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EVIDENCE FOR HETEROCHRONY IN THE CRANIAL EVOLUTION OF FOSSIL CROCODYLIFORMS

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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 processes 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, shifts in timing and rate of development, has been hypothesized to drive major phenotypic modifications in many groups (Gould 1977; McKinney 1988; McNamara & 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 & Butler 2015; Foth *et al.* 2016*a*). In this context, the recent discovery of a beautifully preserved new specimen of the baurusuchid crocodyliform *Pissarrachampsa 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 crocodyliform groups, the notosuchians.

Notosuchia is the most diverse crocodyliform group in the Cretaceous of Gondwana (Turner & Sertich 2010; Godoy *et al.* 2014; Pol *et al.* 2014; Pol & Leardi 2015), showing an extraordinary taxonomical and ecological diversity (Stubbs *et al.* 2013; Bronzati *et al.* 2015; Mannion *et al.* 2015). 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

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FIG. 1. Photographs of the newly reported *Pissarrachampsa sera* juvenile specimen (LPRP/USP 0049) in: A, dorsal; B, ventral; C, lateral view. Scale bar represents 5 cm. Colour online.

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 & 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 & 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 descendant. 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 & 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 abbreviation. LPRP/USP, Laboratório de Paleontologia, Universidade de São Paulo, Ribeirão Preto, Brazil.

SYSTEMATIC PALAEONTOLOGY

CROCODYLIFORMES Benton & Clark, 1988
MESOEUCROCODYLIA Whetstone & Whybrow, 1983
BAURUSUCHIDAE Price, 1945
PISSARRACHAMPSINAE Montefeltro *et al*., 2011
Pissarrachampsa sera Montefeltro *et al*., 2011
Figure 1

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 & Teixeira 2015).

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 subtympanic 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.

METHOD

Heterochronic terminology

It is important to define clearly the peramorphic processes used in the context of this work, as distinct heterochronic processes have been defined using different formalisms (e.g. evolutionary vs developmental concepts) 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 (1998). 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 with the ancestral allometry (size–shape relations), so these changes are not ontogenetically scaled (i.e.

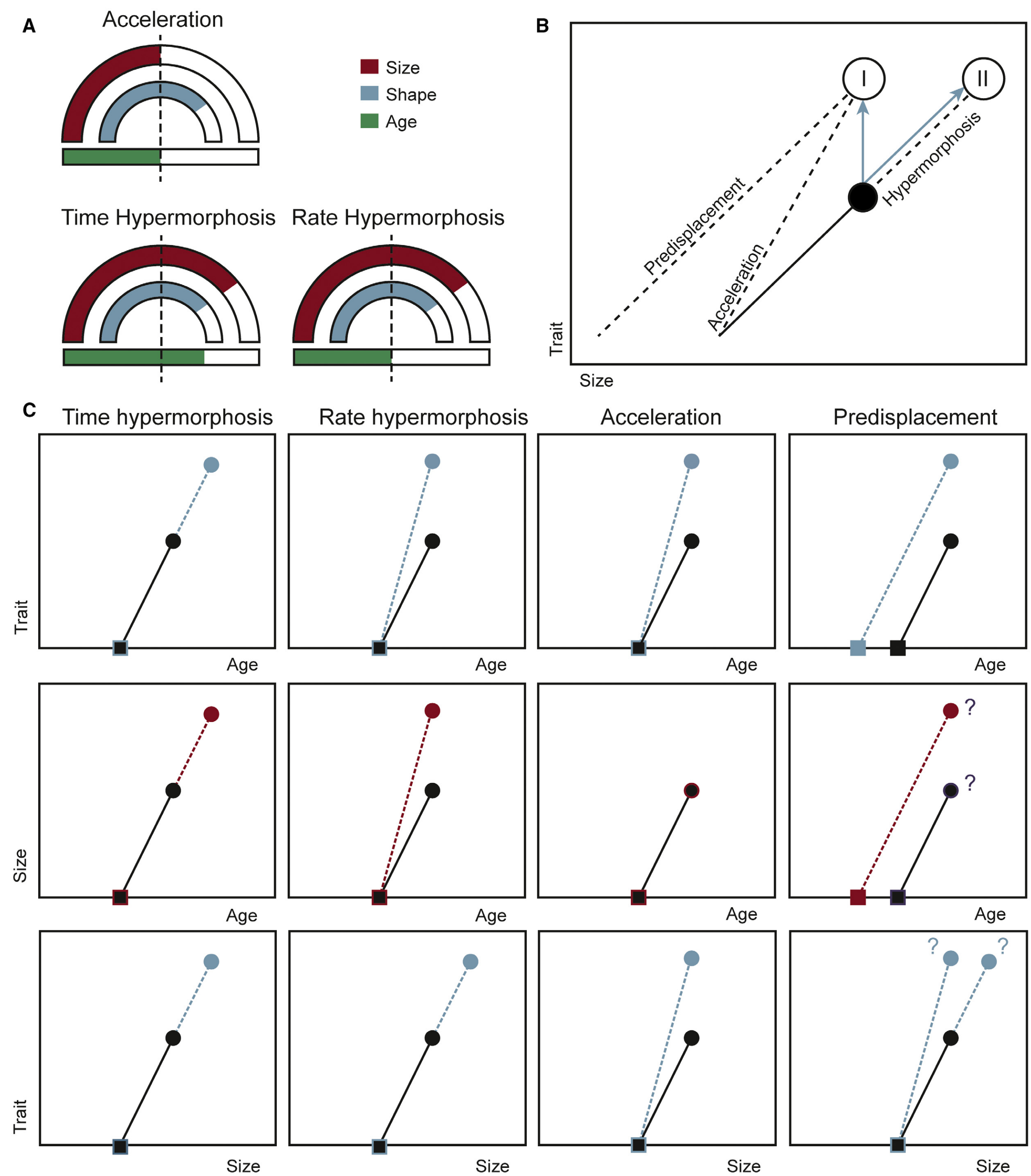

FIG. 2. A, comparison between effects of time hypermorphosis, rate hypermorphosis and acceleration on size (large arch), shape (small arch), and age (bottom bar) of ancestors (dotted midline) and descendants (filled bars), using the clock model devised by Gould (1977). B, representation of morphological evolution and its relationship to ontogenetic scaling (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 age, 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. Colour online.

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 in the descendant starts to develop earlier than in the ancestor. This often leads to a break with 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 whether 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 Godoy *et al.* 2018, 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 (for the position and description of landmarks, see Godoy *et al.* 2018, 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 extracted 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 & Sertich 2010; Andrade *et al.* 2011; Bronzati *et al.* 2012; Montefeltro *et al.* 2013; Pol *et al.* 2014; Sertich & 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 & Lapparent de Broin 2016; Meunier & 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 & 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 (Sereno & Larsson 2009; Montefeltro *et al.* 2013; Wilberg 2015; Meunier & Larsson 2016). It is almost

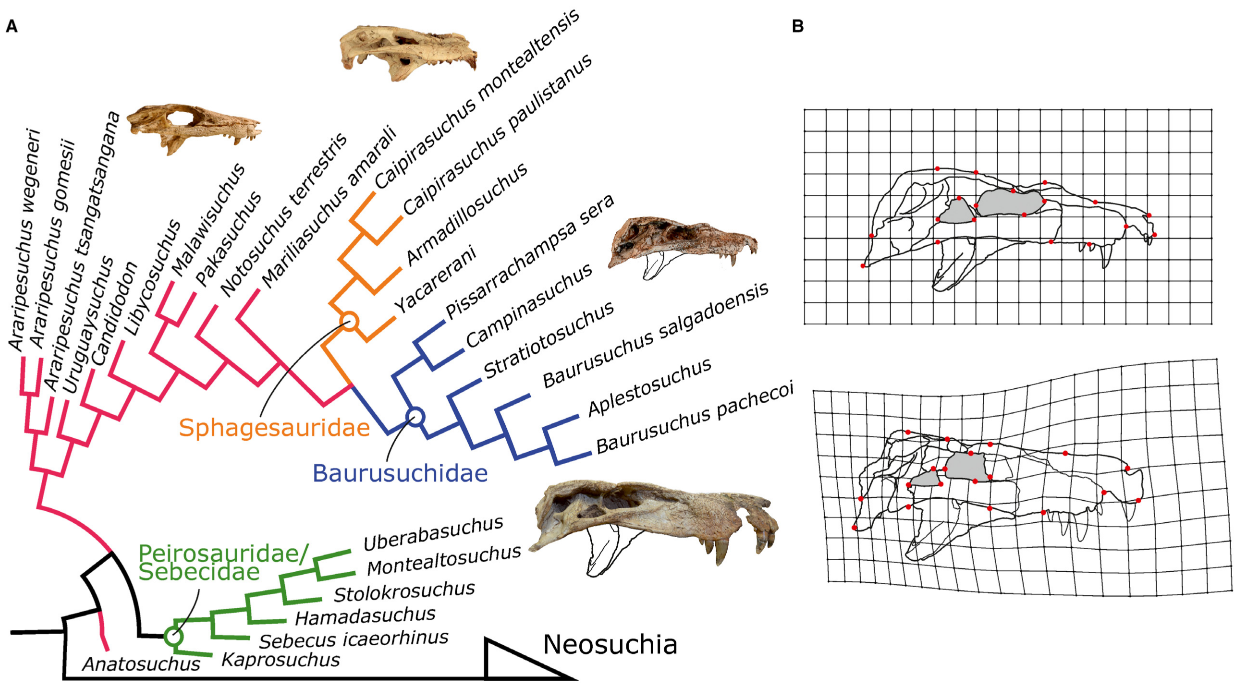

FIG. 3. A, phylogenetic hypothesis of the Notosuchia taxa included in our geometric morphometric analyses (based on Montefeltro *et al.* 2013), with clades Baurusuchidae, Sphagesauridae, and Peirosauridae/Sebecidae indicated, and other notosuchians distributed along the tree; the skulls of some notosuchians (not to scale) were selected to illustrate the cranial disparity of the group (clockwise, from the left): adult *Araripesuchus wegeneri*, adult *Mariliasuchus 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).

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.* 2015*a*, *b*; Martin & 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.

To test the robustness of our results with respect 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.* 2015*a*, *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 the ‘geomorph’ package (Adams & 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 were interested only in interspecific size variation. The residuals from this regression were then used as the input for a second PCA to explore the occupied morphospace after removing the effect of size on the observed variation. As for the first PCA, the specimens were also divided into taxonomic groups using both the primary and alternative phylogenetic frameworks. To test the significance of the differences in the distributions of groups in the morphospace, we used a non-parametric multivariate analysis of variance, NPMANOVA, which, in contrast to a parametric MANOVA, does not require the data to be normally distributed, and tests for significant differences on the basis of permutations (Anderson 2001; Foth *et al.* 2016*b*). These tests were performed in PAST (Hammer *et al.* 2001), and we used the PC scores that represent at least 95% of shape variation. These scores were then transformed into a Euclidean distance matrix (Euclidean similarity index) and permuted with 10 000 replications. Comparisons were made using the Bonferroni correction, to reduce the likelihood of type 1 statistical errors (Rice 1989). Additionally, we projected the topology based on the hypothesis of Montefeltro *et al.* (2013) onto the PC scores (using both dorsal and lateral view datasets), creating a phylomorphospace to explore the evolutionary history of shape changes in the sampled taxa.

To evaluate the specific action of time hypermorphosis, we applied the methodology described by Strelin *et al.* (2016), to test whether the shape modifications seen in the baurusuchid skull evolved by ontogenetic scaling. Time hypermorphosis corresponds to an extension of the ancestral ontogenetic trajectory, a pattern previously detected in other crocodyliforms known to extend the growth period and attain larger body sizes (e.g. Erickson & Brochu 1999). As such, based on whether the differences among taxa remain or not after this procedure, we can reject or confirm hypermorphosis as the sole peramorphic process acting on baurusuchid skull evolution, as this is the only process that extends the ontogenetic trajectory in time.

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 Godoy *et al.* (2018) 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 (Sereno *et al.* 2003; Sereno & 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% of the variation, PC2 = 9.9%) and dorsal views (PC1 = 57.9%, PC2 = 11.3%), 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. 4A), and along both PC1 and PC2 axes for the dorsal view dataset (Godoy *et al.* 2018, 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 (Godoy *et al.* 2018, figs 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% of the variation in the dorsal and lateral view datasets, respectively (for more about this allometric regression see Godoy *et al.* 2018, fig. S5; tables S4, 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%) for baurusuchids, sphagesaurids, and even peirosaurids/sebecids overlapped with the confidence ellipse of other notosuchians (for the phylomorphospaces, see Godoy *et al.* 2018, 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 by rearranging the specimens into different taxonomic groups (see Method, 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 (Godoy *et al.* 2018, figs S7, S8; tables S6, S7).

Finally, the ancestral ontogenetic trajectory was estimated by using the ontogenetic trajectories of *Mariliasuchus amarali* and *Anatosuchus minor* as proxies. First, to confirm 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 Method, 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

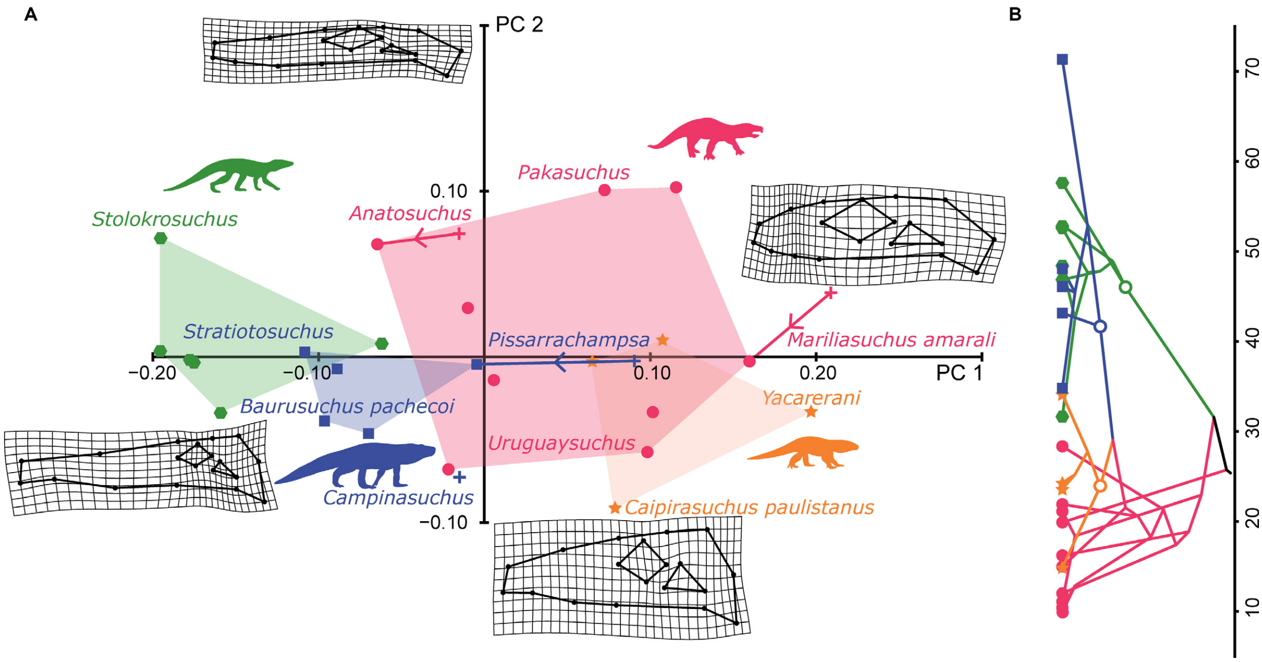

FIG. 4. A, two-dimensional morphospace (PCA results plot) of the first two PCs of the lateral view dataset with deformation grids for hypothetical extremes along the two axes; filled polygons show the morphospace occupation by each of the four groups considered in this study: crosses represent juvenile 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); 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). Colour online.

a different result, with baurusuchid and other notosuchian morphospaces significantly separated (Fig. 5C; Table 1). 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 (Godoy *et al.* 2018, figs S10, S11; tables S10, S11). Finally, to test the influence of the ontogenetic trajectory of *Anatosuchus minor* on our results (given its unique morphology, see Method 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 (Godoy *et al.* 2018, figs S13, S14; tables 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 (Godoy *et al.* 2018, figs 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 *Pissarrachampsa 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 (Godoy *et al.* 2018, fig. S2), in which the PC1 axis also represents rostrocaudal shortening of the rostrum (as in lateral view). The PC2 axis accounts for the

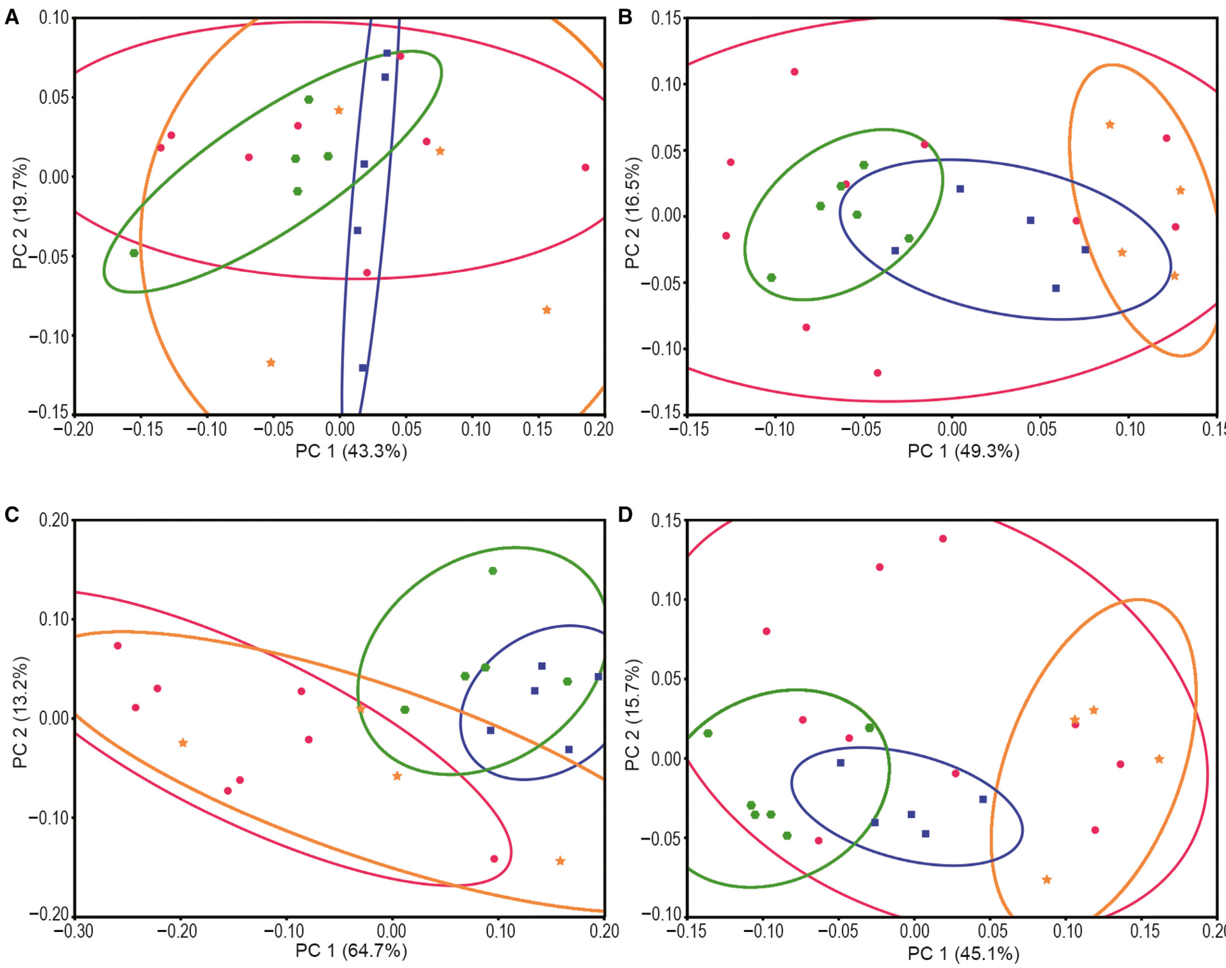

FIG. 5. Two-dimensional morphospace (plot of PCA results) after the size correction (A, dorsal view; B, lateral view) and after the ancestral ontogenetic allometry correction (C, dorsal view; D, lateral view). Average values were used for taxa with more than one adult specimen sampled. The 90% confidence 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). Colour online.

TABLE 1. Pairwise comparison between morphospace occupation of different taxonomic groups.

Groups	*p* 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

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.

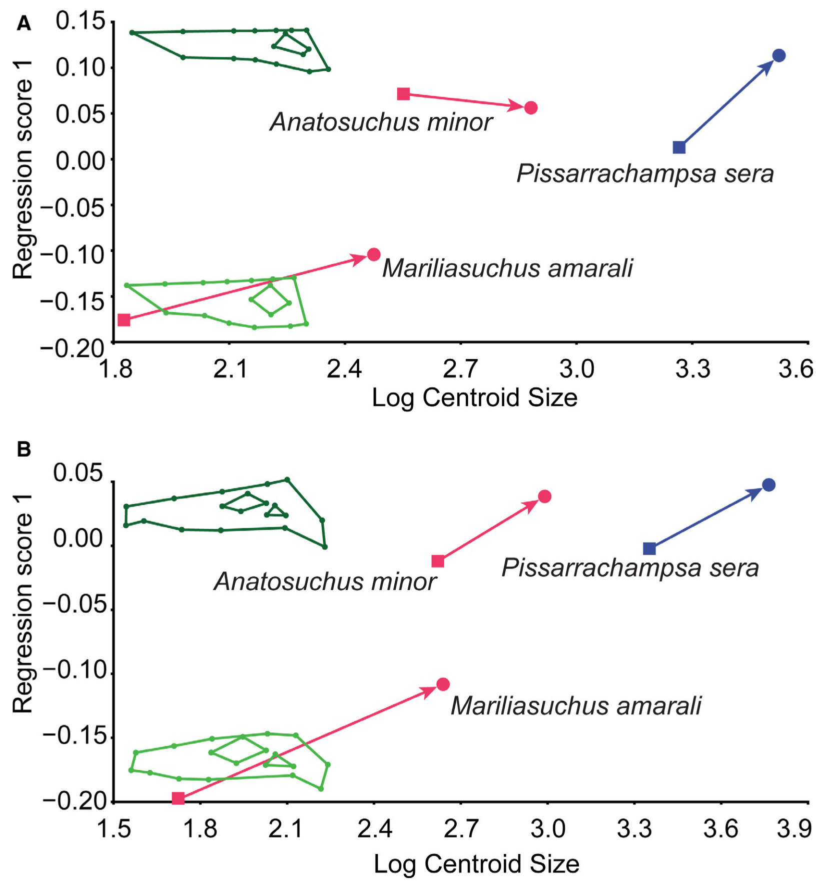

FIG. 6. Comparisons between the ontogenetic trajectories of *Mariliasuchus amarali* and *Anatosuchus minor* (used as proxies for the ancestral ontogenetic trajectory) and that of *Pissarrachampsa sera* (representing the baurusuchid condition), based on regression analyses of Procrustes coordinates against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

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 & 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 are relatively broader later in ontogeny; Bona & Desojo 2011; Foth *et al.* 2017). Nevertheless, quantitative investigations of possible heterochronic processes acting on the evolution of Crocodyliformes are rare (e.g. Gignac & 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 to or within the clade composed of Pissarrachampsinae + Baurusuchinae (Godoy *et al.* 2014). It has been suggested that these two early-diverging species, known from fragmentary remains, are adults but they are substantially smaller than other baurusuchids (estimated as *c.* 50% 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 whether 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 (for further information and results see Godoy *et al.* 2018, figs S9, S12; tables S4, S5, S8, S9, S11, 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 Method, above), the morphospaces of sebecosuchians (which includes baurusuchids) and other notosuchians remain significantly separated (Godoy *et al.* 2018, figs S10, S11; tables S10, S11). The same is observed when we removed the *Anatosuchus minor* specimens from the ancestral ontogenetic trajectory estimation (Godoy *et al.* 2018, figs S13, S14; tables 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 have a diet comprising at least 70% vertebrate flesh. They frequently have a specialized dentition, such as the ziphodont teeth of baurusuchids (Riff & 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 relationship between the reported cranial modifications and size, changes that might have occurred together with the shift to a hypercarnivorous habit. A link between size increase and the evolution of hypercarnivory has been previously documented in other vertebrate lineages, such as carnivoran and creodont mammals (Werdelin 1996; Van

Valkenburgh 1999; Van Valkenburgh *et al.* 2004; Wesley-Hunt 2005). Furthermore, heterochrony is commonly associated with evolutionary trends leading to size increase (McNamara 1982, 1990) and one of the possible triggers of these trends is the positive pressure caused by competition (McKinney 1990; Van Valkenburgh *et al.* 2004).

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* (two to five eggs per clutch; Marsola *et al.* 2016) when compared to fossil neosuchians, such as atoposaurids and dyrosaurids (*c.* 12 eggs per clutch; Russo *et al.* 2014; Srivastava *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 (Brazaitis & 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, probably 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.

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AUTHOR CONTRIBUTIONS

GSF and MCL designed the research. GSF, PLG, FCM and BCVN collected the data. FCM, RJB, and MCL provided evolutionary expertise for the project. GSF and PLG performed the analyses, jointly wrote the manuscript and created the figures and tables. GSF, PLG, FCM, BCVN, RJB and MCL discussed the results and contributed to manuscript revisions.

DATA ARCHIVING STATEMENT

Data for this study, including Supporting Information (supplementary text, tables and figures), 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: https://doi.org/10.5061/dryad.7m48r.

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