

Cranial characters in *Caiman crocodilus* (Crocodylia: Alligatoridae) with emphasis on the subspecies distributed in Colombia

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ABSTRACT

Studies on the biology of *Caiman crocodilus* have drawn attention to its biology with emphasis on systematic, taxonomy and ecology. However, anatomical aspects, such as skull characteristics, have not been studied in detail throughout its geographic range. In this study the skull characteristics for *C. crocodilus* subspecies, *C. c. fuscus*, *C. c. chiapasius*, *C. c. crocodilus*, and *C. c. apaporiensis* were analyzed using geometric morphometrics and descriptive morphology, including geographic and ontogenetic variation. Variation in skull morphology was found between the subspecies analyzed. Trans-Andean subspecies, *C. c. fuscus* and *C. c. chiapasius*, exhibit brevirostrine skulls but they are different in the contact between frontal and nasal bones and the size of the palatine process of the maxilla; therefore, populations in Colombia correspond to *C. c. fuscus* and, *C. c. chiapasius* is not distributed in Colombia. Although cis-Andean subspecies, *C. c. apaporiensis* and *C. c. crocodilus*, have longirostrine skulls, both subspecies differ in the shape of the skull and in osteological characters; then, adults of *C. c. apaporiensis* present frontal and nasal in contact and, V-shape maxillary-premaxillary suture; while *C. c. crocodilus* specimens exhibit a high geographic and ontogenetic variation, supporting the hypotheses that there at least two clades of such subspecies for Colombia. These morphological differences should be considered in future systematics studies and policies on global conservation of the different *C. crocodilus* subspecies.

Key Words: Caimaninae; Skull Variation; Geometric Morphometrics; Ontogeny; Geographic Variation.

Introduction

Caiman crocodilus is the only alligatorid distributed throughout most Latin America, from México to Perú and Brazil (Medem, 1983; Velasco and Ayzarzagüena, 2010). The wide distribution of this species, along with its genetic and morphological variation, has led to the recognition of four subspecies: *C. crocodilus crocodilus*, *C. c. apaporiensis*, *C. c. chiapasius* and *C. c. fuscus* (King and Burke, 1989; Venegas-Anaya *et al.*, 2008; Fig. 1). The recognition of different subspecies has important implications for regional and global conservation policies, and the proposal to maintain the four subspecies has been broadly discussed, (Busack and Pandya, 2001; Venegas-Anaya *et al.*, 2008; Balaguera-Reina *et al.*,

2020). In fact, there are extraction and hunting pressures over *Caiman crocodilus* in Colombia, which are reported from the Late Pleistocene to the present (Balaguera-Reina and González-Maya 2009, 2010; De la Ossa-Lacayo and De la Ossa, 2015; Balaguera-Reina 2019, Morcote-Ríos *et al.*, 2021). Therefore, the delimitation of taxonomic units will allow better planning of the conservation efforts for each subspecies.

The presence of four subspecies in Colombia has been recognized for several decades. Medem (1962) distinguished *C. c. chiapasius* in the Pacific region from *C. c. fuscus* in the Caribbean and Andean region based on skull shape, lepidosis, and



Figure 1. Geographic distribution of *Caiman crocodilus* with natural regions of Colombia.

skin coloration, highlighting differences in the last two characteristics. Subsequently, Medem (1981) published drawings of the skulls and recorded different body measurements and scale counts for the four subspecies.

Bocourt (1876) described *C. c. chiapasius* from Mexico based on five specimens, using coloration and scalation, but the geographical distribution was not discussed (Schmidt, 1928; Medem, 1962; Busack and Pandya, 2001; Venegas-Anaya *et al.*, 2008; Escobedo-Galván *et al.*, 2011, 2015). Venegas-Anaya *et al.* (2008) used mitochondrial DNA from Central American populations to indicate that *C. c. chiapasius* occur in Mexico, Guatemala, and northern El Salvador, excluding the subspecies from Colombia. This taxonomic classification was later supported by Jiménez (2016), who also used mitochondrial DNA, and suggested the populations in the Pacific region of Colombia were *C. c. fuscus*.

The classification of *C. c. apaporiensis* as a subspecies (Medem, 1955) was questioned by Bloor (2013), who suggested it was the same evolutionary significant unit (ESU) as *C. c. crocodilus*, based on mitochondrial DNA. Recently, Balaguera-Reina *et al.* (2020), via mitochondrial molecular markers, suggested that *C. c. apaporiensis* and *C. c. crocodilus* are the same ESU. However, Escobedo-Galván *et al.* (2015) analyzed the skull of *C. c. apaporiensis* and described osteological and morphometric characters that distinguish it from *C. c. crocodilus*, which warrants further investigation into whether both subspecies should be considered as such.

On the other hand, Angulo-Bedoya *et al.* (2019) analyzed the intraspecific variation of onto-

genetic skull development in *C. c. crocodilus*, *C. c. fuscus*, and *C. c. apaporiensis* in Colombia using geometric morphometrics. They confirmed the pattern observed by Escobedo-Galván *et al.* (2015), where *C. c. apaporiensis* differs from *C. c. crocodilus*, and these two subspecies, in turn, differ from *C. c. fuscus*.

Morphological variation in Colombian populations of *C. crocodilus* has not been completely studied (Busack and Pandya, 2001; Escobedo-Galván *et al.*, 2015). Detailed descriptions of the skull are only available for *C. c. apaporiensis*, a questionable subspecies with a restricted geographic range in Colombia (Escobedo-Galván *et al.*, 2015; Fig. 1), while *C. c. fuscus* and *C. c. crocodilus* have a wide distribution (Fig. 1). Here, we analyze the skulls of three subspecies of *C. crocodilus* present in Colombia, the ontogenetic development patterns in the skull, and the variability between populations. These data may provide useful morphological characters for taxonomic and evolutionary studies, which are essential for crocodylian conservation policies in Latin America.

Materials and methods

We analyzed 158 skulls of *C. crocodilus* stored in the Reptile Collection at the Instituto de Ciencias Naturales at Universidad Nacional de Colombia, and photographs of three specimens of *C. c. chiapasius* stored in the Amphibian and Reptile Collection at the National Museum of Natural History of the United States (USNM) (Table 1; Appendix I).

First, we performed a morphometric analysis in a subset of the specimens, composed by 53 skulls of adult specimens of the four subspecies of *C. crocodilus* and compared our results to the patterns described in previous studies (Escobedo-Galván *et al.*, 2015, Angulo-Bedoya *et al.*, 2019). The analysis was performed over photographs of the dorsal and ventral views of the skulls. Nine landmarks were used in dorsal view and 15 landmarks were used in ventral view (Fig. 2; Table 2) based on the protocols of Fernandez Blanco *et al.* (2014) and Okamoto *et al.* (2015). Landmarks were digitized using TPSUtil (Rohlf, 2018) and TPSDig2 (Rohlf, 2017). In order to avoid increasing the degrees of freedom in the analyses (Okamoto *et al.*, 2015) and due to the bilateral symmetry of the skull, landmarks were only digitized on the left side of the skull for each view.

For the geometric morphometric analyses, a Generalized Procrustes Analysis (GPA) and other

Table 1. Analyzed specimens of *Caiman crocodilus*.

Subspecies of <i>C. crocodilus</i>	Total analyzed specimens	Cranial element analyzed in all specimens by region and state	Geometric morphometrics analyzed adult specimens by state	Source
		Caribbean region		
		Bolívar (4)		
		Córdoba (19)		
		Magdalena (1)		
<i>C. c. fuscus</i>	52 Colombia	Pacific region	Bolívar (2)	ICN
		Chocó (16)	Córdoba (12)	
		Cauca (10)	Chocó (6)	
		Andean region		
		Caldas (1)		
		Tolima (1)		
<i>C. c. chiapasius</i>	3 Mexico	Chiapas (3)	Chiapas (3)	USNM
<i>C. c. apaporiensis</i>	44 Colombia	Amazon region		ICN
		Vaupés (44)	Vaupés (15)	
		Amazon region		ICN
		Amazonas (1)		
		Caquetá (2)		
		Guainía (1)	Caquetá (1)	
		Guaviare (2)	Guaviare (2)	
<i>C. c. crocodilus</i>	62 Colombia	Putumayo (1)	Putumayo (1)	
		Vaupés (7)	Vaupés (2)	
			Casanare (1)	
		Orinoco region	Meta (8)	
		Casanare (2)		
		Meta (46)		

statistical and graphic analysis were performed using the software MorphoJ 1.06d (Klingenberg, 2011) and Past 3.20 (Hammer *et al.*, 2001). A Principal Component Analysis (PCA) was performed to detect patterns of change between subspecies and between the two populations of *C. c. fuscus* analyzed, in order to determine if both populations correspond to the same subspecies, as proposed by Jiménez (2016). We used a MANOVA and the Wilk's lambda and Pillai's trace statistics to analyze differences between groups. Subsequently, a paired comparison between subspecies was conducted using the Bonferroni correction for each view. One *C. c. crocodilus* specimen, ICN 8726, showed deterioration in the occipital region of the dorsal view so it was excluded from the morphometric analysis for that view.

We analyzed three morphological skull characteristics in all the specimens: 1) contact between the frontal and nasal bones, 2) the shape of the

premaxillary-maxillary suture in the ventral view, and 3) the variability in the length/width ratio of the palatine process of the maxilla in the four subspecies, based on characters used for distinguishing *C. latirostris* and *C. yacare* (Fernandez Blanco *et al.*, 2018). The three skull characters were examined and compared across geographic distributions (particularly the Colombian populations; Table 1) and through post-hatchling ontogenetic stages to assess the variation among *C. crocodilus* subspecies and to determine the taxonomic utility of the characters. Individuals of each subspecies in Colombia were categorized according to the five geographic regions of the country (Fig. 1). We also used four age classes based on the total length (TL= from the tip of the tail to the tip of snout), according to Reserva de la Biosfera la Encrucijada (2011) which were: hatchlings (between 41 - 80 cm TL); juveniles (between 81 - 120 cm TL); subadults (between 121 - 160 cm TL); and

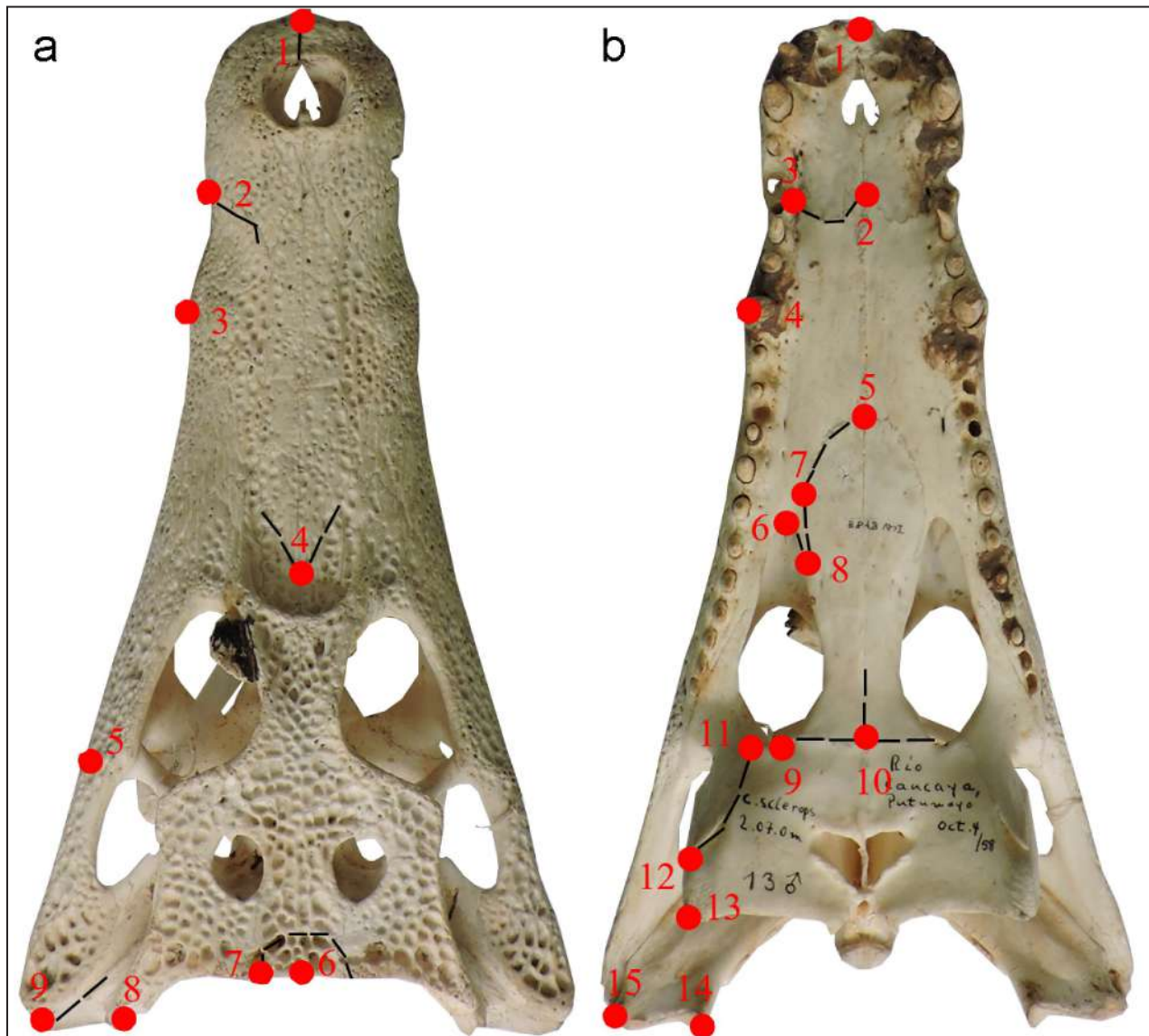


Figure 2. *C. crocodilus* (ICN 8788). Distribution of landmarks. (a). Dorsal view. (b). Ventral view.

adults (161 cm TL or more). Five specimens were excluded from the contact between the frontal and nasal bones analysis, due to the poor condition of the skull or difficulties in the visualization of the suture (noted as unidentified in Tables 5 - 8).

The shape of the ventral premaxillary-maxillary suture was determined by its orientation from the midline to the lateral border of the palate. On the other side, the variation in the palatine process of the maxilla was determined by comparing the length/width ratio of the palatine process in a qualitative way; thus, it ranged from a process as long as the width at the base (i.e., forming a wider and stouter palatine process) to two, three, or four times longer than the width at the base (i.e., forming a narrower palatine process).

For the skull characteristics, the Mexican specimens were analyzed for comparison with the Colombian specimens. We adopted the nomenclature reported by Romer (1956) for bony elements. Maps were built with ArcGIS 10.5 (ESRI, 2017).

Results

Geometric Morphometric analysis

In the PCA for the dorsal view, the first two Principal Components (PCs) accounted for 71.55% of the total variance. Subspecies were separated along the PC1 (Fig. 3a) due to the width of the snout, with *C. c. apaporiensis* and *C. c. crocodilus* specimens located mainly in the negative values of this component due to both subspecies having a longirostrine skull

Table 2. Description of landmarks in dorsal and ventral views.

View	Number	Landmark Definition	Type
Dorsal	1	Most anterior point of the premaxilla.	I
	2	Contact between premaxilla and maxilla in lateral view.	I
	3	Maximum width point of the snout, posterior to the premaxilla-maxilla contact.	II
	4	Anterior contact point between the nasals.	I
	5	Left side of the skull at the posterior point of the orbital bar.	II
	6	Middle point of the posterior margin of the supraoccipital.	II
	7	Contact between supraoccipital and squamosal bones at the posterior margin of the skull table.	I
	8	Most posterolateral point of the squamosal.	II
	9	Most posterolateral point of the quadrate, where it contacts the quadratojugal.	I
Ventral	1	Most anterior point of the premaxilla.	I
	2	Contact between maxilla and premaxilla at the sagittal plane.	I
	3	Contact between maxilla and premaxilla at the lateroventral margin.	I
	4	Lateroventral point of the fourth mandibular tooth.	I
	5	Most anterior point of contact between the palatines.	I
	6	Most anterior point of the suborbital fenestra.	II
	7	Most posterolateral point of the palatine process of the maxilla.	II
	8	Most distal point of the palatine process of the maxilla.	II
	9	Most posterior point of the suborbital fenestra.	II
	10	Contact between palatine and pterygoid at sagittal plane.	I
	11	Apical end of the anterior process of the pterygoid.	II
	12	Most anterior point of the descending process of the ectopterygoid.	II
	13	Most posterior point of the pterygoid wings.	II
	14	Most posteromedial point of the quadrate.	II
	15	Most posterolateral point of the quadrate.	II

(Fig. 3b). In contrast, *C. c. fuscus* specimens from the Caribbean and Pacific regions were located in the positive values of the PC1, having a wider and more robust snout (Fig. 3c), a typical configuration of a brevirostrine skull.

For the ventral view, the first three PCs accounted for 63.8% of the total variance. Subspecies were separated along the PC1 due to the width of the snout (Fig. 4a), with *C. c. fuscus* specimens from the Caribbean and Pacific regions having a brevirostrine skull (Fig. 4b), whereas *C. c. apaporiensis* and *C. c. crocodilus* were grouped into the positive values of the PC1, showing a longirostrine skull (Fig. 4c).

We performed a MANOVA using the loadings of the first two and three PCs in the dorsal and ventral view, respectively. Multinormality was tested ($p < 0.05$) for both views. MANOVA results were statistically significant for the dorsal and ventral views (Table 3). The comparison test using the Bonferroni correction did not show statistical differences neither

between the Caribbean and Pacific populations of *C. c. fuscus* nor between this subspecies and *C. c. chiapasius* for both views (Table 4). There were no statistically significant differences in the skull shape between *C. c. apaporiensis* and *C. c. crocodilus* in the dorsal view, but there was a slight statistically significant difference in ventral view (Table 4). Finally, there were no statistical differences in the skull between *C. c. crocodilus* and *C. c. chiapasius* in ventral view, although there were significant differences in dorsal view (Table 4).

Cranial element analysis

There was morphological variation in the contact of the frontal and nasal bones in the subspecies of *C. crocodilus* (Table 5). In *C. c. fuscus* specimens, the frontal and nasal bones were in contact (i.e., they were not separated by prefrontal bones) (Fig. 5a; Table 5). We observed this characteristic in 50 skulls (Table 5), including specimens from the Andean,

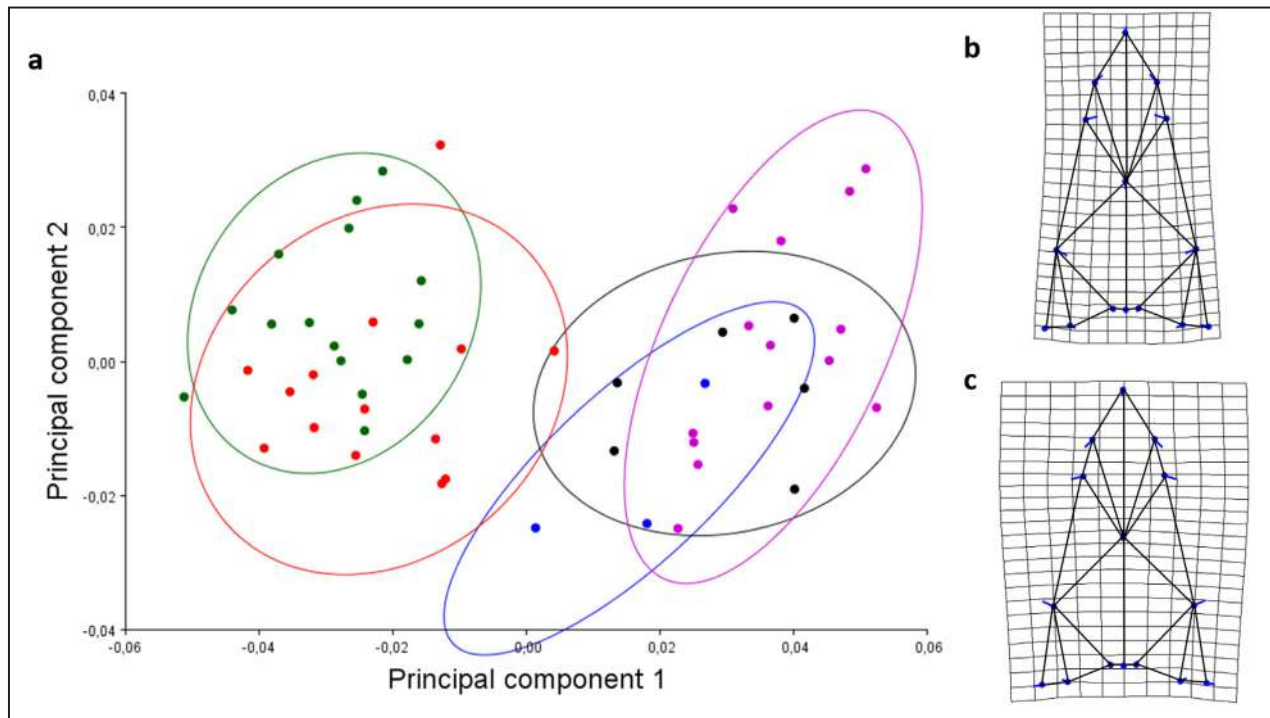


Figure 3. (a). Principal Component Analysis, dorsal view. Scatterplot of the PC1 vs PC2. *C. c. apaporiensis* (green), *C. c. crocodilus* (red), *C. c. chiapasius* (blue), *C. c. fuscus* Pacific region (black), *C. c. fuscus* Caribbean region (purple). (b). Transformation grid of the maximum negative value in the PC1. (c). Transformation grid of the maximum positive value in the PC1.

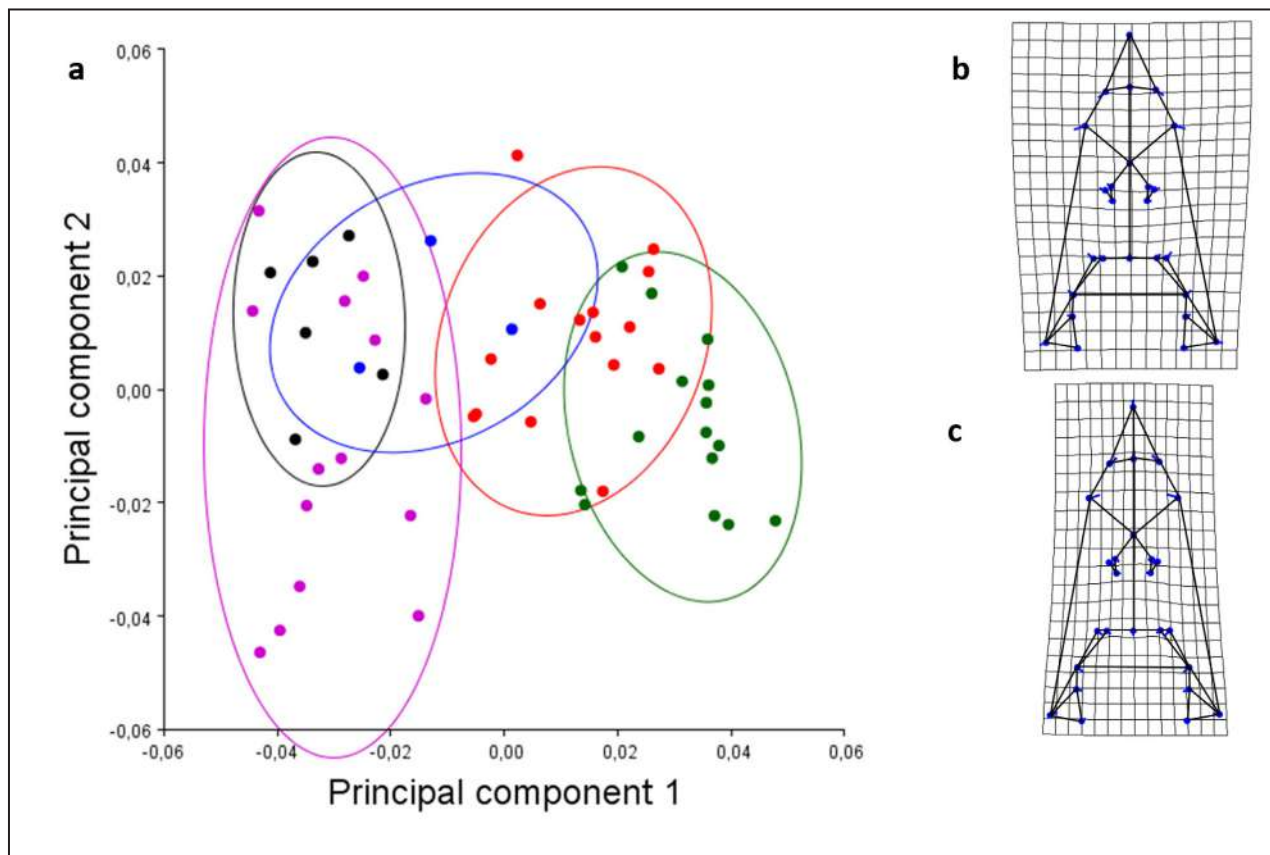


Figure 4. (a). Principal Component Analysis, ventral view. Scatterplot of the PC1 vs PC2. *C. c. apaporiensis* (green), *C. c. crocodilus* (red), *C. c. chiapasius* (blue), *C. c. fuscus* Pacific region (black), *C. c. fuscus* Caribbean region (purple). (b). Transformation grid of the maximum negative value in the PC1. (c). Transformation grid of the maximum positive value in the PC1.

Table 3. MANOVA test results for landmark configurations in dorsal and ventral views of the subspecies of *Caiman crocodilus*.

	Wilk's lambda		Pillai's trace	
	p-value F		p-value F	
Dorsal		1,227 E-18 22,49		3,702 E-10 10,2
Ventral		2,199 E-17 13,53		5,309 E-08 5,715

Table 4. MANOVA pairwise comparisons using Bonferroni's correction. Results of the dorsal landmark analysis (above diagonal) and ventral landmark analysis (below diagonal).

	<i>C. c. apaporiensis</i>	<i>C. c. chiapasius</i>	<i>C. c. crocodilus</i>	<i>C. c. fuscus</i> Pacific	<i>C. c. fuscus</i> Caribbean
<i>C. c. apaporiensis</i>	-	0,000837	0,851*	1,966 E-07	9,234 E-13
<i>C. c. chiapasius</i>	0,00197	-	0,00802	3,316*	0,427*
<i>C. c. crocodilus</i>	0,00513	0,1451*	-	3,355 E-06	4,56 E-11
<i>C. c. fuscus</i> Pacific	1,0002 E-07	2,406*	9,863 E-06	-	4,621*
<i>C. c. fuscus</i> Caribbean	3,885 E-12	1,274*	4,949 E-09	9,7625*	-

* indicates non-significant differences between groups ($p > 0,05$).

Caribbean, and Pacific populations, as well as all ontogenetic stages from hatchlings to adults (Table 6). In the three specimens of adult *C. c. chiapasius*, the frontal and nasal bones were not in contact (Fig. 5b; Table 5).

In the 41 subadult and adult specimens of *C. c. apaporiensis*, the frontal and nasal bones were not in contact (Fig. 5c; Table 5), although they were in contact in a juvenile specimen (Table 7). Most of the specimens of *C. c. apaporiensis* were from the west Vaupés state, municipality of Apaporis, near the type locality of the subspecies; and only three specimens were from Ajajú river (Table 7).

Contact between the frontal and nasal bones varied in *C. c. crocodilus* specimens, both within and between populations. In a sample of 62 specimens from the Amazon and Orinoco regions of Colombia, 45 specimens had contact between the frontal and nasal bones, while 16 specimens did not have contact between these bones (Table 5). Different age groups showed both contact and no contact between the frontal and nasal bones (Table 8). Specimens from populations in the Amazon and Orinoco regions also showed both contact and no contact between the frontal and nasal bones (Fig. 6a; Table 8). However, all the specimens from populations at the east of the Amazon region showed contact between the frontal and nasal bones (Fig. 6a; Table 8).

We found the following variations in the shape of the premaxillary-maxillary suture: almost horizontal (Fig. 7a), U-shaped (Fig. 7b), V-shaped (Fig.

7c), and J-shaped (Fig. 7d). The ventral premaxillary-maxillary suture was U-shaped in 47 *C. c. fuscus* specimens; however, this suture was almost horizontal in two juveniles and a subadult specimen from Cauca state, in the Pacific region (Tables 5 and 6). The U-shaped suture was also observed in the three *C. c. chiapasius* specimens (Fig. 7b; Table 5). The ventral premaxillary-maxillary suture was V-shaped in 43 *C. c. apaporiensis* specimens (Fig. 7c; Table 5) and one subadult *C. c. apaporiensis* specimen from Ajajú river (Vaupés state) had the U-shaped suture (Tables 5 and 7).

The four different morphologies of the ventral premaxillary-maxillary suture were observed in 62 *C. c. crocodilus* specimens (Table 5). The U-shaped suture was the most common pattern (N=33), followed by V-shaped (N=11), almost horizontal (N=9), and J-shaped (N=8, Fig. 6b). Variation was observed in specimens of different ontogenetic stages and even within each ontogenetic stage (Table 8). Regarding the geographic distribution, there was no evident pattern associated with this characteristic in *C. c. crocodilus* (Table 8) however, the U-shaped suture was the most common in most localities (Fig. 6b).

For *C. c. fuscus*, 26 specimens showed a palatine process as long as the width at the base (Fig. 8a; Table 5), whereas 26 specimens showed a process two times longer than the width at the base. In this subspecies, all the hatchlings showed a process two times longer than the width at the base, while juveniles, subadults, and adults showed more variation

Table 5. Variation of the analyzed characters in the subspecies of *C. crocodilus*. Frontal-Nasal bones: FN (in contact); F-N (no contact). Ventral premaxillary-maxillary suture shape: U (U-shaped); V (V-shaped); J (J-shaped); H (almost horizontal). Palatine process: as long as the base width (1X), twice as long as the width of the base (2X), three times longer than the width of the base (3X), four times longer than the width of the base. Unidentified (?).

Character	Snout shape	Frontal-Nasal bones contact	Ventral premaxillary-maxillary suture shape	Palatine process length
Subspecies				
<i>C. c. fuscus</i>		50 FN	3 H	1x (26)
	Brevirostrine	2?	49 U	2x (26)
<i>C. c. chiapasius</i>		3 F-N	3 U	3x (3)
		1 FN	1 U	1x (1)
<i>C. c. apaporiensis</i>		41 F-N	43 V	2x (39)
		2?		3x (2)
				4x (2)
	Longirostrine	45 FN	9 H	1x (12)
		16 F-N	33 U	2x (35)
<i>C. c. crocodilus</i>		1?	8 J	
			11 V	3x (15)
			1?	

in the length/width ratio (Table 6). There was no geographical pattern that distinguished populations, since both wide and narrow palatine processes were identified in all regions (Table 6). In all the three specimens of *C. c. chiapasius*, the palatine process was almost three times longer than the width at the base (Fig. 8b; Table 5).

The *C. c. apaporiensis* specimens showed all the configurations for this character. Most specimens (N=39) had a palatine process almost twice as long as the width at the base (Fig. 8c; Table 5), whereas the remaining configurations were observed only in five specimens (Table 7). There were no clear ontogenetic

trends for this morphological character (Table 7).

In the *C. c. crocodilus* specimens, the palatine process was as long as the width at the base (N=12), two times longer than the width at the base (N=35), and three times longer than the width at the base (N=15, Table 5). There was an ontogenetic trend toward a progressively longer palatine process relative to the width at the base in subadults and adults (Table 8). We did not observe any geographic variation associated with this characteristic (Fig. 6c), since all characteristics were recorded in most populations from both the Orinoco and Amazon regions (Fig. 6c; Table 8).

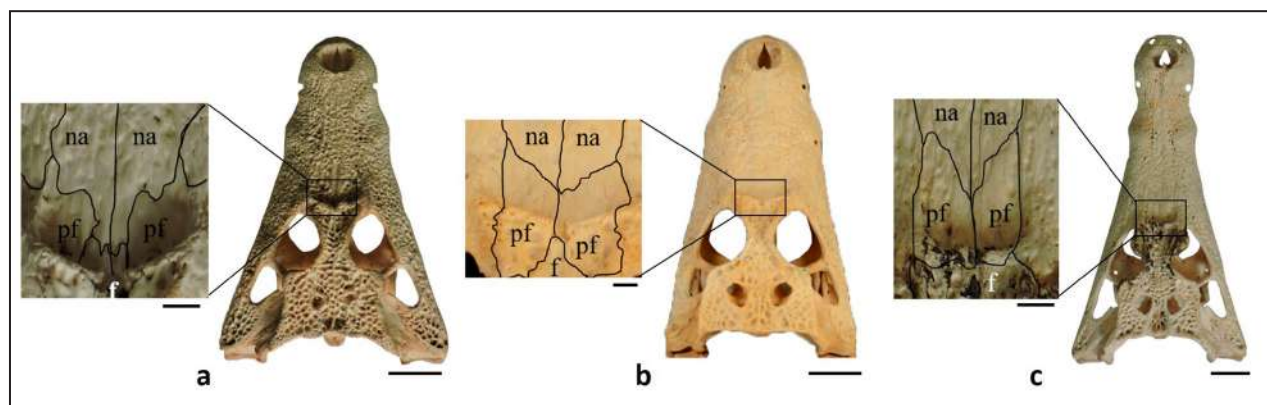


Figure 5. Nasal and frontal bones contact. (a). *C. c. fuscus* (ICN 8886) with frontal and nasals bones in contact. (b). *C. c. chiapasius* (USNM 115335) with frontal and nasals bones separated by prefrontals. (c) *C. c. apaporiensis* (ICN 8730) with frontal and nasals bones separated by prefrontals. Abbreviations: f, frontal; na, nasal, pr, prefrontal. Scale bar equals 5 cm for complete skulls; 1 cm for miniatures.

Table 6. Geographic and ontogenetic variation in *C. c. fuscus*. Frontal-Nasal bones: FN (in contact); F-N (no contact). Ventral premaxillary-maxillary suture shape: U (U-shaped); V (V-shaped); J (J-shaped); H (almost horizontal). Palatine process: as long as the base width (1X), twice as long as the width of the base (2X), three times longer than the width of the base (3X), four times longer than the width of the base. Unidentified (?).

Subspecies	Region						
		Pacific			Caribbean		Andean
<i>C. c. fuscus</i>		Cauca	Chocó	Córdoba	Bolívar	Magdalena	Caldas
Frontal-Nasal bones contact	Ontogenetic stage						
	Hatchling (9)		8FN	1FN			
	Juvenile(14)	5FN	2FN	5FN	2FN		
	Subadult (18)	5FN	2FN	6FN 1?	2FN	1FN	1FN
Adult (11)			4FN	6FN	1?		
Ventral premaxillary-maxillary suture shape	Hatchling (9)		8U	1U			
	Juvenile(14)	2H 3U	2U	5U	2U		
	Subadult (18)	1H 4U	2U	7U	2U	1U	1U
	Adult (11)		4U	6U	1U		
Palatine process length	Hatchling (9)		8(2x)	1(2x)			
	Juvenile (14)	4(1x) 1(2x)	1(1x) 1(2x)	3(1x) 2(2x)	2(1x)		
	Subadult (18)	5(1x)	2(2x)	3(1x) 4(2x)	1(1x) 1(2x)	1(2x)	1(2x)
	Adult (11)		1(1x) 3(2x)	6(1x)	1(2x)		

Discussion

Regarding the geometric morphometric analyses, *C. crocodilus* subspecies showed skull configurations falling into two groups, the longirostrine type and the brevirostrine type (Figs. 3 and 4). Our results are similar to those described by Escobedo-Galván *et al.* (2015) and Angulo-Bedoya *et al.* (2019) for Colombian subspecies, under the taxonomic classification of Venegas-Anaya *et al.* (2008). Therefore, “trans-Andean” subspecies, *C. c. fuscus* and *C. c. chiapasius*, distributed west of the Andes at the Andean, Caribbean, and Pacific regions in Colombia have a brevirostrine skull; while the “cis-Andean” subspecies, *C. c. apaporiensis* and *C. c. crocodilus*, distributed in the Orinoco and Amazon regions have a longirostrine skull.

In the trans-Andean populations, Medem (1962, 1981) reported differences between Pacific and Caribbean populations of *C. crocodilus* and proposed the presence of *C. c. chiapasius* in the country based on skull shape, lepidosis, and coloration. Our morphometric analyses showed no differences between the Pacific and Caribbean populations in Colombia, which is in accordance with the results reported by Jiménez (2016), as the Caribbean, Andean, and Pacific populations of *C. crocodilus* correspond to *C. c. fuscus*, supporting the taxonomic classification of Venegas-Anaya *et al.* (2008). On the other hand, our results showed that *C. c. chiapasius* and *C. c. fuscus* did not differ in the shape of their skulls in either the dorsal or ventral views.

The skulls of *C. c. apaporiensis* and *C. c. crocodilus* did not differ in dorsal view but they did

Table 7. Geographic and ontogenetic variation in *C. c. apaporiensis*. Frontal-Nasal bones: FN (in contact); F-N (no contact). Ventral premaxillary-maxillary suture shape: U (U-shaped); V (V-shaped); J (J-shaped); H (almost horizontal). Palatine process: as long as the base width (1X), twice as long as the width of the base (2X), three times longer than the width of the base (3X), four times longer than the width of the base. Unidentified (?).

Subspecies	Ontogenetic stage	Amazon region	
		Vaupés state: Apaporis	Guaviare state: Ajajú River
<i>C. c. apaporiensis</i>	Juvenile (2)	1FN 1F-N	
	Subadult (14)	12F-N 1?	1F-N
	Adult (28)	27F-N 1?	
Frontal-Nasal bones contact	Juvenile (2)	2V	
	Subadult (14)	13V	1U
	Adult (28)	28V	
Ventral premaxillary-maxillary suture shape	Juvenile (2)	2(2x)	
	Subadult (14)	12(2x) 1(3x)	1(2x)
	Adult (28)	1(1x) 24(2x) 1(3x) 2(4x)	
Palatine process length	Juvenile (2)	2(2x)	
	Subadult (14)	12(2x) 1(3x)	1(2x)
	Adult (28)	1(1x) 24(2x) 1(3x) 2(4x)	

in ventral view (Table 4), according to the results of Angulo-Bedoya *et al.* (2019), which applied a similar methodology as it was used in this study, and Escobedo-Galván *et al.* (2015) which used traditional morphometry. These two subspecies showed a similar skull shape, but they differed in other morphological characteristics analyzed here. They are also distributed in different geographical regions with diverse ecological conditions.

The analysis of skull elements in *C. crocodilus* highlight the importance of studying morphological changes and patterns to distinguish subspecies (Table 5). Differences in skull morphology have been widely studied, due to its application in the taxonomic and systematic study of crocodylians (Mook, 1921; Brochu, 1999, 2001; Pierce *et al.*, 2008; Clarac *et al.*, 2016; Fernandez Blanco *et al.*, 2018; Foth *et al.*, 2018). In this study, we could see that the contact between the frontal and nasal bones allows us to distinguish trans-Andean subspecies. In *C. c.*

chiapasius specimens, the two bones were separated but in *C. c. fuscus* specimens, the two bones were in contact (Table 5).

On the other hand, cis-Andean subspecies also showed variation in the contact between frontal and nasal bones. In the adult forms of *C. c. apaporiensis*, the frontal and nasal bones were separated (Table 7), which is a diagnostic cranial character for this subspecies. However, in *C. c. crocodilus*, both conditions were documented in specimens from the Orinoco and western Amazon populations, with the east Amazon populations tending to have frontal and nasal bones in contact (Fig. 6; Table 8). This geographic pattern is in accordance with Jiménez (2016), who used molecular markers to propose the existence of two clades for *C. c. crocodilus* in Colombia, the western one in the Orinoco region and the Andean piedmont and the eastern one in the Amazon region. This classification is also supported by Roberto *et al.* (2020), who actually reported three lineages for the

Table 8. Geographic and ontogenetic variation in *C. c. crocodilus*. Frontal-Nasal bones: FN (in contact); F-N (no contact). Ventral premaxillary-maxillary suture shape: U (U-shaped); V (V-shaped); J (J-shaped); H (almost horizontal). Palatine process: as long as the base width (1X), twice as long as the width of the base (2X), three times longer than the width of the base (3X), four times longer than the width of the base. Unidentified (?).

Subspecies	Region							
	Orinoco				Amazon			
	Casanare	Meta	Caquetá	Putumayo	Guaviare	Guainía	Vaupés	Amazonas
Frontal-Nasal bones contact	Hatchling (1)		1FN					
	Juvenile (23)	1FN	12FN 3F-N	1FN		1F-N	4FN	1FN
	Subadult (22)	1FN	11FN 5F-N 1?	2FN	1F-N	1FN		
	Adult(16)		5FN 6F-N			1FN	4FN	
Ventral premaxillary-maxillary suture shape	Hatchling (1)		1H					
	Juvenile (23)	1?	1H 8U 2J 4V	1V		1V	3U 1V	1U
	Subadult (22)	1U	3H 9U 5J 1V			1U 1V	1U	
	Adult(16)		3H 6U 2V			1U	1H 2U 1J	
Palatine process length	Hatchling (1)		1(1x)					
	Juvenile (23)	1(2x)	3(1x) 12(2x)	1(2x)		1(1x)	4(2x)	1(2x)
	Subadult (22)	1(1x)	4(1x) 9(2x) 4(3x)	2(2x)	1(2x)		1(2x)	
	Adult(16)		2(1x) 3(2x) 6(3x)			1(3x)	4(3x)	

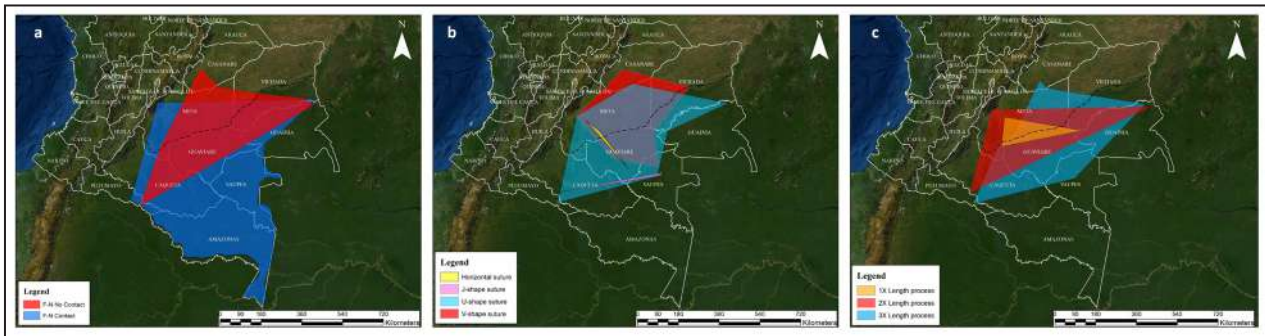


Figure 6. Geographic distribution of the characters in *C. c. crocodilus* in Colombia. (a). Frontal-Nasal contact. (b). Premaxillary-maxillary suture shape. (c). Palatine process length. Discontinuous line in the maps divide Orinoco (northern) and Amazon (southern) regions.

Amazon and Orinoco regions, forming *C. crocodilus sensu stricto*.

A similar pattern of variation was observed in the shape of the ventral premaxillary-maxillary suture. Cis-Andean *C. c. crocodilus* showed four different shapes for this characteristic, the U-shaped suture being the most common. In contrast, *C. c. apaporiensis* showed a V-shaped suture in adults, providing a new characteristic to distinguish this subspecies from *C. c. crocodilus*, along with the characteristics described by Escobedo-Galván *et al.* (2015). Conversely, the trans-Andean subspecies *C. c. chiapasius* and *C. c. fuscus* share a U-shaped

suture, which could be associated with a morphological change from longirostrine skulls in cis-Andean subspecies to brevirostrine skulls in trans-Andean subspecies (Venegas-Anaya *et al.*, 2008; Jiménez, 2016). It is important to examine differences in diet between the subspecies, as different morphologies may represent local adaptations to prey items and postnatal dietary shifts (Ayarzagüena, 1984; Monteiro and Soares, 1997).

Cis-Andean subspecies show enormous variation in the length/width ratio of the palatine process (Table 5). However, in trans-Andean subspecies, we found that *C. c. chiapasius* differs from *C. c. fuscus*

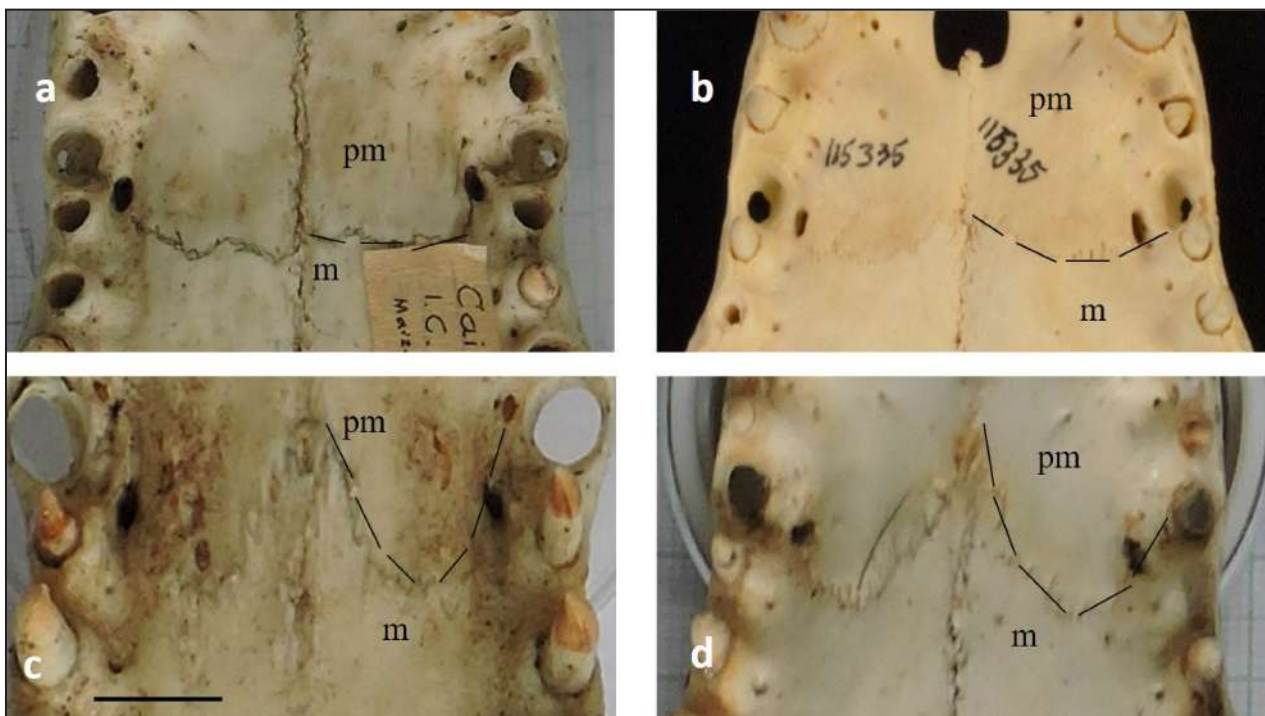


Figure 7. Ventral premaxillary-maxillary suture shape. (a). Almost horizontal suture in *C. c. crocodilus* (ICN 1813); (b). U-shaped suture in *C. c. chiapasius* (USNM 115335); (c). V-shaped suture in *C. c. apaporiensis* (ICN 8730); (d). J-shaped suture in *C. c. crocodilus* (ICN 8825). Abbreviations: m, maxilla; pm, premaxilla. Scale bar equals 1 cm.

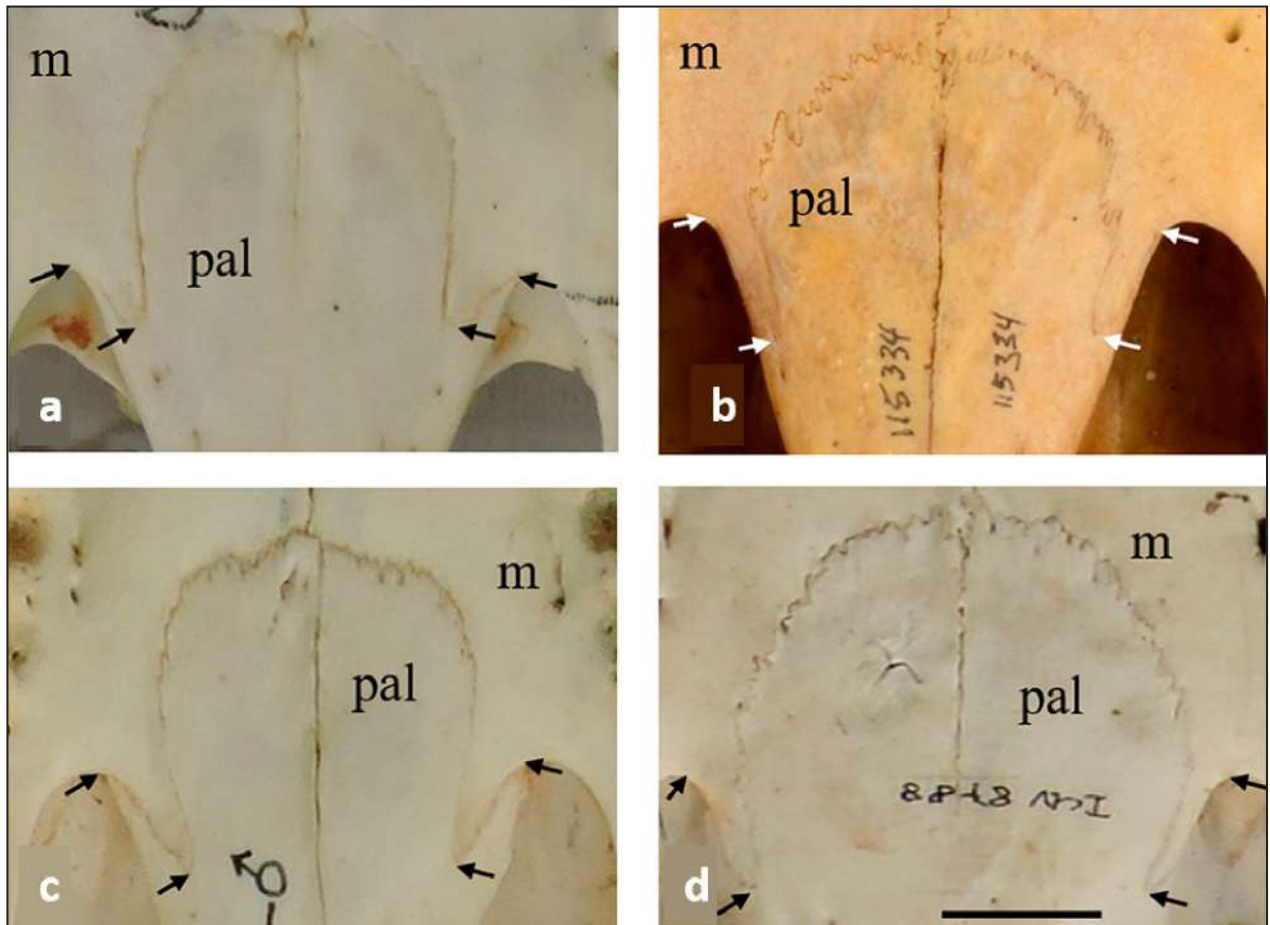


Figure 8. Palatine process of the maxilla in ventral view, arrows show the anterior and posterior portion of the process for each subspecies. (a) *C. c. fuscus* (ICN 1834). (b) *C. c. chiapasius* (USNM 115334). (c) *C. c. apaporiensis* (ICN 8738). (d) *C. c. crocodilus* (ICN 8788). Abbreviations: m, maxilla; pal, palatine. Scale bar equals 1 cm.

in the palatine process. *C. c. chiapasius* has a process three times longer than the base width, while *C. c. fuscus* has a process one or two times longer than the base width.

The three cranial characteristics examined in this study showed minimal variation across the geographic distributions for *C. c. apaporiensis* and *C. c. fuscus*. However, there was a lot of variation for Colombian populations of *C. c. crocodilus*, (Fig. 6; Table 5), which could be in accordance with the wide genetic variation reported for the populations throughout Amazonia, vicariant events of dispersion, and/or different hybridization processes with *C. yacare* (Brazaitis *et al.*, 1998; Farias *et al.*, 2004; Vasconcellos *et al.*, 2006; Hrbek *et al.*, 2008; Jiménez, 2016; Roberto *et al.*, 2020). Therefore, morphological and genetic variation could reveal hidden speciation patterns, similar to those of other alligatorid species in Amazonia (Vasconcellos *et al.*, 2008; Muniz *et al.*, 2017; Bittencourt *et al.*, 2019).

C. c. crocodilus specimens showed significant variation in the three characters throughout its postnatal development (Table 8), which has already been reported for *C. yacare* and *C. latirostris* (Fernandez Blanco *et al.*, 2018) and other crocodylians (Brochu, 1999; Watanabe and Slice, 2014). Therefore, we recommend considering cranial morphological variation during ontogeny to distinguish crocodylian subspecies because, ontogenetic changes in the skull could reveal important anatomical differences, useful for taxonomic classification.

Despite Busack and Pandya's (2001) proposal for maintaining *C. crocodilus* as a unique taxonomic entity (i.e., discouraging the division into subspecies), our results show enough skull morphological differences between the four *C. crocodilus* subspecies, supporting the findings reported by Venegas-Anaya *et al.* (2008), Escobedo-Galván *et al.* (2015), Jiménez (2016), and Angulo-Bedoya *et al.* (2019). Therefore, we argue that morphological analyses of the skull in

C. crocodilus can provide useful information for the taxonomic division of the subspecies.

These morphological analyses reveal that *C. c. apaporiensis* has a different skull shape and other skull elements (i.e., the separation between the frontal and nasal bones; the form of the premaxillary-maxillary suture in ventral view) that distinguish this subspecies from the others in the *C. crocodilus* complex. As in other crocodylians, those differences could be related to geographic distribution and diet (Ayarzagüena, 1984; Muniz *et al.*, 2017; Bittencourt *et al.*, 2019). However, Balaguera-Reina *et al.* (2020) proposed that *C. c. apaporiensis* is not a distinct subspecies from *C. c. crocodilus*, based on mitochondrial DNA. McCurry *et al.* (2017) analyzed the convergent evolution of longirostrine skulls and found that species with riparian habits eat mostly fish and small prey. They also suggested a scenario where biomechanical constraints had shaped the evolution of those ecomorphological patterns, as reported by Fernandez Blanco *et al.* (2018) for *C. yacare* and *C. latirostris*. Thus, the anatomical, ecological, and geographical peculiarities of *C. c. apaporiensis* should be considered in future systematic analysis and conservation policies.

In conclusion, although trans-Andean subspecies *C. c. chiapasius* and *C. c. fuscus* showed a similar skull shape, with a brevirostrine snout and a similar ventral premaxillary-maxillary suture shape, they differ in frontal-nasal contact and length of the palatine process, characters that may be useful in their distinction as taxonomic units. Additionally, all populations with a trans-Andean distribution in Colombia correspond to *C. c. fuscus*. Although cis-Andean subspecies present longirostrine skulls, additional characters support the taxonomic identity for *C. c. apaporiensis*. Variation in the skull characters of *C. c. crocodilus* supports the hypothesis that there are at least two clades in its distribution in Colombia. Our data on skull morphology, ontogeny, and geographic variation provide support for the recognition of *C. crocodilus* subspecies and highlights the importance of an evolutionary perspective in conservation policies, especially in a region with serious conservation challenges.

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Appendix I

***Caiman crocodilus apaporiensis*. ICN.** Colombia: Vaupés: 8669; 8680; 8684; 8690; 8693; 8694; 8701; 8702; 8703; 8705; 8706; 8710; 8712; 8720; 8724; 8727; 8730; 8731; 8732; 8735; 8736; 8738; 8740; 8741; 8743; 8746; 8747; 8750; 8752; 8754;

8762; 8766; 8778; 8779; 8824; 8826; 8827; 8839; 8864; 12393; 12395; 12399; 12400; 12404.

***Caiman crocodilus chiapasius*. USNM.** México: Chiapas 115334; 115335; 115336.

***Caiman crocodilus crocodilus*. ICN.** Colombia: Amazonas: 8836. Caquetá: 8818; 8825. Casanare: 8798; 8840. Guainía: 8880. Guaviare: 8790; 8822. Meta: 1782; 1786; 1788; 1789; 1790; 1791; 1793; 1796; 1813; 1819; 1825; 1826; 1829; 1835; 1836; 1837; 8726; 8794; 8800; 8808; 8811; 8814; 8817; 8819; 8838; 8841; 8842; 8845; 8846; 8847; 8858; 8860; 8862; 8872; 8877; 8884; 8897; 12383; 12390; 12398; 12401; 12402; 12403; 12416; 12418; 12419. Putumayo: 8815. Vaupés: 8681; 8793; 8801; 8813; 8830; 8869; 12394.

***Caiman crocodilus fuscus*: ICN.** Colombia: Bolívar: 1834; 8771; 8849; 8856. Caldas: 1856. Cauca: 8685; 8688; 8689; 8691; 8699; 8707; 8708; 8709; 8711; 8716. Chocó: 1784; 1785; 1798; 1811; 1822; 1843; 1844; 1845; 1846; 1847; 1855; 8799; 8857; 8870; 8873; 12384. Córdoba: 1797; 1814; 1821; 1823; 1827; 1828; 1832; 1833; 1838; 8700; 8756; 8802; 8823; 8863; 8867; 8871; 8883; 8886; 12389. Magdalena: 8821. Tolima: 12385.

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