Zoomorphology (2019) 138:387–397
https://doi.org/10.1007/s00435-019-00448-2

ORIGINAL PAPER

Unveiling the cryptic morphology and ontogeny of the Colombian *Caiman crocodilus:* a geometric morphometric approach

Mónica Angulo-Bedoya[1] · **Santiago Correa**[1] · **Hugo A. Benítez**[2]

Received: 7 February 2019 / Accepted: 30 April 2019 / Published online: 9 May 2019

Abstract

Caiman crocodilus is an alligatoroid broadly distributed in the neotropics from Mexico to Brazil, where Colombia is the only country that has the complete subspecies complex distributed in its territory. This species has been the focus of many genetic, ecological and morphological studies. However, these studies are limited to traditional morphology methods or have limitations to examine interspecific variation among the four subspecies reported in Colombia. This is the first study of intraspecific variation in the skull of *Caiman crocodilus* complex distributed in Colombia, using a two-dimensional approach of geometric morphometric on 122 post-hatching ontogenetic cranial series. Morphological differences between species and changes during ontogeny (snout increases its length and, skull roof and orbits decrease their proportions) that represents part of morphological changes in the cranial ontogeny of crocodilians were found. In the morphospace, there was a significant differentiation of *C. crocodilus apaporiensis* and *C. crocodilus crocodilus* from *C. crocodilus fuscus* and *C. crocodilus chiapasius*. Results from this study revealed that *C. crocodilus apaporiensis* is a differentiated group from the global complex as well as that the specimens of *C. crocodilus chiapasius* collected from Medem in Colombia may be showing cryptic morphology in some traits.

Keywords Geometric morphometrics · *Caiman crocodilus* · Colombian biodiversity · Cranial variation · Ontogeny

Introduction

The most geographically variable crocodilian species in the Neotropical region is *Caiman crocodilus* Linnaeus 1758, a species extensively distributed from Mexico to Brazil. This species has four recognized subspecies systematically distributed in this region; nonetheless the entire complex has been reported to inhabit exclusively Colombia: *Caiman crocodilus fuscus* Cope 1868, in the Caribbean and Magdalena basins; *Caiman crocodilus chiapasius* Bocourt 1876, on the Pacific side; *Caiman crocodilus crocodilus* Linnaeus 1758, all across the Amazonas and Orinoco; and *Caiman crocodilus apaporiensis* Medem 1955, apparently endemic of the Apaporis River region (Amazon basin) (Medem 1955, 1960, 1981). A variety of morphometric divergences of the *Caiman crocodilus* complex in Colombia might be explained because of the country geographical barriers such as the Andean Mountains (Fig. 1) (Busack and Pandya 2001).

Surveys of the Apaporis River caiman were taken back in the 1950's and individuals where only present in the upper and middle Apaporis River, and some adjacent areas. In 1969 a different species from *Caiman crocodilus apaporiensis* was found inhabiting this territory, thus it is believed that this subspecies might be hybridized (Medem 1955, 1971). Another survey at similar places was taken between 1994 and 1997 where the researchers found 497 crocodilian specimens but only 42 were suspected of being the Apaporis River caiman (Rodríguez Melo 2000).

Although taxonomic classification of this species complex is based predominantly on morphological characters—linear measurements of the skull, scute pigmentation and scalation—there is not a consensus between these studies on the presence and distribution of this species in the

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00435-019-00448-2) contains supplementary material, which is available to authorized users.

✉ Hugo A. Benítez
hbenitez@uta.cl

[1] Engineering Faculty, Universidad EAFIT, Medellín, Colombia

[2] Departamento de Biología, Facultad de Ciencias, Universidad de Tarapacá, Velasquez 1775, Arica, Chile

Fig. 1 Geographical distribution of the *Caiman crocodilus* complex in Colombia

Colombian territory (Busack and Pandya 2001; Velasco et al. 2010; Morales-Betancourt et al. 2013; Escobedo-Galvan et al. 2015). Furthermore, mtDNA analyses have shown that *C. crocodilus* complex is more diverse than previous studies revealed (Venegas-Anaya et al. 2008). Unfortunately, this genetic study lacks an adequate number of specimens collected in Colombia, leaving some uncertainty about the presence or absence of some subspecies in this territory.

Geometric morphometrics (GM) is a powerful tool for taxonomic identification and functional analyses (Amavet et al. 2009; Fernandez Blanco et al. 2018; Foth et al. 2019). GM measures differences in shape among skulls using homologous landmark localizations, outlines, and semi-landmarks, among others; that captures relevant information about shape variability and it has the ability to describe evolutionary and genetic effects on morphological shape (Klingenberg 2010). Furthermore, morphological data and morphological patterns may provide a baseline when genetic information is not available, mainly in fossils and cryptic species (Böhmer et al. 2015). Although morphological comparisons of the *Caiman crocodilus* head and skull have been performed (Monteiro and Soares 1997; Busack and Pandya 2001; Escobedo-Galvan et al. 2015), there are serious limitations of these studies as they used traditional morphometrics (linear measurements, angles). This approach does not quantify an organism complete shape and the measurements are often analyzed as independent of one another even though they are all part of the same structure. Such data sets contain relatively little information about the shape and some of them are unclear. Moreover, some of the information that is necessary for morphological analysis is missing from this type of measurement system (Zelditch et al. 2012; Cooke and Terhune 2015; McNulty and Vinyard 2015).

In spite of the several previous studies of skull analysis and intraspecific variation, evolution and morphology of extant crocodilians (Iordansky 1973; Medem 1981; Busbey 1995; Monteiro and Soares 1997; Brochu 1999; Sadlier and Makovicky 2008), there are insufficiency morphology studies and there are not enough data available because most of the osteological herpetological collections are outside South America (Foth et al. 2015).

Medem (1981) published a research compilation of 30 years studying Colombian crocodilians. In his book, he detailed diet, distribution, taxonomic descriptions and the ecology of the *Caiman crocodilus* complex. During his expeditions, Medem collected more than 480 specimens of the four subspecies of *Caiman crocodilus* and deposited most of the osteological samples at the Field Museum of Natural History (FMNH) in Chicago, USA.

The main goal of this study is to describe and quantify the intraspecific skull morphological variation in the *Caiman crocodilus* complex, evaluating those areas possibly significant to systematics and morphological changes during ontogeny. For that purpose, a two-dimensional approach of geometric morphometrics were conducted on three different views: cranium dorsal and ventral views, and mandible dorsal view; on post-hatching ontogenetic series. In addition, we included three more species of the Alligatoridae family to test the validity of currently recognized subspecies.

By analyzing exclusively, the specimens collected in Colombia and deposited by Medem at FMNH, we have the original assignation of each specimen to the taxonomic categories by the same researcher criteria. Then, we intend to perform the first study including exclusively Colombian specimens, of the intraspecific variation of the skull of *Caiman crocodilus* subspecies using geometric morphometric approaches.

Materials and methods

Specimen sampling

Crania skulls of 122 Colombian specimens were used including the four subspecies of the *Caiman crocodilus* complex (*Caiman crocodilus crocodilus*, *Caiman crocodilus fuscus*, *Caiman crocodilus chiapasius* and *Caiman crocodilus apaporiensis*) and three outgroup species *Paleosuchus trigonatus*, *Paleosuchus palpebrosus* and *Caiman yacare*, all of them belonging to the Alligatoridae family. Skulls are deposited at FMNH in Chicago, USA, which owns the largest collection of *Caiman crocodilus* skulls from Colombia in the world; and six specimens of *Caiman crocodilus apaporiensis* are housed in "Senckenberg, Forschungsinstitute und Naturmuseen" in Frankfurt, Germany (Supplementary Table S1).

From the total of specimens: 9 of *C. c. crocodilus*; 30 of *C. crocodilus fuscus*; 51 of *C. crocodilus chiapasius*; 24 of *C. crocodilus apaporiensis*; 3 of *P. trigonatus* and *P. palpebrosus*, and 2 of *C. yacare* were included in the analysis.

Specimen information is based on collection data and historical notes (Medem 1981), and age was calculated according to Medem (1981), based on head and body measurements. *Caiman crocodilus* complex specimens with a Snout-Vent Length $\mathrm{SVL} \leq 75$ cm were assessed as juveniles; $75\ \mathrm{cm} < \mathrm{SVL} > 120$ cm were assessed as subadults, and $\mathrm{SVL} \geq 120$ cm as adults. *Paleosuchus* spp specimens with $\mathrm{SVL} \leq 70$ cm were considered as juveniles, $70\ \mathrm{cm} < \mathrm{SVL} > 130$ cm were considered as subadults, and $\mathrm{SVL} \geq 130$ cm as adults (Medem 1981). Both *Caiman yacare* specimens were adults (Supplementary Table S1).

Morphometric data

The 122 skulls were analyzed using a two-dimensional geometric morphometric approach. Dorsal and ventral views were used for the cranium (upper jaw), and dorsal view for the mandible. Specimens with incomplete views were not used to avoid missing landmarks (Supplementary Table S1). Skull shape was taken using 40 (cranium, dorsal view), 35 (cranium, ventral view) and 16 (mandible, dorsal view) landmarks. (Figure 2—See Supplementary Table S2, S3 for full description of landmarks). Landmarks were digitized using the software tpsDig2 (Rohlf 2017). All the morphometric analyses were performed using MorphoJ software, version 1.06d (Klingenberg 2011). The *Paleosuchus* spp. landmarks 9, 10, 11, 12, 15 and 16 were over located on the right/left same midpoint (joined suture between parietal, squamosal and postorbital as the supratemporal fenestra is enclosed by these three bones), as the specimens included in this study lack a fully developed supratemporal fenestra.

Each landmark configuration was superimposed using a generalized procrustes analysis (Rohlf and Slice 1990) to remove non-shape variation caused by size, orientation and scale. This procedure standardizes the sample by translating, scaling and rotating it to a unit centroid size (Dryden and Mardia 1998). To discard problems at the digitizing procedures, a measurement error was analyzed where the complete dataset was re-digitized and analyzed using Procrustes ANOVA. A Principal Component Analysis (PCA) was performed using the covariance matrix of the skull shape individual to simulate the shape space and their scatterplot was performed to analyze shape raw variation.

Ontogenetic analysis

With the purpose of observing shape changes related to ontogenetic changes in skull shape, a multivariate regression was completed using the centroid size as an independent variable and shape as a dependent variable. If an ontogenetic signal is present, then a statistical relationship between centroid size and shape should be measurable. A statistical test of permutation with 10.000 rounds was performed to calculate the significance of the ontogenetic allometry in the data (Drake and Klingenberg 2008).

Since age can modify the results of the previous PCA data, a covariance matrix of regression residuals was performed to use the data without the allometric influence.

Results

The Procrustes ANOVA for the measurement error showed that the mean square for individual variation is bigger than the amount of error for the three views: upper jaw (cranium) dorsal (0.0001046840 > 0.0000045264), upper jaw ventral 0.0000550731 > 0.0000016696), and lower jaw dorsal (0.0001463042 > 0.0000023716), indicating that this error is negligible.

Upper jaw dorsal view (UJD)

The PCA of the variation in the upper jaw for the dorsal view between taxa, uncorrected for size, showed that 70.96% of the total variation is explained by the first three

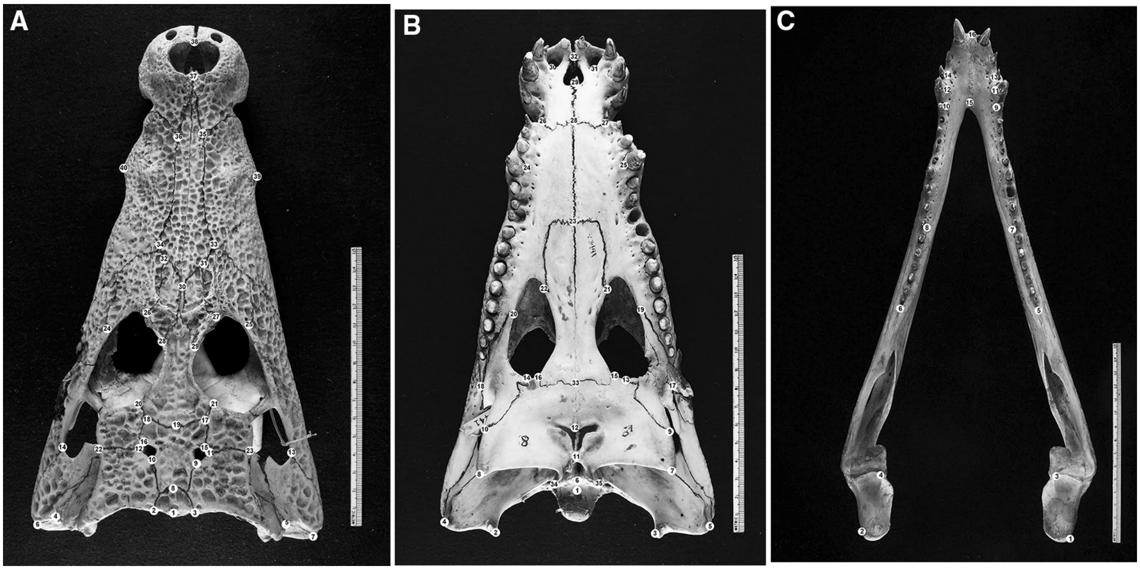

Fig. 2 Landmarks used in this study (See Supplementary Table 2 and Supplementary Table 3 for details) shown on cranial specimens from the FMNH, Chicago, USA. **a** Upper jaw dorsal view (FMNH 73685); **b** upper jaw ventral view (FMNH 73685); and **c** lower jaw dorsal view (FMNH 69831)

PCs (PC1 = 47.9%; PC2 = 15.99%; PC3 = 7.04%). The first PC axis changes across the relative width of the snout, the relative size and position of the orbit influencing the relative length of the nasal and the cranium; the parietal width and length, the relative width of the skull roof table and the change of the angle from the orbit along the jugal edge in a posterolateral direction. The second PC axis is mainly associated with the length of the snout and the width of the orbit influencing the total width at the most posterior point of the quadratojugal-quadrate (Fig. 3).

Upper jaw ventral view (UJV)

The variation in the upper jaw for the ventral view between taxa, uncorrected for size, showed that 67.24% of the total variation is explained by the first three PCs (PC1 = 36.10%; PC2 = 22.91%; PC3 = 8.24%). The first PC axis is mostly associated with the relative width of the suborbital fenestra, influencing the length and width of the lateral margin of the cranium with changes in the relative width between both fourth cranium teeth. There are also changes on the relative length of the infratemporal fenestra at the tip of the snout; and the shape and width of the pterygoid. The second PC axis mainly explains changes on the relative length and width on the pterygoid, influencing the length and position of the quadrate. The relative length of the choana in an anteroposterior direction, the relative distance between the most posterior point of the choana and the eustachian foramen, and the relative length or presence of the pterygoid flanges posterior to the choana can also be explained by the second PC axis (Fig. 4).

Lower jaw, dorsal view (LJ)

The PCA of the variation in the lower jaw for the dorsal view between taxa, uncorrected for size, showed that 84.4% of the total variation is explained by the first three PCs (PC1 = 45.3%; PC2 = 29.8%; PC3 = 9.1%). The first PC axis is associated with the relative width between the articular, splenial and dentary influencing the total length of the dentary, and the relative shape and width between both of foramen aërum. The second PC axis explains shape and relative length of the dentary influencing the relative width of the dentary, the relative length from the splenial-dentary

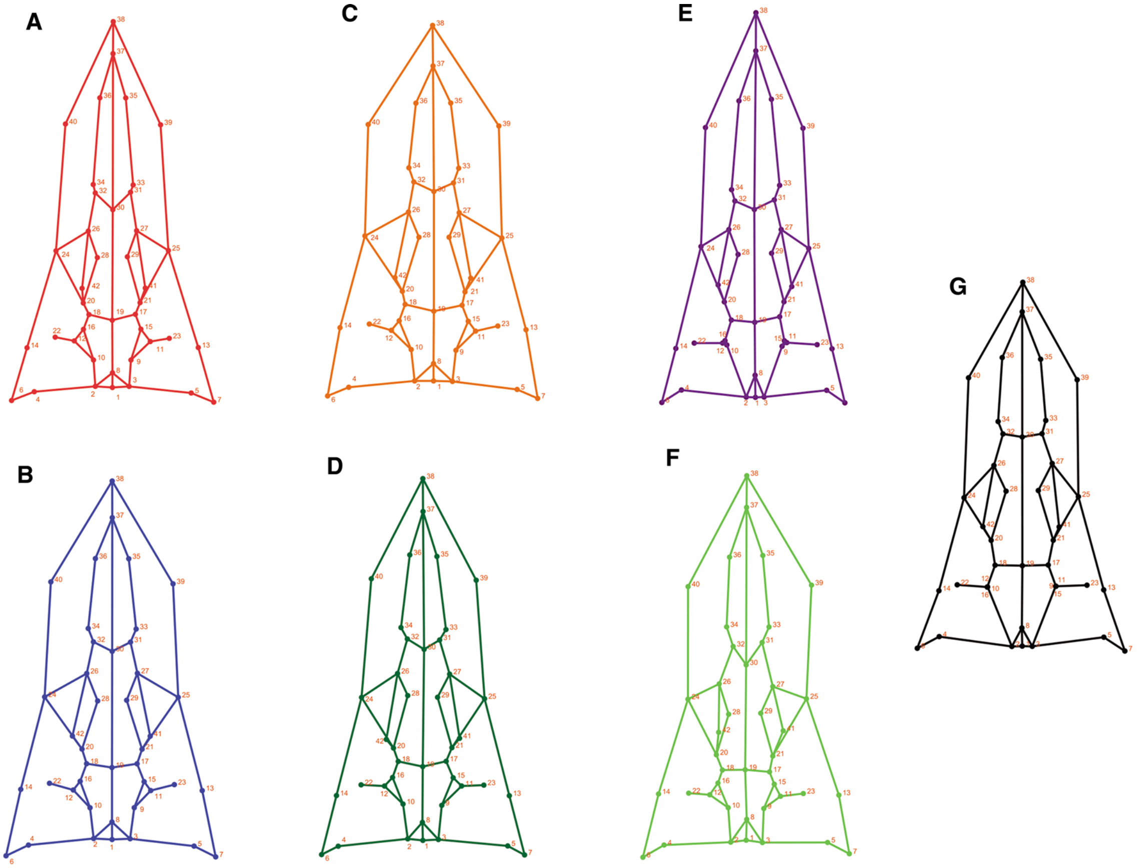

Fig. 3 Wireframe representation of the average cranial shape variation and their corresponding landmarks for the upper jaw dorsal view. **a** *Caiman crocodilus apaporiensis* (red), **b** *Caiman crocodilus chiapasius* (blue), **c** *Caiman crocodilus fuscus* (orange), **d** *Caiman crocodilus crocodilus* (green), **e** *Paleosuchus trigonatus* (purple), **f** *Caiman yacare* (light green), **g** *Paleosuchus palpebrosus* (black)

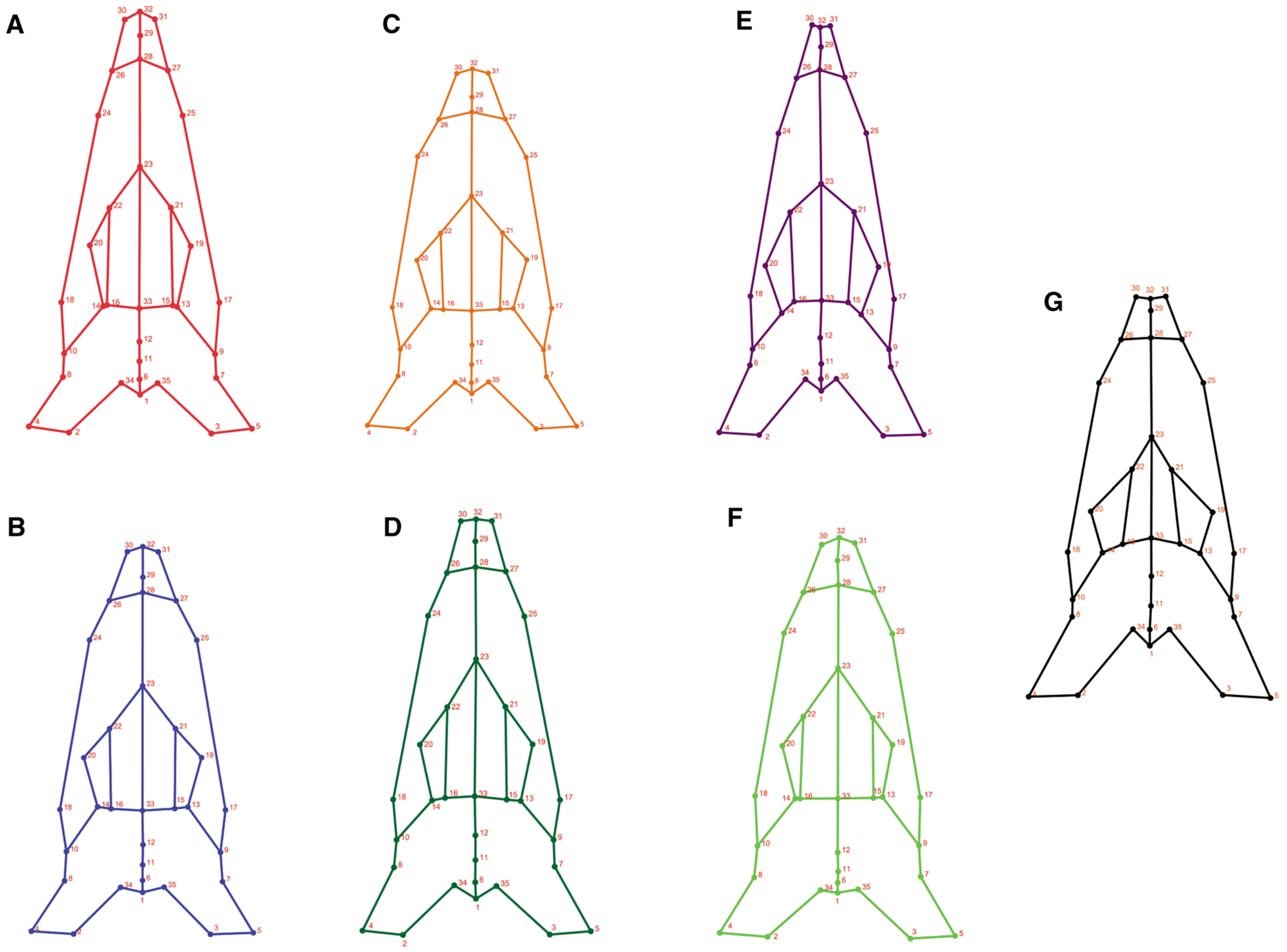

Fig. 4 Wireframe representation of the average cranial shape variation and their corresponding landmarks for the upper jaw ventral view. **a** *Caiman crocodilus apaporiensis* (red), **b** *Caiman crocodilus chiapasius* (blue), **c** *Caiman crocodilus fuscus* (orange), **d** *Caiman crocodilus crocodilus* (green), **e** *Paleosuchus trigonatus* (purple), **f** *Caiman yacare* (light green), **g** *Paleosuchus palpebrosus* (black)

junction in an anteroposterior direction to the last alveolar midpoint (Fig. 5).

Ontogenetic analysis

The ontogenetic analysis showed a higher and significant relationship between the shape and CS, with a clear differentiation of the skull of juveniles, subadults and adults (Fig. 6). A positive allometry was noticeable for the three views, with a higher explanation of shape by allometry [UJD 35.7%, p value: <0.0001 (Fig. 6a). UJV 20.7%, p value: <0.0001 (Fig. 6b); LJ 24.1%, p value: <0.0001 (Fig. 6c)]. The influence of centroid size by ontogeny on the different skull views was eliminated from the analyses using the multivariate regression residual, and the PCA analyses were all corrected by size (Fig. 7), where the accumulated percentage of variation for the first three PCA decrease as follows: UJD 57.3% (Fig. 7a); UJV 62.4% (Fig. 7b); LJ 80.4%; (Fig. 7c).

Discussion

A geometric morphometric approach was used to investigate the variation in skull shape and ontogeny of the subspecies of *Caiman crocodilus* and related species according to their distribution in Colombia. The power of this technique was useful to corroborate the presence of morphotypes for the Colombian Caiman in three cranial views, describing a clear variation for *Caiman crocodilus* that may confirm the first taxonomic classification results proposed by Medem (1981).

Comparing the cranial morphospace was possible to distinguish two clear point clouds that represents the two genera *Caiman* and *Paleosuchus*. Observing the morphometric variation within the genus *Caiman*, another two large point clouds separate the species groups from their geographic history. The morphometrics structure in all views shows a notorious separation of *C. crocodilus apaporiensis* (separated point cloud at the right side in the three views—red dots)

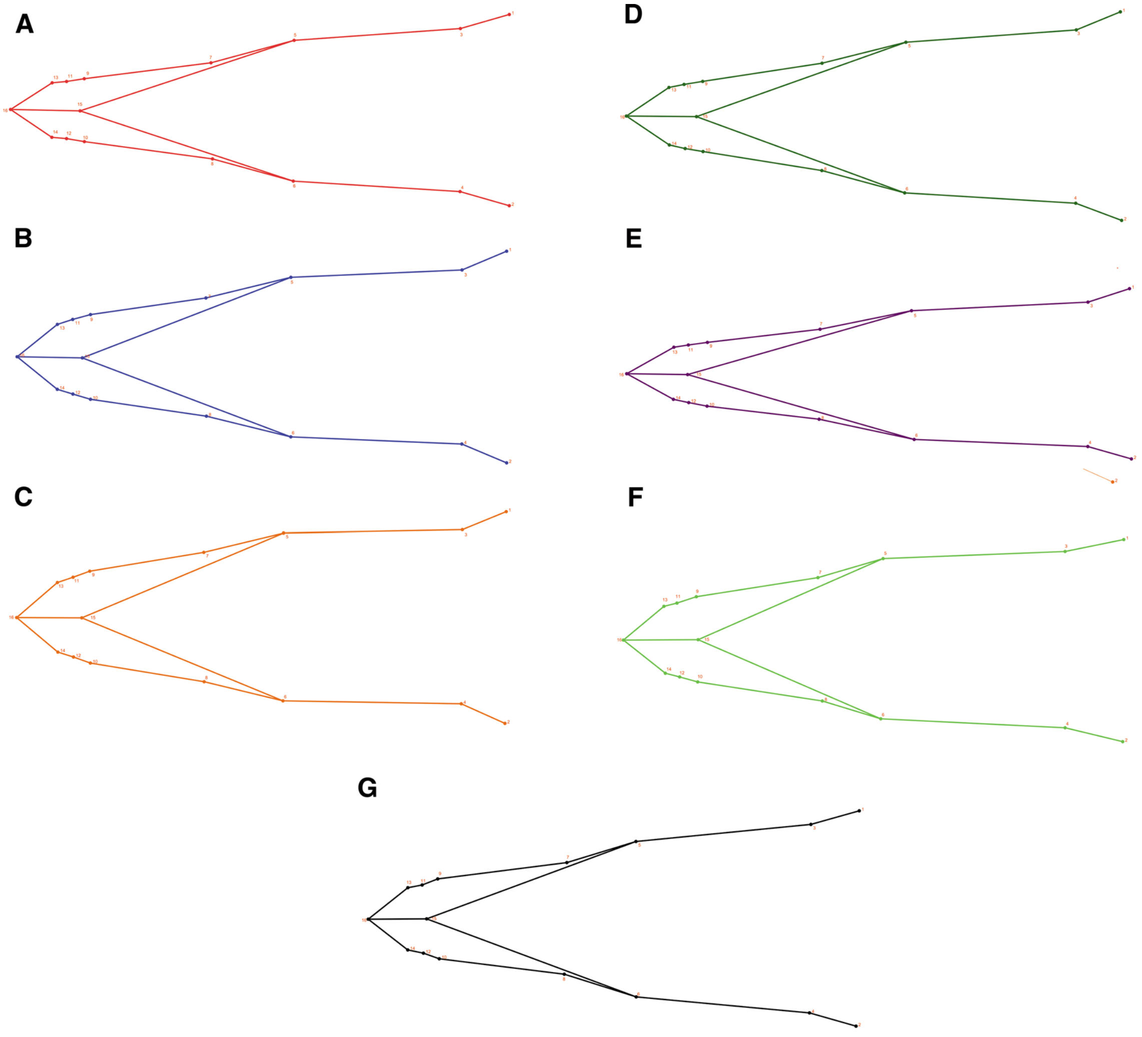

Fig. 5 Wireframe representation of the average cranial shape variation and their corresponding landmarks for the lower jaw dorsal view. **a** *Caiman crocodilus apaporiensis* (red), **b** *Caiman crocodilus chiapasius* (blue), **c** *Caiman crocodilus fuscus* (orange), **d** *Caiman crocodilus crocodilus* (green), **e** *Paleosuchus trigonatus* (purple), **f** *Caiman yacare* (light green), **g** *Paleosuchus palpebrosus* (black)

(Fig. 7). This subspecies was described by Medem as the last of the four subspecies described for the *C. crocodilus* complex (Medem 1955); however, its limited geographic distribution has clearly shown that it may be a different species and our results confirm those statements. The geographical isolation effects found on *C. crocodilus apaporiensis* are because it is spread only in the high areas of the Apaporis River, where water flows have strong currents that prevent them from migrate, especially the water fall called Raudal de Jirijirimo.

The second evident group includes the morphotypes at the left side of the morphospace, which is composed of the subspecies *C. crocodilus fuscus* and *C. crocodilus chiapasius*, which have generated deep controversy in literature caused by their close morphological similitude, and limited genetic evidence has caused that all of them are considered just as *C. crocodilus fuscus* (Busack and Pandya 2001; Venegas-Anaya et al. 2008). For this controversy, the morphometric analyses had interesting results, depicting a small differentiation between the groups in the LJ and UJD views, where the individuals have a small overlap between one another, evidencing a cryptic morphology where the small morphological differences previously analyzed could be detected based on their cranial geometry, and this differentiation does not have external influences associated with them (e.g. centroid size). For UJV, the differentiation was less evident, with a larger overlap between individuals.

Singular cases can be observed in the other subspecies groups studied, where *C. crocodilus crocodilus* repeats a cranial shape behavior for the different views, that is located between these two large species groups previously described but keeping a single morphological identity that maintains them apart from all the groups previously mentioned. These specimens are spread below the eastern mountain range

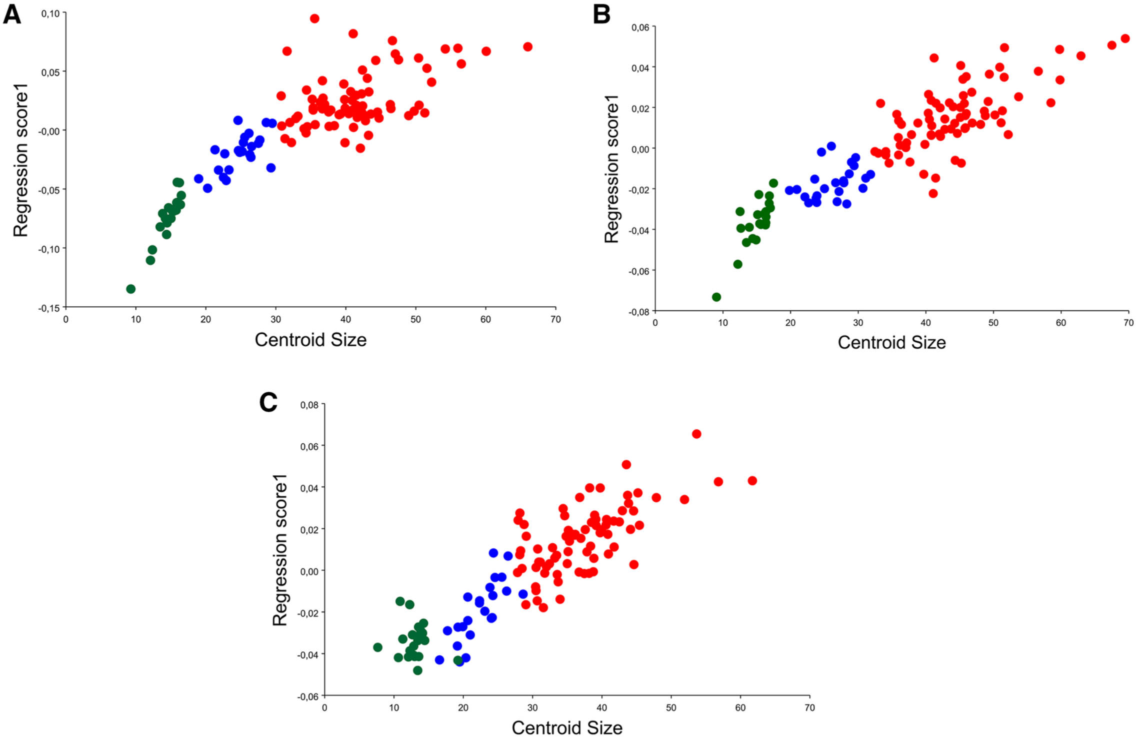

Fig. 6 Analysis of multivariate regression of the procrustes coordinates versus centroid size. Juveniles (green), subadults (blue), adults (red), **a** upper jaw dorsal view; **b** upper jaw ventral view; and **c** lower jaw dorsal view

towards the Amazon and are more clearly separated from *C. crocodilus fuscus*, which is spread throughout the Magdalena river towards the Atlantic coast.

The geologic history of the Andes mountain range in Colombia may have had a strong influence in the isolation of this subspecies, and with their morphological adaptation. This can be directly observed in the point groups of the three PCs views for the skull, where the main differences are observed between a first group of "*C. crocodilus apaporiensis* and *C. crocodilus crocodilus*" and a second group compound by "*C. crocodilus fuscus* and *C. crocodilus chiapasius*". The major isolation may come from the mountain range formation, where the groups *C. crocodilus fuscus* and *C. crocodilus chiapasius* became isolated in the north cross section to the east of the country, and the other two subspecies would have stayed below the eastern mountain range.

Relatively few studies about cranial shape of the species *C. crocodilus* have been reported in literature (Monteiro et al. 1997; Busack and Pandya 2001; Escobedo-Galvan et al. 2015). However, those studies have had some limitations in their sampling geographically, statistically and in the experimental design, which have weakened their impact of the conclusions on the morphologic differences between the subspecies. The first morphological description of the species *C. crocodilus* referenced as *Jacare sclerops* was made in 1921, by recording nine measures of the cranium of seven specimens from five museums in the US (Mook 1921). Those cranial measurements were not compared between individuals or statistically processed. The second cranial morphology study was conducted with nine measurements on the subspecies *C. crocodilus apaporiensis* (Medem 1955). Unfortunately, the measures reported are only from one specimen (the holotype FMH69812) and the study does not compare them morphologically to other species or subspecies in the area. Subsequently, in 2001, there was a study that intended to compare the cranial morphology of the species *Caiman crocodilus* and *Caiman yacare*, taking linear measures from more than 35 specimens maintained in alcohol (Busack and Pandya 2001). That study found significant differences between both species but did not mention differences among the subspecies of *C. crocodilus* and the specimens evaluated were mainly from outside Colombia. Nine years later, Velasco et al. (2010) published the ecology, natural history and conservation of *C. crocodilus*, confirming the geographical distribution originally stated in 2001, paving the road for Escobedo-Galvan et al. (2015) team, whom using conventional morphometrics of the cranium tried to cover the weaknesses of the article by Busack and Pandya (2001), by including the four subspecies. Escobedo-Galvan et al. (2015) results suggested that the geographic isolation may have given rise to this morphologic separation of the *C. crocodilus* complex, where they found some differences

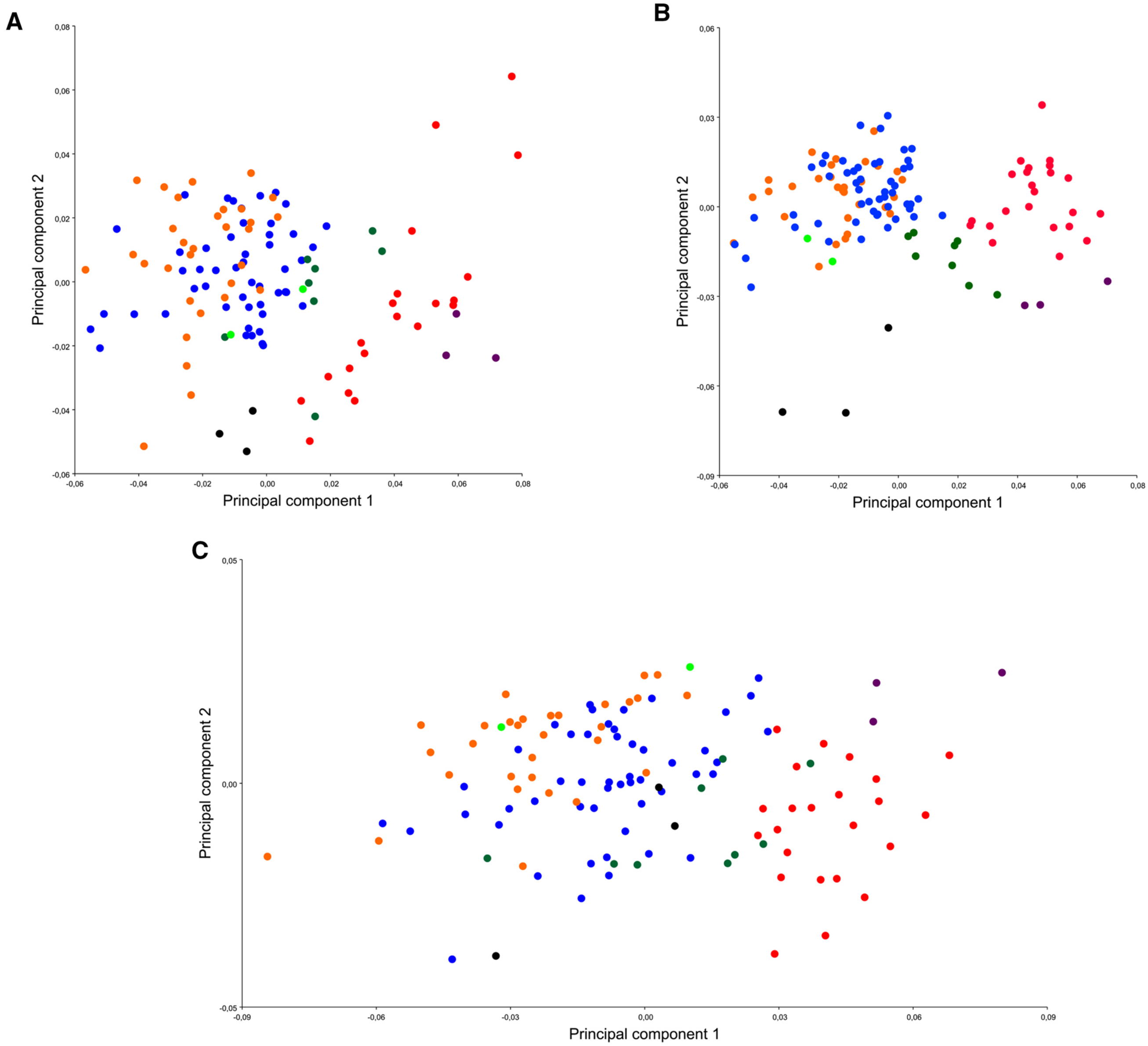

Fig. 7 Scatterplot of the Principal Component Analysis showing a two-dimensional cranial morphospace using the residuals of the multivariate regression (corrected by size). **a** Upper jaw dorsal view; **b** upper jaw ventral view; and **c** lower jaw dorsal view. Species used in this study are represented by different colors: *Caiman crocodilus apaporiensis* (red), *Caiman crocodilus chiapasius* (blue), *Caiman crocodilus fuscus* (orange), *Caiman crocodilus crocodilus* (green), *Paleosuchus trigonatus* (purple), *Caiman yacare* (light green), *Paleosuchus palpebrosus* (black)

between *C. crocodilus apaporiensis* and *C. yacare;* all these data were confirmed, and the differences completely justified in our results with cranial geometric morphometrics.

From the ontogenetic standpoint, our results showed a clear positive allometry were the effect from size is apparent in the different ontogenetic stages of the analyzed specimens. However, the ontogenetic traits are clearly not having a direct influence on the cranium shape at the species level, but this trait was not a limitation to detect the morphometric variation exclusively in the cranium shape for the groups studied. Juveniles, subadults and adults were easily distinguished by means of multivariate regression of shape, depicting a clear association of size during growth periods. However, the cranial shape resulting from the ontogenetic variation would not have a strong influence as a descriptive trait. This statement can be confirmed with the results achieved by Watanabe and Slice (2014), using 3D geometric morphometrics where their analyses largely demonstrated a lack of significant phylogenetic signal, indicating that ontogenetic shape changes contain little phylogenetic information.

Thus, using geometric morphometrics as a tool to capture geometric information of structures, this research was, therefore, capable of provide valuable information to differentiate groups of the *C. crocodilus* complex, showing substantial evidence about the subspecies *C. crocodilus apaporiensis* as a group differentiated from the global complex mainly due to the isolation suggested by the environmental heterogeneity. However, despite the climatic differences, further investigation will be necessary to examine possible differences in the gene pools of these populations, to determine the genetic structure of all the *C. crocodilus* complex in Colombia and its relationship with morphology.

Acknowledgements We thank Alan Resetar, Joshua Mata and John Bates for their amazing support with this project. We also thank to the Senckenberg, Forschungsinstitute und Naturmuseen for their help. MAB is a PhD student thanks to the grant program No 647, 2014, from COLCIENCIAS, Colombia. This project was partially supported by a Field Museum of Natural History's Science Visiting Scholarship in 2018. HB thanks to the FONDECYT DE INCIACION No. 11180366 and Proyecto Redes de Investigación REDI170182 from CONICYT.

Author contributions MAB designed the study, collected the samples and performed morphometric measurements of sampled material and data analyses, MAB and HAB performed statistical analysis; MAB, SC and HAB wrote the manuscript; all authors contributed in improving the draft of the manuscript by adding valuable comments.

Funding This project was partially funded by a Science Visiting Scholarship from the Field Museum of Natural History; by FONDECYT DE INCIACION No. 11180366 and Proyecto Redes de Investigación REDI170182 from CONICYT.

Data accessibility The datasets generated during the current study are going to be available in the [name] repository, [Persistent web link to datasets]. Details with the link will be added upon acceptance of publishing.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No live animals were used in this study. The Field Museum of Natural History allowed MAB to use their collection for this project.

References

Amavet P, Vilardi JC, Rosso E, Saidman B (2009) Genetic and morphometric variability in caiman latirostris (broad-snouted caiman), reptilia, alligatoridae. J Exp Zool Part A Ecol Genet Physiol 311:258–269. https://doi.org/10.1002/jez.523

Böhmer C, Rauhut OWM, Wörheide G (2015) Correlation between Hox code and vertebral morphology in archosaurs. Proc R Soc B Biol Sci 282:20150077

Brochu CA (1999) Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. J Vertebr Paleontol 19:9–100. https://doi.org/10.1080/02724634.1999.10011201

Busack SD, Pandya S (2001) Geographic variation in *Caiman crocodilus* and *Caiman yacare* (Crocodylia: Alligatoridae): systematic and legal implications. Herpetologica 57:294–312

Busbey AB (1995) Structural consequences of skull flattening in crocodilians. In: Thomason JJ (ed) Functional morphology in vertebrate paleontology. Cambridge University Press, New York, pp 173–192

Cooke SB, Terhune CE (2015) Form, function, and geometric morphometrics. Anat Rec 298:5–28. https://doi.org/10.1002/ar.23065

Drake AG, Klingenberg CP (2008) The pace of morphological change: historical transformation of skull shape in St Bernard dogs. Proc R Soc B Biol Sci 275:71–76. https://doi.org/10.1098/rspb.2007.1169

Dryden IL, Mardia KV (1998) Statistical shape analysis. John Willey, London

Escobedo-Galvan AH, Velasco JA, Gonzalez-Maya JF, Resetar A (2015) Morphometric analysis of the Rio Apaporis Caiman (Reptilia, Crocodylia, Alligatoridae). Zootaxa 4059:541–554

Fernandez Blanco MV, Cassini GH, Bona P (2018) Skull ontogeny of extant caimans: a three-dimensional geometric morphometric approach. Zoology 129:69–81. https://doi.org/10.1016/j.zool.2018.06.003

Foth C, Bona P, Desojo JB (2015) Intraspecific variation in the skull morphology of the black caiman *Melanosuchus niger* (Alligatoridae, Caimaninae). Acta Zool 96:1–13. https://doi.org/10.1111/azo.12045

Foth AC, Rauhut OWM, Foth C, Rauhut OWM (2019) A Morphometric approach macroevolutionary and morphofunctional patterns in theropod skulls: a morphometric approach. Acta Palaeontol Pol 58:1–16

Iordansky NN (1973) The skull of the crocodilia. Biol Reptil 4:201–261

Klingenberg CP (2010) Evolution and development of shape: integrating quantitative approaches. Nat Rev Genet 11:623–635. https://doi.org/10.1038/nrg2829

Klingenberg CP (2011) MorphoJ: an integrated software package for geometric morphometrics. Mol Ecol Resour 11:353–357. https://doi.org/10.1111/j.1755-0998.2010.02924.x

McNulty KP, Vinyard CJ (2015) Morphometry, geometry, function, and the future. Anat Rec Integr Anat Evol Biol 298:328–333. https://doi.org/10.1002/ar.23064

Medem F (1955) A new subspecies of *Caiman sclerops* from Colombia. Fieldiana Zool 37:339–344

Medem F (1960) Datos zoo-geográficos y ecológicos sobre los Crocodylia y Testudinata de los ríos Amazonas, Putumayo y Caquetá. Caldasia 8:341–351

Medem F (1971) Situation report on Crocodilians from three South American countries. In: Crocodiles. Proceedings of the first working meeting of crocodile specialists sponsored by the New York Zoological Society and organized by the Survival Service Commission, lUCN, at the Bronx Zoo, New York 15–17 March 1971. l-191. lUCN Publication New Series, New York, p 32:152–158

Medem F (1981) Los Crocodylia de Sur América. Volumen 1 Los Crocodylia de Colombia. Ministerio de Educación Nacional, Colciencias, Bogotá

Monteiro LR, Soares M (1997) Allometric analysis of the ontogenetic variation and evolution of the skull in Caiman spix, 1825 (Crocodylia: Alligatoridae). Herpetologica 53:62–69

Monteiro LR, Cavalcanti MJ, Sommer HJSS (1997) Comparative ontogenetic shape changes in the skull of Caiman species (Crocodylia. Alligatoridae). J Morphol 231:53–62. https://doi.org/10.1002/(sici)1097-4687(199701)231:1%3c53:aid-jmor5%3e3.0.co;2-p

Mook CC (1921) Skull characters of recent crocodilia with notes on the affinities of the recent genera. Bull Am Museum Nat Hist XLIV:123–268

Morales-Betancourt MA, Lasso CA, De La Ossa VJ, Fajardo-Patiño A (2013) VIII. Biología y conservación de los Crocodylia de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH)., Bogotá, DC, Colombia

Rodríguez Melo MA (2000) Estado y distribución de los Crocodylia en Colombia. Ministerio del Medio Ambiente, Bogotá

Rohlf FJ (2017) TpsDig, version 2.30. Department of Ecology and Evolution, State University of New York at Stony Brook, New York

Rohlf FJ, Slice D (1990) Extensions of the procrustes method for the optimal superimposition of landmarks. Soc Syst Biol 39:40–59

Sadleir RW, Makovicky PJ (2008) Cranial shape and correlated characters in crocodilian evolution. J Evol Biol 21:1578–1596. https://doi.org/10.1111/j.1420-9101.2008.01602.x

Velasco A, Ayarzagüena J, Manolis S, Stevenson C (2010) Spectacled caiman *Caiman crocodilus*. In: Crocodiles, status survey and conservation action plan, pp 10–15

Venegas-Anaya M, Crawford AJ, Galvan AHE et al (2008) Mitochondrial DNA phylogeography of *Caiman crocodilus* in Mesoamerica and South America. J Exp Zool Part A Ecol Genet Physiol 309A:614–627. https://doi.org/10.1002/jez.502

Watanabe A, Slice DE (2014) The utility of cranial ontogeny for phylogenetic inference: a case study in crocodylians using geometric morphometrics. J Evol Biol 27:1078–1092. https://doi.org/10.1111/jeb.12382

Zelditch ML, Swiderski DL, Sheets HD (2012) Chapter 1 - Introduction. Geometric morphometrics for biologists, 2nd edn. Academic Press, San Diego, pp 1–20