



Ontogenetic variation in the skulls of *Caiman*: the case of *Caiman latirostris* and *Caiman yacare* (Alligatoridae, Caimaninae)

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Caiman is one of the five extant genera of alligatorid crocodylians. While several quantitative and qualitative studies exist on morphological variation in the genus, little is known about ontogenetic effects. Here, we quantify ontogenetic variation in morphology for *Caiman yacare* and *C. latirostris* in a phylogenetic context. A linear regression analysis on twelve skull measurements of *C. yacare* and *C. latirostris* against a measure of size (the first axis of a PCA of all variables) showed high correlation coefficients ($r^2=0.89-0.99$) and negative allometry. Eight allometric trajectories showed common slopes at different intercepts, reflecting a common ontogenetic pattern of morphological growth fixed early in ontogeny. The anterior width of the snout and the posterior width of the skull table are suitable to discriminate between the two species. The relationship between snout width and snout length is isometric in *C. latirostris* while it is negatively allometric in *C. yacare*. These results confirm that the snout shape is a distinctive feature between species established early in ontogeny. The narrowing and lengthening of the snout in *C. yacare* during ontogeny results in adult forms widely represented in other extant taxa within the genus. The broader and shorter snout in *C. latirostris* is probably an autapomorphic feature of this species within Caimaninae.

Key words: allometry, *Caiman latirostris*, *Caiman yacare*, cranial variation, ontogeny

INTRODUCTION

The skull of Crocodylia is a characteristic anatomical structure that has been the focus of many phylogenetic (e.g., Clark, 1994; Brochu, 1997, 1999) and morpho-functional analyses (e.g., Busbey, 1994; Daniel & McHenry, 2001; Erickson et al., 2003; Metzger et al., 2005; McHenry et al., 2006). Systematic studies in crocodyliforms, including extinct species, are mostly based on cranial morphology (e.g., Brochu, 1999, 2003, 2010, 2011; Cleuren & de Vree, 2000; Bona & Paulina Carabajal, 2013; Foth et al., 2013; Pol et al., 2013). There is considerable variation in craniofacial morphology over the crocodylian phylogeny, and it is easier to identify species based on skull morphology than on the relatively conserved postcranium. Moreover, skulls are more commonly preserved in herpetological collections and the fossil record.

The cranial morphology of Crocodylia has been long debated. Based on the snout shape, crocodylian species were informally divided into two categories, longirostrine and brevirostrine (e.g., Lydekker, 1888; von Zittel, 1890). Busbey (1994) described the rostral shape based on dimensions of the lateral view and the length of the skull and the snout, using the expressions platyrostral and oreinirostral. Both of them could be short, normal or long, and platyrostral shapes can be subdivided into broad,

tubular and narrow categories. More recently, Brochu (2001) proposed five new morphotypes that included the categories defined by Busbey. Later, McHenry et al. (2006) defined a different classification based on ecomorphotypes. Finally, Pierce et al. (2008) carried out a quantitative analysis and developed a morphospace for crocodylian species. Based on a sample representing all 23 extant crocodylian species these authors placed Alligatoridae, Gray 1844 and even all species belonging to Caimaninae (sensu Brochu, 1999) in short/narrow and short/broad quadrants, with *Caiman latirostris* being the shortest and broadest form (Table 1).

Caimanines are a clade of neotropical alligatorids distributed mainly in South America and include the genera *Paleosuchus*, *Melanosuchus* and *Caiman* with living species. This group is known from South America since the lower Paleocene (Bona, 2007; Brochu, 2011). The crown group of caimans (sensu Brochu, 1999) has been the focus of numerous morphological studies (e.g., Mook, 1921; Kälin, 1933; Medem, 1963; Bona & Desojo, 2011) but only in a few of them ontogenetic variation is discussed (Monteiro et al., 1997; Monteiro & Soares, 1997). Monteiro & Soares (1997) proposed that skull differences appear early in ontogeny for *Caiman yacare* and *C. latirostris*, suggesting that a heterochronic mechanism is involved in the evolution of the latter species. The authors

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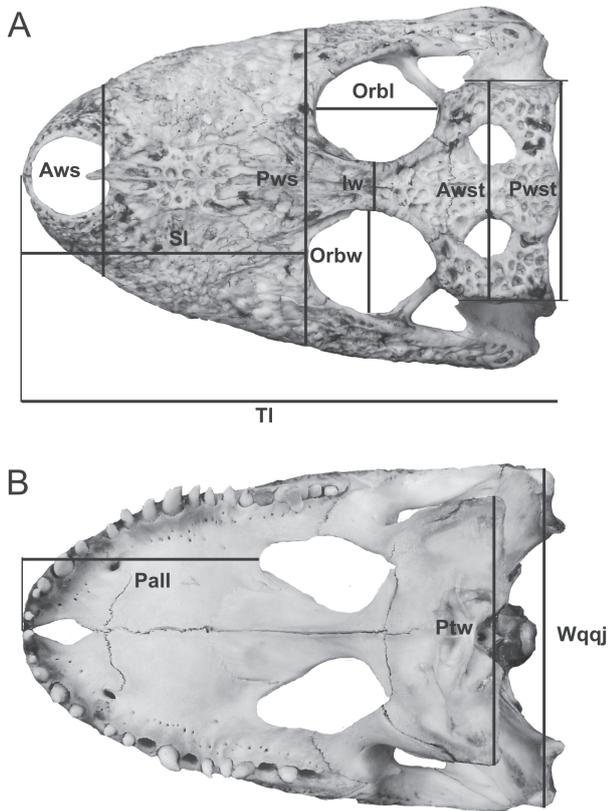


Fig. 1. Skull measurements in *Caiman*. Dorsal (A) and ventral (B) views of skull. Aws, anterior width of the snout; Awst, anterior width of the skull table; lw, interorbital width; Orbl, orbital length; Orbw, orbital width; Pall, palatine length; Ptw, pterygoid width; Pws, posterior width of the snout; Pwst, posterior width of the skull table; SI, snout length; TI, total length; Wqqj, width at quadrate-quadratojugal contact.

also hypothesised that the process that contributes to a broader skull is probably a derived condition (apomorphy) of *C. latirostris*, whereas the ontogenetic process that involves the elongation of the skull present in *C. yacare* is likely plesiomorphic for the group.

The main goal of this study is to describe and quantify the inter- and intraspecific skull morphological disparity in two post-hatching ontogenetic series of *Caiman* and to test the variation of snout proportions among caimans in a phylogenetic context.

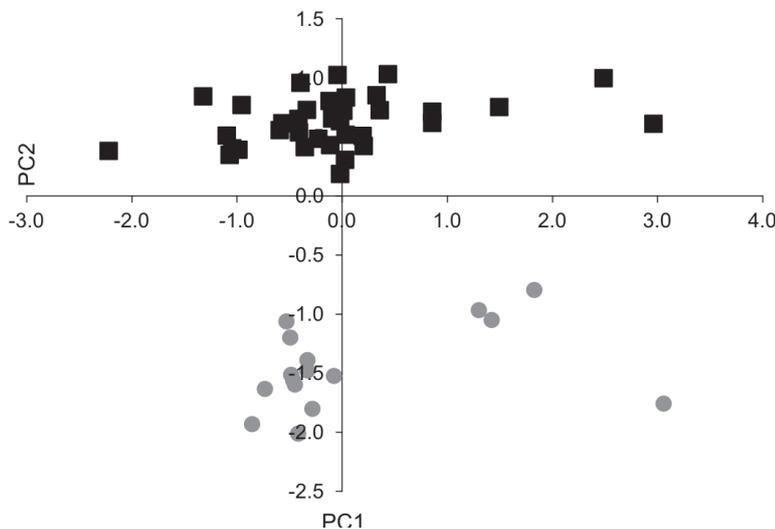
MATERIALS AND METHODS

Specimen sampling

We analysed two post-hatching ontogenetic series of 75 skulls belonging to *C. yacare* and 26 to *C. latirostris* housed in the Herpetological Collection of the Museo de La Plata (MLP) and the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN). Because some skulls were broken, a linear morphometric analysis was carried out on 37 and 16 specimens of *C. yacare* and *C. latirostris*, respectively (Online Appendix 1). We chose these species because they represent the two extremes of the skull shape variation in living caimans (Monteiro & Soares, 1997). Unfortunately, specimens were not sexed. Total skull lengths ranged from approximately 90 to 292 mm. Different sizes can be interpreted as juvenile and adult states. Specimens were collected in different provinces of Argentina (Online Appendix 1).

Regression analysis

A total of 12 cranial linear measurements (Table 2; Fig. 1) that express the variation in skull shape were considered. Four measures of lengths and eight measurements of widths (longitudinal and transverse in relation to the long axis, respectively) were taken with a steel Vernier caliper (0.01 mm precision). These variables were selected based on previous morphological studies (Monteiro & Soares, 1997; Bona & Desojo, 2011). Inter- and intraspecific post-hatching ontogenetic cranial variation was first assessed by a principal component analysis (PCA) of the variance-covariance matrix with \log_{10} transformed values (Neff & Marcus, 1980). The first principal component (PC1) belongs to the major axis of variation within the set of variables and was interpreted as a size factor because all their coefficients had high loadings (0.930–0.993)



	PC 1	PC 2
TI	0.973	0.215
Wqqj	0.993	-0.009
SI	0.952	0.292
Orbl	0.956	0.211
Pall	0.930	0.354
Aws	0.953	-0.249
Pws	0.936	-0.334
Awst	0.987	-0.031
Pwst	0.960	-0.173
Orbw	0.934	-0.244
lw	0.969	0.104
Ptw	0.986	-0.138
Eigenvalue	11.083	0.595
Total variance	92.4%	5%

Fig. 2. Results of PCA. Black squares belong to *Caiman yacare* and grey circles to *C. latirostris*.

Table 1. Classifications of the crocodylian skulls according to different authors.

Author	Classification							
Informal classification (e.g., Lydekker, 1888; von Zittel, 1890)	Longirostrine (elongated, tubular rostra) Brevirostrine (short or moderately elongated)							
Busbey, 1994	<table border="0"> <tr> <td>Long >70%, normal 55-70% or short <55% (ratio rostral-to-skull length)</td> <td>Platyrostral (dorsoventrally compressed)</td> <td rowspan="3">Tubular (dorsoventral and lateromedial diameters are subequal)</td> </tr> <tr> <td>Oreinirostral (mediolaterally compressed)</td> <td>Broad (lateromedial diameter more than twice the dorsoventral one)</td> </tr> <tr> <td></td> <td>Narrow (lateromedial diameter between 1,2 and 1,9 times the dorsoventral one)</td> </tr> </table>	Long >70%, normal 55-70% or short <55% (ratio rostral-to-skull length)	Platyrostral (dorsoventrally compressed)	Tubular (dorsoventral and lateromedial diameters are subequal)	Oreinirostral (mediolaterally compressed)	Broad (lateromedial diameter more than twice the dorsoventral one)		Narrow (lateromedial diameter between 1,2 and 1,9 times the dorsoventral one)
Long >70%, normal 55-70% or short <55% (ratio rostral-to-skull length)	Platyrostral (dorsoventrally compressed)	Tubular (dorsoventral and lateromedial diameters are subequal)						
Oreinirostral (mediolaterally compressed)	Broad (lateromedial diameter more than twice the dorsoventral one)							
	Narrow (lateromedial diameter between 1,2 and 1,9 times the dorsoventral one)							
Brochu, 2001	<p>Generalised (dorsoventrally compressed snout that tapers toward the narial region)</p> <p>Longirostrine and slender-snouted (narrow and tubular snout. Reduced in size teeth. Few elongate too with numerous teeth)</p> <p>Blunt-snouted (rostrum shortened relative to skull length. Broad platyrostrate snout. Flattened skull table with abrupt margins. Enlarged posterior teeth)</p> <p>Ziphodont (deep, laterally compressed snouts. Flattened serrated teeth)</p> <p>Duck-faced (long, very broad, platyrostrate snouts. Skull table reduced in size and teeth are small but numerous)</p>							
McHenry et al., 2006	<p>Longirostrine (elongated rostra. Specialist piscivores)</p> <p>Mesorostrine (snout shorter than in the longirostrine skull. Generalist. From narrower and taller to broader and flatter. Essentially platyrostral)</p> <p>Brevirostrine (small aquatic invertebrates and terrestrial vertebrates)</p>							
Pierce et al., 2008	<p>PCA</p> <p>Short/narrow morphotype</p> <p>Short/broad morphotype</p> <p>Long/narrow morphotype</p> <p>Long/broad morphotype</p>							

with the same sign. PC1 was used in the following regression analyses as the overall skull size proxy. The relationship between each variable (y) and the overall skull size represented by PC1 (x) was analysed through the \log_{10} transformed allometric equation $\log y = \log a + b \log x$, where $\log a$ is the y -intercept or elevation, and b is the slope of the line (allometric coefficient). Allometric equations were calculated using Model II regressions (standardised major axis) given that both variables were considered as random and measured with error (Legendre & Legendre, 1998). Variations in intercept and slope were tested for evolutionary changes in allometric trajectories (Klingenberg, 1998; Verzi et al., 2010). Differences between these parameters were assessed by heterogeneity tests. Similarity in slopes was tested by likelihood-ratio test (Warton et al., 2006). Where no significant heterogeneity in slope was found among species (e.g., when the direction of trajectories was conserved; $p_b > 0.05$), a Wald test was used. This test was conducted in order to evaluate significant differences between intercepts of the allometries (e.g., looking for lateral transposition of ontogenies; $p_a < 0.05$) for each pairwise species comparison (Warton et al., 2006). These

analyses were performed using the software SMATR v. 2.0 (Falster et al., 2006). The 95% confidence interval of the slope includes the value of 1.0, indicating an isometric scaling relationship. Departures from isometry (positive and negative allometry) were assessed by inspection the values that result excluded of the 95% confidence intervals.

To test ontogenetic variation in snout shape, a second regression analysis between widths of the snout (Aws and Pws) and its length (SI) was carried out.

Character mapping

To test the pattern of change of snout proportions among caimans, the ancestral snout index was reconstructed on the Alligatoroidea phylogeny (Brochu, 1999) as a continuous character by linear parsimony (Swofford & Maddison, 1987) using TNT v. 1.1 (Goloboff et al., 2008). Snout indexes were obtained by the quotient of anterior snout width / total snout length (Aws/SI). A total of 19 alligatoroids were considered (Fig. 5). The Aws was measured at the level of the maxilla-premaxilla suture and SI was measured from the posterior border of the skull table to the anterior border of the premaxillae. We

Table 2. Description of the cranial measurements.

Abbreviation	Description of measurements
TI	Total length, length from the tip of the snout to the posterior part of the supraoccipital
SI	Snout length, length from the tip of the snout to the front of the orbits
Pall	Palatine length, length from the tip of the snout to the anterior part of the palatine fenestra
Orbl	Orbital length, length at the longer part of the orbit measured in a longitudinal plane in relation to the body
Orbw	Orbital width, width at the wider part of the orbit measured in a transversal plane in relation to the body
Iw	Interorbital width, width between orbits at the narrowest part of the frontal
Aws	Anterior width of the snout, width of the snout at the level of the contact between premaxillar and maxillar
Pws	Posterior width of the snout, width of the snout at the level of the anterior part of the orbits
Ptw	Pterygoid width, width between end of pterygoid wings
Awst	Anterior width of the skull table, width measured in the most external and anterior part of the skull table at the level of the contact between postorbital and squamosal
Pwst	Posterior width of the skull table, width measured at the most lateral edge of squamosals at the level of the posterior margin of supraoccipital
Wqqj	Width at quadrate-quadratojugal contact, width measured at the posterior and outermost part of the contact between quadrate and quadrate-jugal

used a Vernier caliper (0.01 mm precision) to directly measure cranial material and skull photographs in dorsal view.

RESULTS

The first principal component (PC1) corresponded to the major axis of variation within the set of variables and accounted for the 92.4% of variation present in the sample (Fig. 2). Along the PC1 axis, specimens were sorted from small to large skull size. The second principal component (PC2) accounted for the 5% of variation present in the sample; nevertheless it separated the two species. Loadings on PC2 were generally low with the highest being 0.35 for Pall and the lowest -0.33 for Pws.

Allometric analysis of skull variables

Values of PC1 scores and variables used in the regression analyses are provided in Online Appendix 2. All the variables analysed showed r^2 between 0.89–0.99 and negative allometry (Fig. 3). It was previously demonstrated that in caimanines (*Melanosuchus niger*) sexual dimorphism is primarily size related (Foth et al., 2013). The comparative analyses of trajectories between species exhibited three patterns (Fig. 3): Group 1, lateral transposition (Klingenberg, 1998), with a common slope and significant shift in elevation, i.e., different intercept ($p_b > 0.05$, $p_\sigma < 0.05$); Group 2, ontogenetic scaling (Klingenberg, 1998), common slope and no elevation shift, i.e. common intercept ($p_b > 0.05$, $p_\sigma > 0.05$); and Group 3, change in slope (Klingenberg, 1998, $p_b < 0.05$).

Variables with lateral transposition (Group 1) were TI, Orbl, SI, Pall, Orbw, Iw, Pws and Ptw (Fig. 3A). Trajectories of length variables from this group (TI, SI, Pall, Orbl) presented higher intercept values in *Caiman yacare* than in *C. latirostris*, and trajectories of width

variables (Pws and Ptw) showed higher intercept values in *Caiman latirostris* than in *C. yacare*. The other two width variables of Group 1 (Orbw and Iw) almost overlap in their trajectories. Variables with ontogenetic scaling (Group 2) were Awst and Wqqj (Fig. 3B) and those with a change in slope (Group 3) were Aws and Pwst (Fig. 3C). Each variable of Group 2 behaves in the same way in the two species because there is no difference in slope and intercept. Regarding Group 3, Aws exhibited the highest slope and Pwst the lowest one in *C. latirostris*. Specifically, the anterior width of the rostrum shows growth acceleration in *C. latirostris*.

Allometric analysis of the snout and character mapping

The allometric analysis of the anterior width (Aws) and posterior width (Pws) of the snout vs snout length (SI) displayed isometry in *C. latirostris* ($b_{\text{AWS}} = 1.02$; $b_{\text{PWS}} = 0.93$) and negative allometry in *C. yacare* ($b_{\text{AWS}} = 0.84$; $b_{\text{PWS}} = 0.89$) (Fig. 4). When comparing slopes of these variables with the overall skull size in both species, Aws is characterised by a change in slope and Pws by lateral transposition. Both trajectories of *C. latirostris* showed higher values of slope and intercept than *C. yacare* (Fig. 4).

Within a phylogenetic context and considering a hypothetical ancestral condition of low values of snout index, an Aws/SI of 0.3 (similar to the crocodylian *Leydiosuchus canadensis*: 0.26), Globidontia (Brochu, 1999) acquires a snout index of 0.51–0.53 which remains as the hypothetical ancestral condition of the clades Alligatoridae and Alligatorinae. This trend is more pronounced in derived groups of alligatorines, such as the crown *Alligator*, with values ranging from 0.65 to 0.66 (Fig. 5). The ancestral snout ratio assumed for Caimaninae is 0.51 to 0.53 and it is present in basal forms such as *Eocaiman cavernensis* (0.53). In this clade there is a tendency to decrease the snout index, given by the

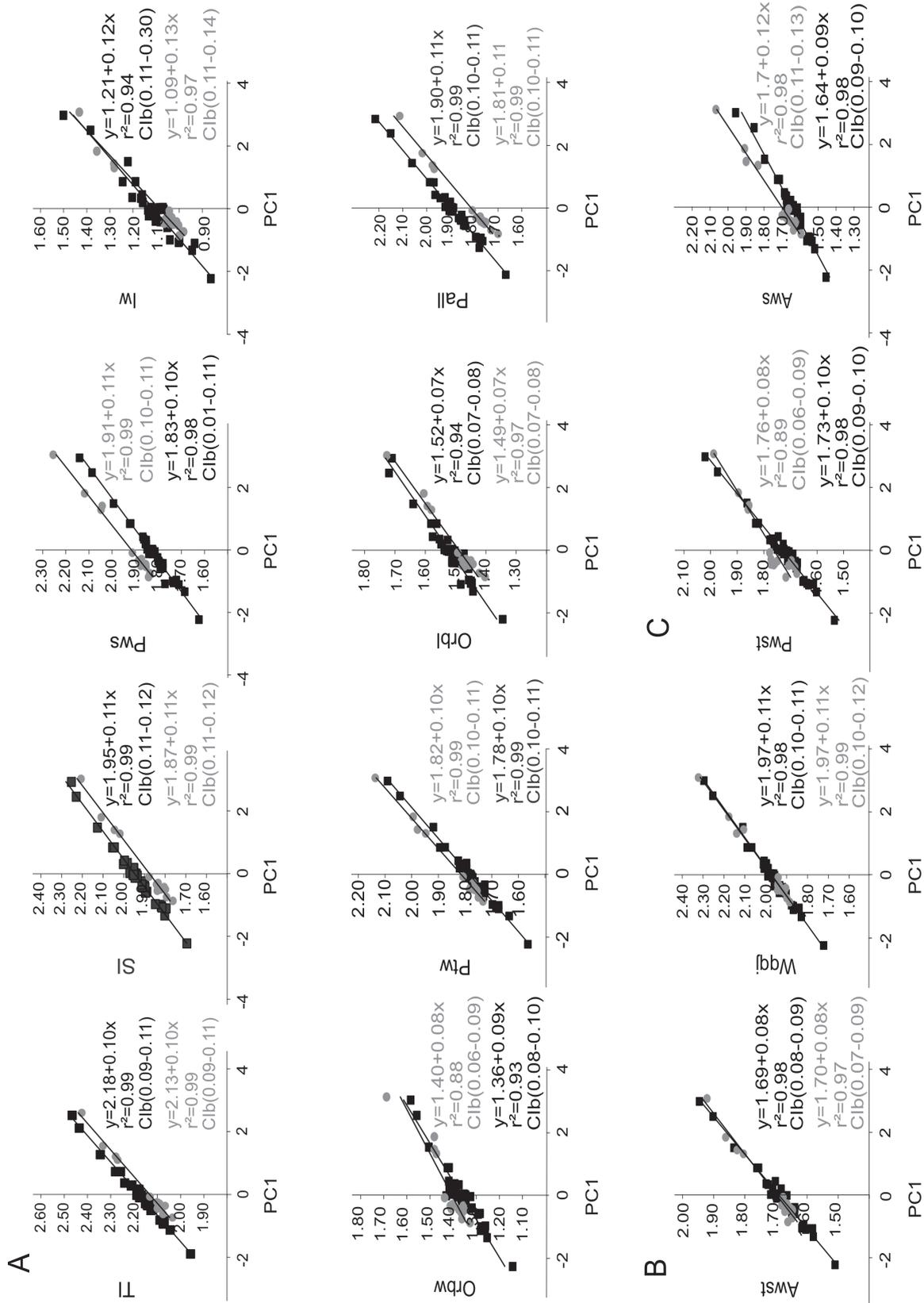


Fig. 3. Allometric relationships (standardised major axis regressions) of \log_{10} -transformed skull measurements versus PC1 scores for *Caiman latirostris* (grey circles) and *C. yacare* (black squares). A, lateral transposition; B, ontogenetic scaling and C, change in slope. Allometric equation $\log y = \log a + b \log x$, where $\log a$ is the y-intercept or elevation, and b is the slope of the line (allometric coefficient). Clb, confidence interval of slope (b).

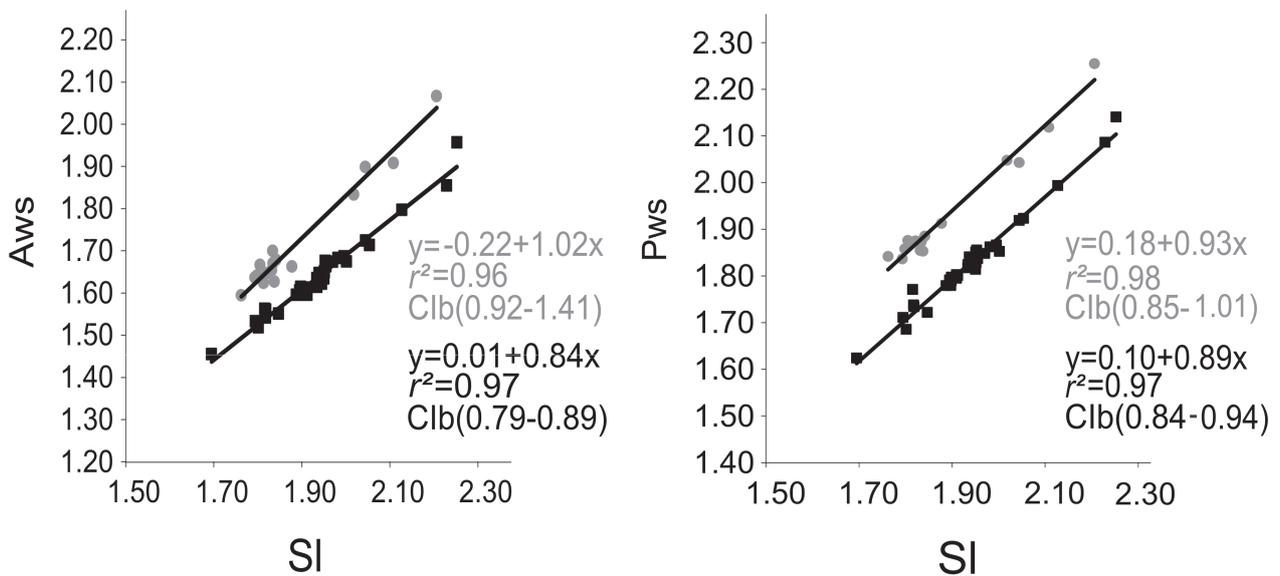


Fig. 4. Allometric analysis of width vs length of the snout in *Caiman latirostris* (grey circles) and *C. yacare* (black squares).

values of 0.48 in *Paleosuchus* and 0.48–0.53 in the clade *Purussaurus* + *Mourasuchus* + *Jacarea* (Brochu, 1999). This trend is very marked in the lineage *Purussaurus* + *Mourasuchus*, with index ranges between 0.38–0.53 (e.g., *Mourasuchus nativus*: 0.32; *Purussaurus mirandai*: 0.29). However, in derived taxa of crown group caimans this rate increases (*C. latirostris* and *C. cf. lutescens* have values of 0.70 and 0.67, respectively; Fig. 5).

DISCUSSION

Based on the regression analyses, the similar ontogenetic trajectories found in most variables reflect a common ontogenetic pattern of change in the skull shape of *Caiman latirostris* and *C. yacare*. This confirms that the snout shape is a distinctive feature of species established early in the ontogeny. Variables with the same trajectories (ontogenetic scaling, Klingenberg, 1998) express that both species have the same pattern of change in the anterior width of the skull table and the posterior width of the skull at the mandibular joint (quadrate-quadratojugal contact). Differences in intercepts (lateral transpositions, Klingenberg, 1998) observed in the trajectories of width and length variables reveal that main morphological skull differences become established in early stages of development of both species (see Monteiro & Soares, 1997). *Caiman yacare* differs from *C. latirostris* by longer skulls, orbits, snouts and palates (TI, Orbl, SI and Pall, respectively) throughout post-hatching ontogeny. Likewise, *C. latirostris* differs by the widest posterior area of the snout and the widest space between the pterygoid wings (Pws and Ptw). Some measurements, such as the orbital and interorbital widths (Orbw and Iw), are not useful to delimit species, suggesting that these are constrained. A similar situation is observed for Awst and Wqqj which exhibit the same slopes and intercepts in both species.

The anterior width of the snout (Aws) and the posterior width of the skull table (Pwst) have different ontogenetic

trajectories represented by a change in slope, allowing the separation of adult specimens of both species. However, it should be noted that during ontogeny both trajectories come together, rendering the species indistinguishable. Thus, part of the snout morphology (Aws) of adults is acquired during post hatching ontogeny.

Adults of *C. latirostris* represent a brevirostrine condition among extant species (Pierce et al., 2008). At the beginning of development, young individuals of *C. latirostris* have higher snout widths than *C. yacare* (Fig. 4). This difference is exaggerated through ontogeny, when the snout of *C. latirostris* becomes broader. Regression analyses of the anterior and posterior width of the snout against snout length reveal that growth of the snout is isometric in *C. latirostris*, showing that there is a balance in the growth of length and width. Furthermore, our data set shows that snout proportions are established early in the ontogeny and stay without modification during growth in this species. In contrast, the snout proportions in *C. yacare* change with negative allometry and the snout becomes narrower in relation to its length. Monteiro & Soares (1997) pointed out that the retention of juvenile characters in adults (with subsequent ontogenetic re-patterning; Wake, 1989) can explain such divergence in the ontogenetic trajectory of *C. latirostris*. In this way, the isometric relationship between width and length of the snout could reflect the retention of juvenile proportions of the snout in adult specimens. This condition contrasts the negative allometry observed for *C. yacare*, indicating a progressive elongation of the skull (narrowing-lengthening) previously demonstrated by Monteiro & Soares (1997). These findings should be tested with more exhaustive methods, such as a geometric morphometric analysis.

According to Monteiro & Soares (1997) the elongation of the skull observed in *C. yacare* is probably the plesiomorphic condition in *Caiman* because it also occurs in *Melanosuchus niger* considered to be the sister taxon of the group. In this scenario, the broader skull would

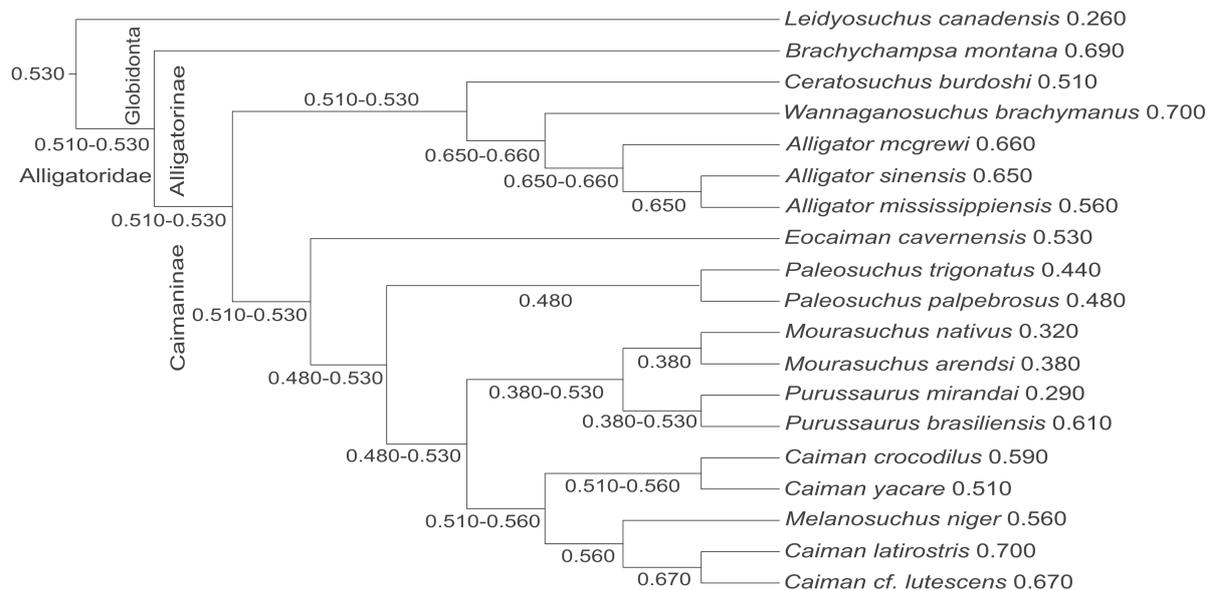


Fig. 5. Phylogenetic relationships of alligatoroids (taken from Brochu, 1999) displaying the optimisation of Aws/SI.

be an autapomorphy of *C. latirostris* (Monteiro et al., 1997) within the Caimaninae. However, plesiomorphic and apomorphic conditions in relation to snout proportions are difficult to distinguish from each other in Caimaninae when taking extinct forms into account (Table 1). Pierce et al. (2008) presented the variation of extant crocodylian skulls in a morphospace and Alligatoridae was located in the short/narrow and short/broad quadrants. If fossil alligatorids are also considered, then Caimaninae skulls would present not only short snout morphologies (short/narrow and short/broad) but also long/broad morphologies in the duck-faced forms (sensu Brochu, 2001), as is the case for the extinct *Mourasuchus*. According to the results obtained in the character mapping, there is a trend to reduce the snout index Aws/SI in Caimaninae, opposite to what occurs in Alligatorinae. This trend is especially marked in the lineage of the crown group caimans *Purussaurus* and *Mourasuchus*, probably through the development of broad but elongated snouts. Nevertheless, in the caimanines *Jacarea* (Brochu, 1999), this trend is reversed in the clade *C. latirostris*-*C. cf. lutescens* (Fig. 5), which has the broadest/shortest snout of the group. The generalised snout proportions of *C. yacare*, *C. crocodilus* and *Melanosuchus niger* present similar values to most clades of Alligatorinae and to the extinct basal caimanines, such as *Eocaiman*.

Along the phylogeny of crocodylian species, similar snout morphologies can appear multiple times (Kälin, 1955; Langston, 1973; Busbey, 1994; Russell & Wu, 1997; Cleuren & de Vree, 2000; Brochu, 2001, 2003; Pierce et al., 2008). Here, two species of closely related caimans have readily distinguishable snout proportions (Fig. 5). Cranial disparity can be related to diet (Neill, 1971; Lordansky, 1973; Diefenbach, 1979; Thorbjarnarson, 1990, 1993; Pooley, 1992; Monteiro et al., 1997; Cleuren & de Vree, 2000) or foraging strategies (Busbey, 1994; Brochu, 2001; McHenry et al., 2006; Pierce et al., 2008). We suggest that the observed differences in the rostrum in the present study are attributable to different ecological requirements related with the type

of habitat and foraging strategies. Both species develop different skull morphologies and eat similar food items (insects, molluscs, snails, birds, mammals, crustaceans, amphibians, reptiles and fishes: Carvalho, 1951; Vanzolini & Gomes, 1979; Ayarzagüña, 1983; Monteiro & Soares, 1997; Melo, 2002; Borteiro et al., 2008). Moreover, they undergo the same ontogenetic shift in their diet, from feeding primarily on invertebrates to vertebrates (Melo, 2002; Borteiro et al., 2008), a generalised pattern for crocodylians (Dodson, 1975; Pooley & Gans, 1976; Taylor, 1979; Webb et al., 1982; Delany & Abercombie, 1986; Hutton, 1987; Magnusson et al., 1987; Thorbjarnarson, 1993; Da Silveira & Magnusson, 1999; Delany et al., 1999; Cleuren & de Vree, 2000). Normally both species overlap in their distribution. Although, *Caiman latirostris* generally prefers shallow and usually heavily vegetated aquatic environments, *C. yacare* is often associated with deep water bodies (Larriera & Imhof, 2006). In this context, we consider that morphological skull differences reflect ecological separation in association with habitat preference and foraging behaviours. It is likely that the source of cranial variation resides in how the species interact with different types of environments which encompasses a hydrodynamic aspect. *Caiman yacare* develops a more triangular elongated snout-pointed skull and lives in deep waters. In contrast, *C. latirostris* possesses a more robust skull, remaining less aquatic than *C. yacare* among superficial aquatic vegetation (see also Magnusson et al., 1987; 1998). Nevertheless, there is a complete lack of information about hydrodynamic traits of crocodylian skull and more investigation is needed regarding feeding behaviors and techniques for capturing prey.

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