paper are not yet published and this temporary link should not be shared without the express permission of the author]

REFERENCES

ADAMS, D. C. and OTÁROLA-CASTILLO, E. 2013. geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology & Evolution*, **4**, 393–399.

ALBERCH, P., GOULD, S. J., OSTER, G. F. and WAKE, D. B. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology*, **5**, 296–317.

ANDERSON, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.

ANDRADE, M. B., EDMONDS, R., BENTON, M. J. and SCHOUTEN, R. 2011. A new Berriasian species of *Goniopholis* (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus. *Zoological Journal of the Linnean Society*, **163**, 66–108.

BARRIOS, F., PAULINA-CARABAJAL, A. and BONA P. 2016. A New Peirosaurid (Crocodyliformes, Mesoeucrocodylia) from the Upper Cretaceous of Patagonia, Argentina. *Ameghiniana*, **53**, 14–25.

BATEZELLI, A. 2017. Continental systems tracts of the Brazilian Cretaceous Bauru Basin and their relationship with the tectonic and climatic evolution of South America. *Basin Research*, **29**, 1–25.

BENTON, M. and CLARK, J. M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. 295–338. In BENTON, M. (ed). *The phylogeny and classification of the tetrapods*. Clarendon Press, Oxford.

BHULLAR, B. A., MARUGÁN-LOBÓN, J., RACIMO, F., BEVER, G. S., ROWE, T. B., NORELL, M. A. and ABZHANOV, A. 2012. Birds have paedomorphic dinosaur skulls. *Nature*, **487**, 223–226.

BONA, P. and DESOJO, J. B. 2011. Osteology and cranial musculature of *Caiman latirostris* (Crocodylia: Alligatoridae). *Journal of Morphology*, **272**, 780–795.

BOOKSTEIN, F. L. 1991. *Morphometric tools for landmark data*. Cambridge University Press, New York, NY.

BRAZAITIS, P. and WATANABE, M. E. 2011. Crocodilian behaviour: a window to dinosaur behaviour? *Historical Biology*, **23**, 73–90.

- BRONZATI, M., MONTEFELTRO, F. C. and LANGER, M. C. 2012. A species-level  
supertree of Crocodyliformes. *Historical Biology*, **24**, 598–606.
- --- 2015. Diversification events and the effects of mass extinctions on Crocodyliformes  
evolutionary history. *Royal Society open science*, **2**, 140385.
- CARVALHO, I. S., VASCONCELLOS, F. M. and TAVARES, S. A. S. 2007.  
*Montealtosuchus arrudacamposi*, a new peirosaurid crocodile (Mesoeucrocodylia) from  
the Late Cretaceous Adamantina Formation of Brazil. *Zootaxa*, **1607**, 35–46.
- TEIXEIRA, V. P. A., FERRAZ, M. L. F., RIBEIRO, L. C. B., MARTINELLI, A. G.,  
NETO, F. M., SERTICH, J. J. W., CUNHA, G. C., CUNHA, I. C. and FERRAZ, P. F.  
2011. *Campinasuchus dinizi* gen. et sp. nov., a new Late Cretaceous baurusuchid  
(Crocodyliformes) from the Bauru Basin, Brazil. *Zootaxa*, **2871**, 19–42.
- CUBO, J., KÖHLER, M. and BUFFRENIL, V. 2017. Bone histology of *Iberosuchus*  
*macrodon* (Sebecosuchia, Crocodylomorpha). *Lethaia*, **50**, 495–503.
- ERICKSON, G. M. and BROCHU, C. A. 1999. How the ‘terror crocodile’ grew so big.  
*Nature*, **398**, 205–206.
- MAKOVICKY, P. J., CURRIE, P. J., NORELL, M. A., YERBY, S. A. and BROCHU, C.  
A. 2004. Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs.  
*Nature*, **430**, 772–775.
- GIGNAC, P. M., STEPPAN, S. J., LAPPIN, A. K., VLIET, K. A., BRUEGGEN, J. D.,  
INOUE, B. D., KLEDZIK, D. and WEBB, G. J. 2012. Insights into the ecology and  
evolutionary success of crocodylians revealed through bite-force and tooth-pressure  
experimentation. *PLoS One*, **7**, e31781.
- EZCURRA, M. D. and BUTLER, R. J. 2015. Post-hatchling cranial ontogeny in the Early  
Triassic diapsid reptile *Proterosuchus fergusi*. *Journal of Anatomy*, **226**, 387–402.
- FOTH, C., BONA, P. and DESOJO, J. B. 2015. Intraspecific variation in the skull  
morphology of the black caiman *Melanosuchus niger* (Alligatoridae, Caimaninae). *Acta*  
*Zoologica*, **96**, 1–13.
- HEDRICK, B. P. and EZCURRA MD. 2016a. Cranial ontogenetic variation in early  
saurischians and the role of heterochrony in the diversification of predatory dinosaurs.  
*PeerJ*, **4**, e1589.
- FERNANDEZ BLANCO, M. V., BONA, P. and SCHEYER, T. M. 2017. Cranial shape  
variation in jacarean caimanines (Crocodylia, Alligatoroidea) and its implications in the  
taxonomic status of extinct species: The case of *Melanosuchus fisheri*. *Journal of*  
*Morphology*. Published online on 15 November 2017 (doi: 10.1002/jmor.20769).

- EZCURRA, M. D., SOOKIAS, R. B., BRUSATTE, S. L. and BUTLER RJ. 2016b. Unappreciated diversification of stem archosaurs during the Middle Triassic predated the dominance of dinosaurs. *BMC Evolutionary Biology*, **16**, 188.
- GASPARINI, Z. B. 1971. Los Notosuchia del Cretácico de América del Sur como un nuevo Infraorden de los Mesosuchia (Crocodilia). *Ameghiniana*, **8**, 83–103.
- GIGNAC, P. and O'BRIEN, H. 2016. Suchian Feeding Success at the Interface of Ontogeny and Macroevolution. *Integrative and Comparative Biology*, **56**, 449–458.
- GODOY, P. L., MONTEFELTRO, F. C., NORELL, M. A. and LANGER, M. C. 2014. An additional Baurusuchid from the cretaceous of Brazil with evidence of interspecific predation among crocodyliformes. *PLoS One*, **9**, e97138.
- BRONZATI, M., ELTINK, E., MARSOLA, J. C. A., CIDADE, G. M., LANGER, M. C. and MONTEFELTRO, F. C. 2016. Postcranial anatomy of *Pissarrachampsia sera* (Crocodyliformes, Baurusuchidae) from the Late Cretaceous of Brazil: insights on lifestyle and phylogenetic significance. *PeerJ*, **4**, e2075.
- GOULD, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biological reviews of the Cambridge Philosophical Society*, **41**, 587–640.
- 1977. *Ontogeny and phylogeny*. Harvard University Press, Cambridge, MA.
- 2000. Of coiled oysters and big brains: how to rescue the terminology of heterochrony, now gone astray. *Evolution & Development*, **2**, 241–248.
- HAMMER, Ø., HARPER, D. A. T. and RYAN, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Paleontologia Electronica*, **4**, 1–9.
- KELLNER, A. W., PINHEIRO, A. E. and CAMPOS, D. A. 2014. A new sebecid from the paleogene of Brazil and the crocodyliform radiation after the K-Pg boundary. *PLoS One*, **9**, e81386.
- KLINGENBERG, C. P. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biological reviews of the Cambridge Philosophical Society*, **73**, 79–123.
- 2011. MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology Resources*, **11**, 353–357.
- 2016. Size, shape, and form: concepts of allometry in geometric morphometrics. *Development Genes and Evolution*, **226**, 113–137.
- DUTTKE, S., WHELAN, S. and KIM, M. 2012. Developmental plasticity, morphological variation and evolvability: a multilevel analysis of morphometric integration in the shape of compound leaves. *Journal of Evolutionary Biology*, **25**, 115–129.

- KOYABU, D., WERNEBURG, I., MORIMOTO, N., ZOLLIKOFER, C. P., FORASIEPI, A. M., ENDO, H., KIMURA, J., OHDACHI, S. D., SON, N. T. and SANCHEZ-VILLAGRA, M. R. 2014. Mammalian skull heterochrony reveals modular evolution and a link between cranial development and brain size. *Nature Communications*, **5**, 3625.
- LEARDI, J. M., FIORELLI, L. E. and GASPARINI, Z. 2015a. Redescription and reevaluation of the taxonomical status of *Microsuchus schilleri* (Crocodyliformes: Mesoeucrocodylia) from the Upper Cretaceous of Neuquén, Argentina. *Cretaceous Research*, **52**, 153–166.
- POL, D., NOVAS, F. E. and SUÁREZ RIGLOS, M. 2015b. The postcranial anatomy of *Yacarerani boliviensis* and the phylogenetic significance of the notosuchian postcranial skeleton. *Journal of Vertebrate Paleontology*, **35**, e995187.
- MANNION, P. D., BENSON, R. B., CARRANO, M. T., TENNANT, J. P., JUDD, J. and BUTLER, R. J. 2015. Climate constrains the evolutionary history and biodiversity of crocodylians. *Nature Communications*, **6**, 8438. (doi:10.1038/ncomms9438)
- MARSOLA, J. C. A., BATEZELLI, A., MONTEFELTRO, F. C., GRELLT-TINNER, G. and LANGER, M. C. 2016. Palaeoenvironmental characterization of a crocodilian nesting site from the Late Cretaceous of Brazil and the evolution of crocodyliform nesting strategies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **457**, 221–232.
- MARTIN, J. E. and LAPPARENT DE BROIN, F. A. 2016. A miniature notosuchian with multicuspid teeth from the Cretaceous of Morocco. *Journal of Vertebrate Paleontology*, **36**, e1211534.
- MCKINNEY, M. L. 1988. Classifying heterochrony: allometry, size, and time. 17–34. In MCKINNEY, M. L. (ed). *Heterochrony in evolution. A Multidisciplinary Approach*. Plenum Press, New York, NY.
- 1990. Classifying and analyzing evolutionary trends. 28–58. In MCNAMARA, K. J. (ed). *Evolutionary trends*. The University of Arizona Press, Tucson, AZ.
- MCNAMARA, K. J. 1982. Heterochrony and phylogenetic trends. *Paleobiology*, **8**, 130–142.
- 1986. A guide to the nomenclature of heterochrony. *Journal of Paleontology*, **60**, 4–13.
- 1990. The role of heterochrony in evolutionary trends. 59–74. In MCNAMARA, K. J. (ed). *Evolutionary trends*. The University of Arizona Press, Tucson, AZ.
- and MCKINNEY, M. L. 2005. Heterochrony, disparity, and macroevolution. *Paleobiology*, **31**, 17–26.
- MÉNDEZ, A. H., NOVAS, F. E. and IORI FV. 2012. First record of Megaraptora (Theropoda, Neovenatoridae) from Brazil. *Comptes Rendus Palevol*, **11**, 251–256.

- MEUNIER, L. and LARSSON, H. C. 2016. Revision and phylogenetic affinities of *Elosuchus* (Crocodyliformes). *Zoological Journal of the Linnean Society*, **179**, 169–200.
- MONTEFELTRO, F. C., LARSSON, H. C. and LANGER, M. C. 2011. A new baurusuchid (Crocodyliformes, Mesoeucrocodylia) from the late cretaceous of Brazil and the phylogeny of Baurusuchidae. *PLoS One* **6**, e21916.
- ANDRADE, D. V. and LARSSON, H. C. 2016. The evolution of the meatal chamber in crocodyliforms. *Journal of Anatomy*, **228**, 838–863.
- LARSSON, H. C. FRANCA, M. A. and LANGER, M. C. 2013. A new neosuchian with Asian affinities from the Jurassic of northeastern Brazil. *Naturwissenschaften*, **100**, 835–841.
- MONTEIRO, L. R. 1999. Multivariate regression models and geometric morphometrics: the search for causal factors in the analysis of shape. *Systematic Biology*, **48**, 192–199.
- O'CONNOR, P. M., SERTICH, J. J. W., STEVENS, N. J., ROBERTS, E. M., GOTTFRIED, M. D., HIERONYMUS, T. L., JINNAH, Z. A., RIDGELY, R., NGASALA, S. E., and TEMBA, J. 2010. The evolution of mammal-like crocodyliforms in the Cretaceous Period of Gondwana. *Nature*, **466**, 748–751.
- OPENSHAW, G. H., D'AMORE, D. C., VIDAL-GARCÍA, M., and KEOGH, J. S. 2016. Combining geometric morphometric analyses of multiple 2D observation views improves interpretation of evolutionary allometry and shape diversification in monitor lizard (*Varanus*) crania. *Biological Journal of the Linnean Society*, **120**, 539–552.
- ÖSI, A. 2014. The evolution of jaw mechanism and dental function in heterodont crocodyliforms. *Historical Biology*, **26**, 279–414.
- PIRAS, P., COLANGELO, P., ADAMS, D. C., BUSCALIONI, A., CUBO, J., KOTSAKIS, T., MELORO, C. and RAIA, P. 2010. The *Gavialis–Tomistoma* debate: the contribution of skull ontogenetic allometry and growth trajectories to the study of crocodylian relationships. *Evolution & Development*, **12**, 568–579.
- POL, D. and LEARDI, J. M. 2015. Diversity patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) during the Cretaceous of Gondwana. 172–186. In FERNÁNDEZ, M. and HERRERA, Y. (eds). *Reptiles Extintos - Volumen en Homenaje a Zulma Gasparini*. Publicación Electrónica de la Asociación Paleontológica Argentina, Buenos Aires, Argentina.
- NASCIMENTO, P. M., CARVALHO, A. B., RICCOMINI, C., PIRES-DOMINGUES, R. A. and ZAHER, H. 2014. A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. *PLoS One*, **9**, e93105.



- PRICE, L. I. 1945. A new reptil from the Cretaceous of Brazil. *Divisão de Geologia e Mineralogia, Notas Preliminares e Estudos*, **25**, 1–8.
- R CORE TEAM. 2017. R: A language and environment for statistical computing. v. 3.4.1. <https://www.R-project.org/>.
- REVELL, L. J. 2009. Size-correction and principal components for interspecific comparative studies. *Evolution*, **63**, 3258–3268.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- RIFF, D. and KELLNER AWA. 2011. Baurusuchid crocodyliforms as theropod mimics: clues from the skull and appendicular morphology of *Stratiotosuchus maxhechti* (Upper Cretaceous of Brazil). *Zoological Journal of the Linnean Society*, **163**, 37–56.
- ROHLF, F. J. 2015. *tpsDig v. 2.22, digitize landmarks and outlines*. Department of Ecology & Evolution, State University of New York at Stony Brook, <http://life.bio.sunysb.edu/morph>.
- RUSSO, J., MATEUS, O., BALBINO, A. and MARZOLA, M. 2014. Crocodylomorph eggs and eggshells from the Lourinhã Fm. (Upper Jurassic), Portugal. *Comunicações Geológicas*, **101**, 563–566.
- SCHOCH, R. R. 2010. Heterochrony: the interplay between development and ecology exemplified by a Paleozoic amphibian clade. *Paleobiology*, **36**, 318–334.
- SERENO, P. and LARSSON, H. 2009. Cretaceous crocodyliforms from the Sahara. *ZooKeys*, **28**, 1–143.
- SIDOR, C. A., LARSSON, H. C. E. and GADO, B. 2003. A new notosuchian from the Early Cretaceous of Niger. *Journal of Vertebrate Paleontology*, **23**, 477–482.
- SERTICH, J. J. W. and O’CONNOR, P. M. 2014. A new crocodyliform from the middle Cretaceous Galula Formation, southwestern Tanzania. *Journal of Vertebrate Paleontology*, **34**, 576–596.
- SHEA, B. T. 1983. Allometry and heterochrony in the African apes. *American Journal of Physical Anthropology*, **62**, 275–289.
- SRIVASTAVA, R., PATNAIK, R., SHUKLA, U. K., and SAHNI, A. 2015. Crocodilian nest in a Late Cretaceous sauropod hatchery from the type Lameta Ghat locality, Jabalpur, India. *PLoS One*, **10**, e0144369.
- STRELIN, M. M., BENITEZ-VIEYRA, S., FORNONI, J., KLINGENBERG, C. P. and COCUCCI, A. A. 2016. Exploring the ontogenetic scaling hypothesis during the diversification of pollination syndromes in *Caiophora* (Loasaceae, subfam. Loasoideae). *Annals of Botany*, **117**, 937–947.

1  
2  
3 STUBBS, T. L., PIERCE, S. E., RAYFIELD, E. J. and ANDERSON, P. S. 2013.  
4 Morphological and biomechanical disparity of crocodile-line archosaurs following the  
5 end-Triassic extinction. *Proceedings of the Royal Society of London B*, **280**, 20131940.  
6  
7 TURNER, A. H. 2015. A review of *Shamosuchus* and *Paralligator* (Crocodyliformes,  
8 Neosuchia) from the Cretaceous of Asia. *PLoS One*, **10**, e0118116.  
9  
10 TURNER, A. and SERTICH, J. J. W. 2010. Phylogenetic history of *Simosuchus clarki*  
11 (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Journal of*  
12 *Vertebrate Paleontology*, **30**, 177–236.  
13  
14 VAN VALKENBURGH, B. 1991. Iterative evolution of hypercarnivory in canids  
15 (Mammalia: Carnivora): evolutionary interactions among sympatric predators.  
16 *Paleobiology*, **17**, 340–361.  
17  
18 --- 1999. Major patterns in the history of carnivorous mammals. *Annual Review of Earth and*  
19 *Planetary Sciences*, **27**, 463–493.  
20  
21 --- WANG, X. and DAMUTH, J. 2004. Cope's rule, hypercarnivory, and extinction in North  
22 American canids. *Science*, **306**, 101–104.  
23  
24 WATANABE, A. and SLICE, D. E. 2014. The utility of cranial ontogeny for phylogenetic  
25 inference: a case study in crocodylians using geometric morphometrics. *Journal of*  
26 *Evolutionary Biology*, **27**, 1078–1092.  
27  
28 WERDELIN, L. 1996. Carnivoran ecomorphology: a phylogenetic perspective. 582–624. In  
29 GITTLEMAN, J. (ed). *Carnivore Behavior, Ecology and Evolution*. Cornell University  
30 Press, Ithaca, NY.  
31  
32 WESLEY-HUNT, G. D. 2005. The morphological diversification of carnivores in North  
33 America. *Paleobiology*, **31**, 35–55.  
34  
35 WHETSTONE, K. N. and WHYBROW, P. J. 1983. A "cursorial" crocodilian from the  
36 Triassic of Lesotho (Basutoland), southern Africa. *Occasional Papers of the Museum of*  
37 *Natural History of University of Kansas*, **106**, 1–37.  
38  
39 WILBERG, E. W. 2015. What's in an outgroup? The impact of outgroup choice on the  
40 phylogenetic position of Thalattosuchia (Crocodylomorpha) and the origin of  
41 Crocodyliformes. *Systematic Biology*, **64**, 621–637.  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60



## FIGURES AND TABLE CAPTIONS

FIG. 1. Photographs of the newly reported *Pissarrachampsia sera* juvenile specimen (LPRP/USP 0049) in dorsal (A), ventral (B) and lateral (C) views. Scale bar equals 5 cm.

FIG. 2. Comparison between effects of time hypermorphosis, rate hypermorphosis and acceleration (A) on size (large arch), shape (small arch), and age (bottom bar) of ancestors (dotted midline) and descendants (filled bars), using the clock model devised by Gould (1977). Representation of morphological evolution and their relations to ontogenetic scaling (B) (modified from Strelin *et al.* 2016). Full black circle and line represent the ancestor and ancestral ontogenetic trajectory, respectively. Dotted lines are descendant trajectories, and arrows are the deviations from the ancestral ontogenetic trajectory. Circles I and II represent modifications not predicted and modifications predicted by the ontogenetic scaling hypothesis, respectively. (C) Pairwise comparison of the effects of time hypermorphosis, rate hypermorphosis, acceleration, and predisplacement on size, shape (trait) and ages, using hypothetical ontogenetic trajectories (lines), from the onset (square) to the offset of growth (circles) of ancestors (full lines) and descendants (dashed lines). The effects of predisplacement on size are not completely known and can potentially occur in two forms: size and shape (trait) growth are coupled and both are “predisplaced” in time (age); (i.e. the onset in descendant occurs earlier than in the ancestor), or size and trait growth are decoupled and predisplacement affects only descendant’s shape, and size growth follows the same ancestral path.

FIG. 3. (A) Phylogenetic hypothesis of the *Notosuchia* taxa included in our geometric morphometric analyses (based on Montefeltro *et al.* 2013), with clades Baurusuchidae,

Sphagesauridae, and Peirosauridae/Sebecidae indicated, and other notosuchians distributed along the tree. The skulls of some notosuchians (not to scale) were selected to illustrate the cranial disparity of the group (clockwise, from the top left): adult *Araripesuchus wegeneri*, adult *Marillasuchus amarali*, juvenile *Pissarrachampsa sera*, and an undescribed adult baurusuchid (LPRP/USP 0697). (B) Morphological transformation during *Pissarrachampsa sera* ontogeny, shown by the results of the thin plate spline analysis with the juvenile (top) and adult (bottom) specimens, also illustrating the position of the landmarks (in lateral view).

FIG. 4. Two-dimensional morphospace (PCA results plot) of the first two PCs of the lateral view dataset (A), with deformation grids for hypothetical extremes along the two axes. The coloured polygons show the morphospace occupation by each of the four groups considered in this study. Crosses represent juvenile specimens, squares, stars, hexagons and circles represent adults of Baurusuchidae, Sphagesauridae, Peirosauridae/Sebecidae and other notosuchians, respectively (average values were used for taxa with more than one adult specimen sampled). The arrows represent an ontogenetic trajectory along this two-dimensional morphospace. (B) Topology based on the phylogenetic hypothesis of Montefeltro *et al.* (2013) projected onto the log-transformed centroid size. The centroid size was obtained from the lateral view dataset using only adults. Silhouettes from Godoy *et al.* (2014).

FIG. 5. Two-dimensional morphospace (plot of PCA results) after the size-correction (A, dorsal view; B, lateral view) and after the ancestral ontogenetic allometry correction (C, dorsal view; D, lateral view). Average values were used for taxa with more than one adult specimen sampled. The 90 per cent confidence ellipses were added for each of the four groups considered in the other analyses: Peirosauridae/Sebecidae (hexagons), Baurusuchidae (circles), Sphagesauridae (stars), and other notosuchians (squares).

FIG. 6. Comparisons between the ontogenetic trajectories of *Mariliasuchus amarali* and *Anatosuchus minor* (used as a proxies of the ancestral ontogenetic trajectory) and that of *Pissarrachampsa sera* (representing the baurusuchid condition), based on regression analyses of Procrustes coordinates against log-transformed centroid size, in both dorsal (A) and lateral (B) views. Squares and circles represent juveniles and adults, respectively.

TABLE 1. Pairwise comparison between morphospace occupation of different taxonomic groups. Bonferroni-corrected *P* values obtained from npMANOVA, using PC scores of all specimens after both size and ancestral ontogenetic allometry corrections, with lateral and dorsal view datasets. Taxonomic groups based on the phylogenetic framework from Montefeltro *et al.* (2013). Significant differences are indicated by an asterisk.

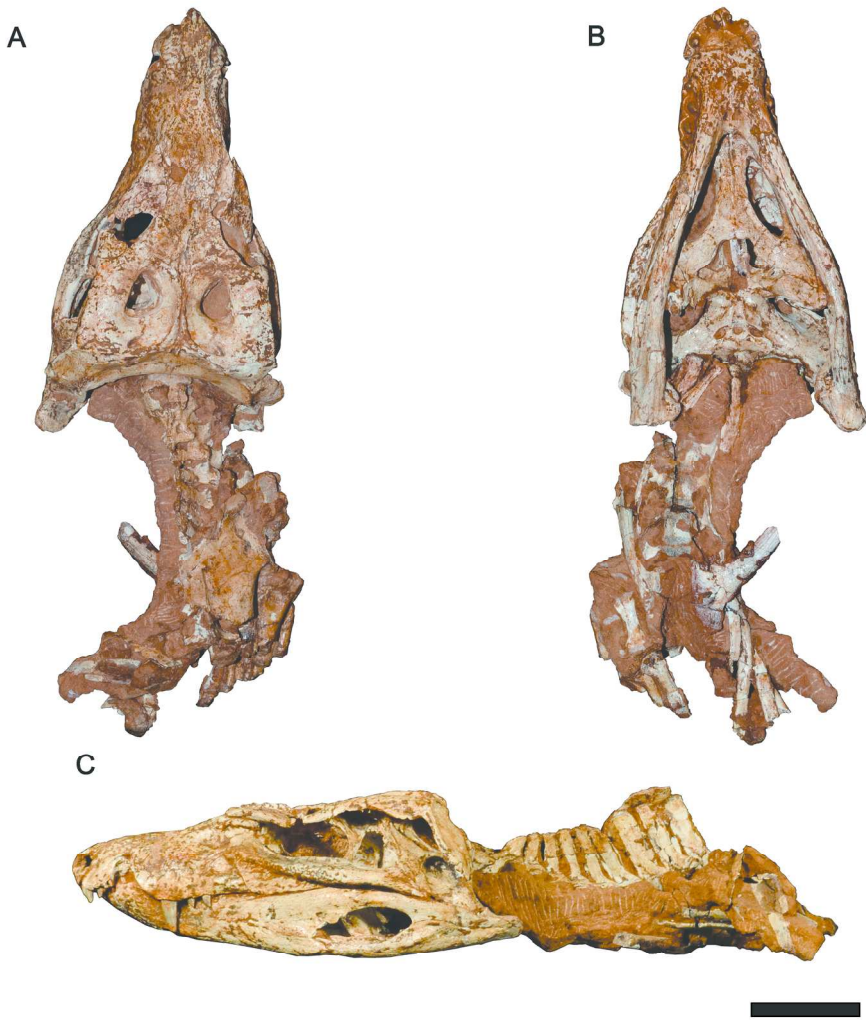


FIG. 1. Photographs of the newly reported *Pissarrachampsia sera* juvenile specimen (LPRP/USP 0049) in dorsal (A), ventral (B) and lateral (C) views. Scale bar equals 5 cm.

179x192mm (300 x 300 DPI)

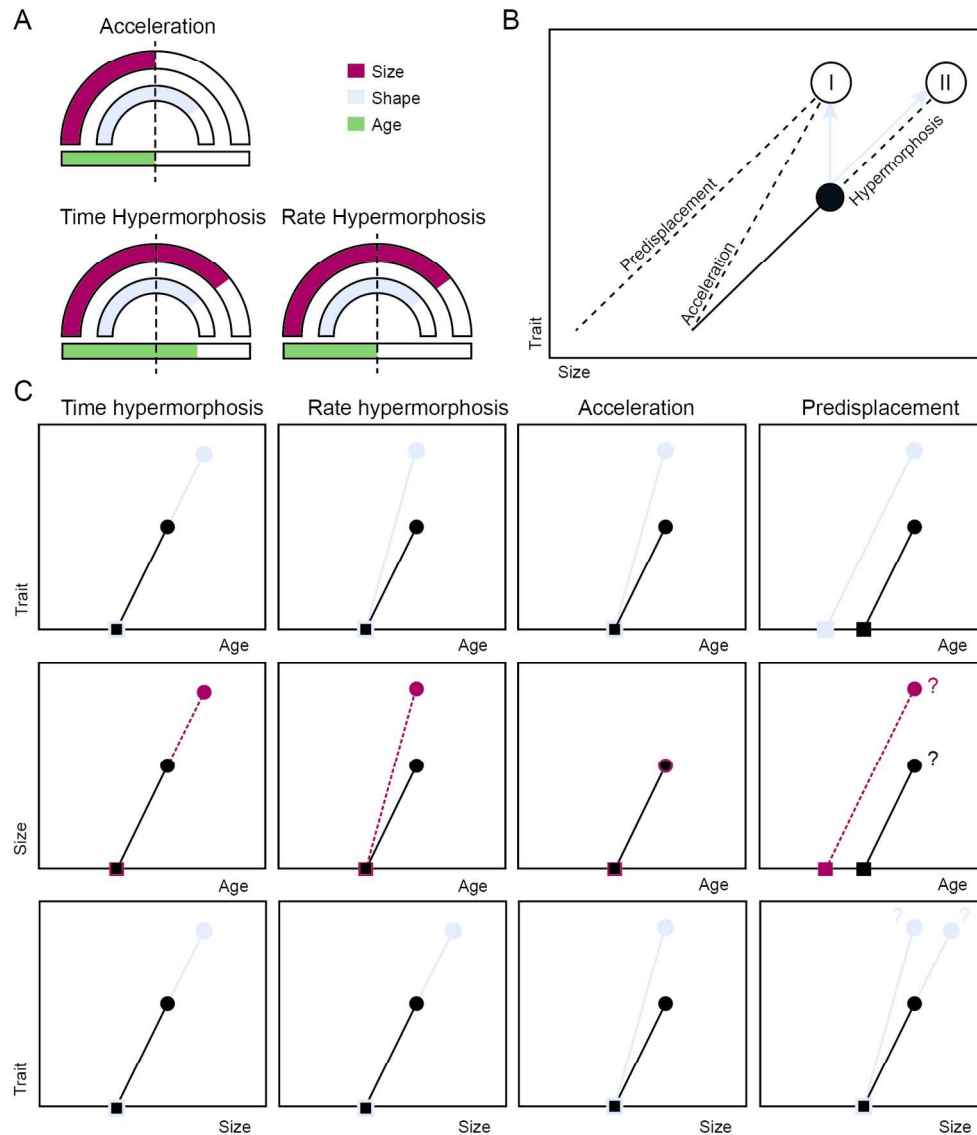


FIG. 2. Comparison between effects of time hypermorphosis, rate hypermorphosis and acceleration (A) on size (large arch), shape (small arch), and age (bottom bar) of ancestors (dotted midline) and descendants (filled bars), using the clock model devised by Gould (1977). Representation of morphological evolution and their relations to ontogenetic scaling (B) (modified from Strelin et al. 2016). Full black circle and line represent the ancestor and ancestral ontogenetic trajectory, respectively. Dotted lines are descendant trajectories, and arrows are the deviations from the ancestral ontogenetic trajectory. Circles I and II represent modifications not predicted and modifications predicted by the ontogenetic scaling hypothesis, respectively. (C) Pairwise comparison of the effects of time hypermorphosis, rate hypermorphosis, acceleration, and predisplacement on size, shape (trait) and ages, using hypothetical ontogenetic trajectories (lines), from the onset (square) to the offset of growth (circles) of ancestors (full lines) and descendants (dashed lines). The effects of predisplacement on size are not completely known and can potentially occur in two forms: size and shape (trait) growth are coupled and both are “predisplaced” in time (age); (i.e. the onset in descendant occurs earlier than in the ancestor), or size and trait growth are

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

decoupled and predisplacement affects only descendant’s shape, and size growth follows the same ancestral path.

199x240mm (300 x 300 DPI)

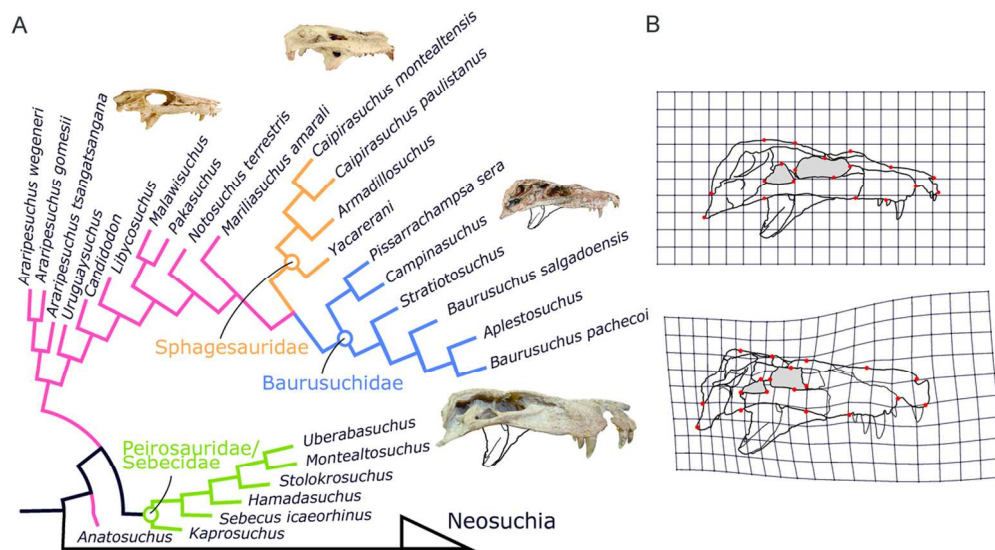


FIG. 3. (A) Phylogenetic hypothesis of the Notosuchia taxa included in our geometric morphometric analyses (based on Montefeltro et al. 2013), with clades Baurusuchidae, Sphagesauridae, and Peirosauridae/Sebecidae indicated, and other notosuchians distributed along the tree. The skulls of some notosuchians (not to scale) were selected to illustrate the cranial disparity of the group (clockwise, from the top left): adult *Araripesuchus* *wegeneri*, adult *Mariliasuchus* *amarali*, juvenile *Pissarrachampsia* *sera*, and an undescribed adult baurusuchid (LPRP/USP 0697). (B) Morphological transformation during *Pissarrachampsia* *sera* ontogeny, shown by the results of the thin plate spline analysis with the juvenile (top) and adult (bottom) specimens, also illustrating the position of the landmarks (in lateral view).

112x63mm (300 x 300 DPI)

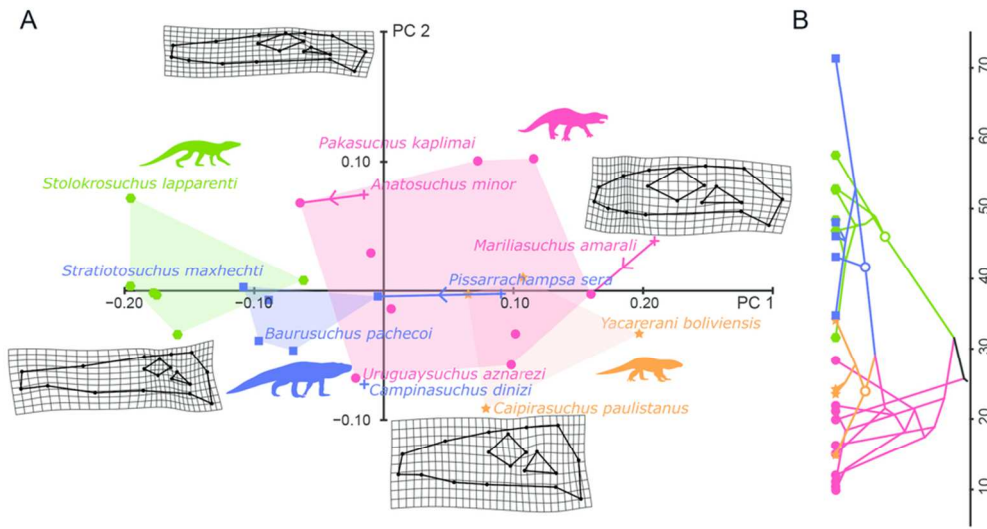


FIG. 4. Two-dimensional morphospace (PCA results plot) of the first two PCs of the lateral view dataset (A), with deformation grids for hypothetical extremes along the two axes. The coloured polygons show the morphospace occupation by each of the four groups considered in this study. Crosses represent juvenile specimens, squares, stars, hexagons and circles represent adults of Baurusuchidae, Sphagesauridae, Peirosauridae/Sebecidae and other notosuchians, respectively (average values were used for taxa with more than one adult specimen sampled). The arrows represent an ontogenetic trajectory along this two-dimensional morphospace. (B) Topology based on the phylogenetic hypothesis of Montefeltro et al. (2013) projected onto the log-transformed centroid size. The centroid size was obtained from the lateral view dataset using only adults. Silhouettes from Godoy et al. (2014).

88x48mm (300 x 300 DPI)



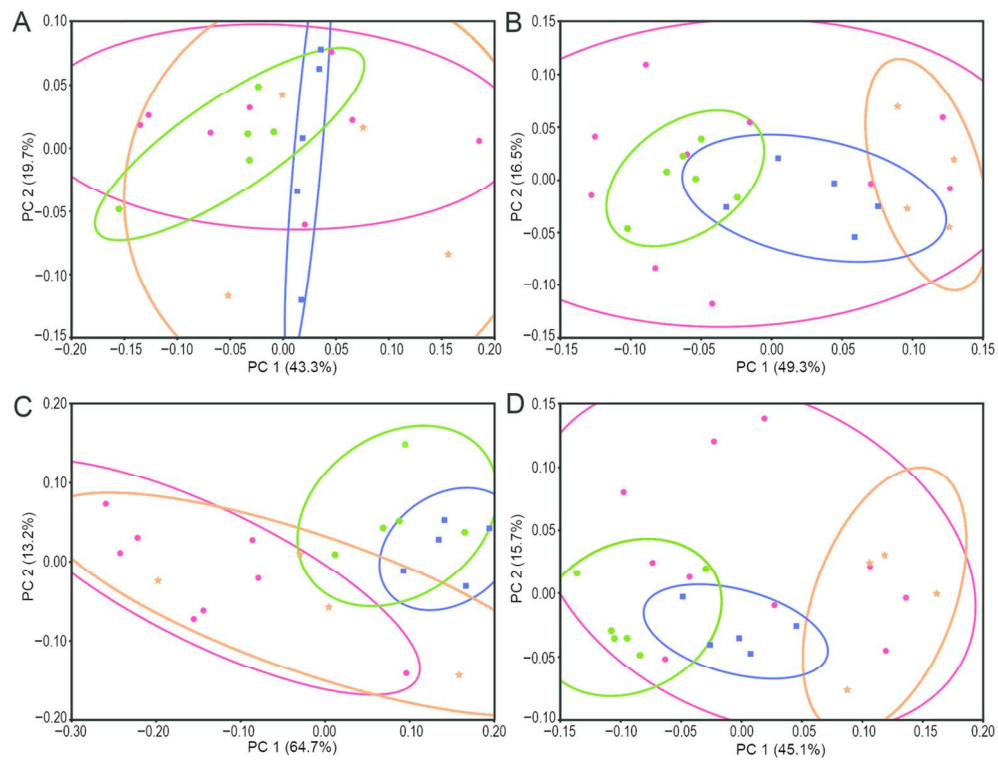


FIG. 5. Two-dimensional morphospace (plot of PCA results) after the size-correction (A, dorsal view; B, lateral view) and after the ancestral ontogenetic allometry correction (C, dorsal view; D, lateral view). Average values were used for taxa with more than one adult specimen sampled. The 90 per cent confidence ellipses were added for each of the four groups considered in the other analyses: Peirosauridae/Sebecidae (hexagons), Baurusuchidae (circles), Sphagesauridae (stars), and other notosuchians (squares).

127x97mm (300 x 300 DPI)

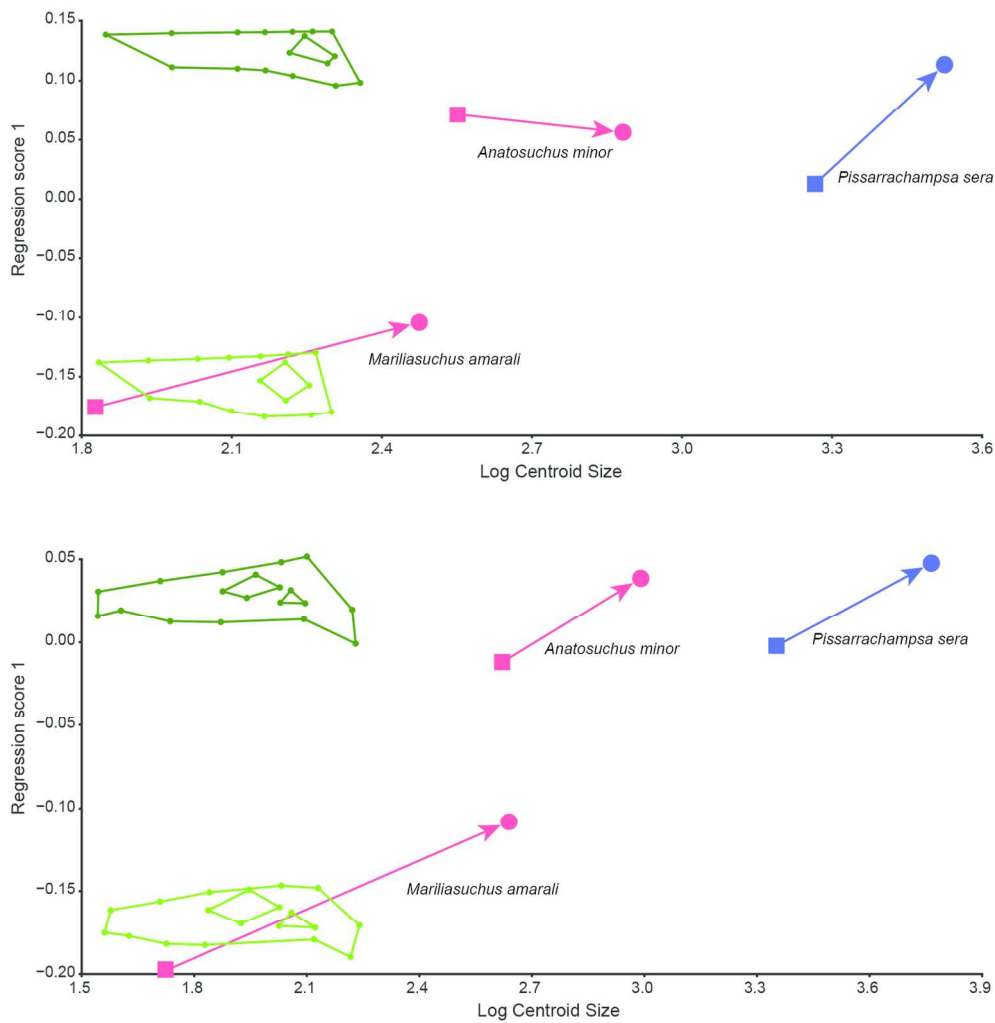


FIG. 6. Comparisons between the ontogenetic trajectories of *Mariliasuchus amarali* and *Anatosuchus minor* (used as a proxies of the ancestral ontogenetic trajectory) and that of *Pissarrachampsia sera* (representing the baurusuchid condition), based on regression analyses of Procrustes coordinates against log-transformed centroid size, in both dorsal (A) and lateral (B) views. Squares and circles represent juveniles and adults, respectively.

159x162mm (300 x 300 DPI)

Groups	<i>P</i> values			
	Size correction		Ancestral ontogenetic allometry correction	
	Dorsal view	Lateral view	Dorsal view	Lateral view
Baurusuchidae – other notosuchians	1	0.9923	0.0126*	0.06419
Baurusuchidae – Peirosauridae/Sebecidae	0.1122	0.008399*	0.267	0.0192*
Baurusuchidae – Sphagesauridae	1	0.048*	0.1416	0.048*
Peirosauridae/Sebecidae – other notosuchians	1	1	0.0138*	0.0138*
Peirosauridae/Sebecidae – Sphagesauridae	0.3732	0.0402*	0.1836	0.0402*
Sphagesauridae – other notosuchians	1	0.1668	0.0126*	0.1944