Paleobiogeography of Cretaceous South American Mesoeucrocodylia and your Contribution to the Knowledge of Biogeographical History of Gondwana and Laurasia

Paleobiogeography of Cretaceous South American Mesoeucrocodylia

Caio Fabricio Cezar Geroto^{1*}

¹Universidade Paulista, Instituto de Ciências e Saúde, Ciências Biológicas, Laboratório de Ecologia Estrutural e Funcional de Ecossistemas, Avenida Independência 210, Éden, Sorocaba 18087-101, São Paulo, Brasil. E-mail: cgeroto@gmail.com

*Corresponding author

ACKNOWLEDGEMENTS

The author like to acknowledgment to Fabio Carbonaro with the discussion and revision of the results are insightful to the conclusions of this paper. To the anonymous reviews with contributed with suggestions to improve of the work.

Aim: Despite Mesoeucrocodylia been the most expressive faunal elements in outcrops of Gondwana, with special attention to South American basin like Bauru Group in Parana Basin and Neuquén Group in Neuquén Basin the biogeographical studies has been almost descriptive. These studies point the hypothesis that vicariance, specially the event of breakup of Gondwana, occupy a main role in speciation and diversification of Mesoeucrocodylia in Cretaceous. The present research investigates the possibility of this hypothesis been true use two complementary methods of biogeographic analysis *a priori*.

Location: The studied reach the sedimentary basins for Gondwana and Laurasia when Mesoeucrocodylia fossils are found (South America, Africa and Eurasia continents)

Methods: Brook Parsimony Analysis, with use maximum parsimony, Bayesian Binary Method for Ancestral State, a maximum like hood method to large data set, and S-DIVA to test the vicariance hypothesis. The area cladograms area time calibrating used the Temporal Calibrating GACs.

Results: Allow reconstruct the ancestral area to the ancestral lineages and track the origin of “Gondwanasuchia” mesoeucrocodylian to African portion, posterior dispersion to South America. Notosuchia had an almost South American history with only peripheral ancestral reach Africa and Peirosauridae divide in two lineages, Peirosaurinae developed almost in Africa and reach South America in Early Cretaceous and Pepesuchinae an endemic South American lineage.

Main Conclusions: Dispersal, not vicariance, take the main role in the diversification of the Mesoeucrocodylia during the Cretaceous. Three migration routes between drain channels take place in Early Cretaceous, one of Peirosaurinae from Araripe Basin to southern portion of South America, another from Pepesuchinae to Bauru Group and the last one of Araripesuchidae from Neuquén Basin do Araripe Basin. With the isolation of Bauru Group in Santonian a series of sympatric speciation take place in Mesoeucrocodylia lineages and other groups like titanosaurids. These sympatric events need future investigations.

Keywords: Atlantogea, Baurusuchidae, Early Cretaceous, Gondwana, Laurasia, Late Cretaceous, Mesoeucrocodylia, Notosuchia, Peirosauridae, Pepesuchinae, Peirosaurinae, Sebecia

INTRODUCTION

Mesoeucrocodylian is a group with a relevant role in the Cretaceous paleofauna records of South America. The fossils can be found in the main outcrops of Parana Basin, Neuquén Basin and Araripe Basin (Leanza, Apesteguía, Novas, & Fuente, 2004; Maissey, 1991; Menegazzo, Catuneanu, & Kiang, 2016). Faunal endemism has been considered to the group, since the first taxa discovered shows a unique setting of morphological characteristics (Romer, 1997), like *Sebecus icaeorhinus* Simpson, 1937, *Baurusuchus pachecoi* Price, 1945, *Notosuchus terrestris* Woodward, 1896) and *Itasuchus jesuinoi* Price, 1955. However, taxa discovered in Africa, Europe and Asia have strict morphological similarities, revealing a closer relationship with South American representatives and supporting a cosmopolitan distribution of those groups, confirmed by all recent phylogenetical analysis (Larsson & Gado, 2018; Larsson & Sues, 2007; Felipe C. Montefeltro, Larsson, & Langer, 2011; Pol, Leardi, Lecuona, & Krause, 2012; P. C. Sereno, Sidor, Larsson, & Gado, 2003; P C Sereno, Larsson, Sidor, & Gado, 2001). These taxa are grouped in a clade that is at times called “Gondwanasuchia” (Carvalho, Ribeiro, & Avilla, 2004), comprising all Mesoeucrocodylia except for Thalattosuchia and Neosuchia (Felipe Chinaglia Montefeltro, 2013).

Gondwanasuchia comprise the well resolve Notosuchia, which include the Notosuchidae and Baurusuchidae families, as well as Peirosauridae (Geroto & Bertini, 2019) and some disputable families like Araripesuchidae, Uruguaysuchidae, Libycosuchidae and Itasuchidae. Sebecosuchia, a clade formed by Baurusuchidae sister group of Sebecidae, are commonly found by some phylogenetics analyses (Pol et al., 2014). However some works found Sebecosuchia merophiletic (Geroto & Bertini, 2019; Godoy, Montefeltro, Norell, & Langer, 2014). Trematochampsidae recently are considering a non-validity family since *Trematochampsia taqueti* is a *nomen dubium* (Meunier & Larsson, 2017). In the same time *Chimaerasuchus paradoxus* Wu, Sues, & Sun, 1995, *Neuquensuchus universitas* Calvo, 2007 and *Razanandrongobe sakalavae* Maganuco, Dal Sasso, & Pasini, 2006 showing like taxa dubious associate with Notosuchia (Dal Sasso, Pasini, Fleury, & Maganuco, 2017).

Recent biogeographical hypothesis proposed some solutions for the irradiation and the role of dispersion and vicariance in the speciation process of Mesoeucrocodylia (Buffetaut & Rage, 1993; Colbert, 1984, 2006; Zulma Gasparini, 1996; Krause, Sertich, Connor, Rogers, & Rogers, 2019; Ortega, Gasparini, Buscalioni, & Calvo, 2000; Paul C Sereno et al., 2009; Sill, 2006; Upchurch, 1995). Most of the hypothesis are literal descriptions based only in the distribution of the fossils and the phylogenetical construction of relationships. Further works, like Turner (2004), apply a methodological analysis to test the vicariance events, suggesting that these events are related to the Gondwana broken up and thus may have a larger role in the geographical distribution of Mesoeucrocodylia. However, the mentioned literature does not develop the idea of irradiation of the lineage inside the continental mass, only between the separations of major areas.

Furthermore, three models try to explain the separation of Gondwana based in fossil distribution (Krause et al., 2019), the Africa-first (Hay et al., 1999; Krause et al., 2006, 2019; Sampson et al., 1998) and Pan-Gondwana (P. C. Sereno, Wilson, & Conrad, 2004) hypothesis admit an initial separation from Gondwana and Laurasia but differ in

time and sequence of separation from Gondwana land. The Africa-first asserts a loss of connection between Africa and South American first in the Albian and the Antarctica/Indo-Madagascar only in the Paleocene. The Pan-Gondwana hypothesis instead admits a concomitant broken up of Gondwana in the Albian. Both agree in an early loss of connection with Laurasia in the Jurassic. The third and more recent hypothesis is the Atlantogea model from Ezcurra & Agnolin (2012) and assume a separation in the Late Jurassic of Asiamerican from Gondwana/Europe, followed by a separation from Europe from Africa, its connection with Asiamerican in Hauterivian and a reconnection of Europe with Gondwana through Africa in the Campanian-Maastrichtian until the Eocene. The paleogeography of continents occupies a main role in biogeography of Mesoeucrocodylia since the break up and approximation of continents create and destroy dispersion routes or cause vicariance events.

In this contribution, I used the Brooks Parsimony Analysis (BPA) and Bayesian Binary MCMC (BBM) to evaluate the pattern of vicariance and dispersion events in irradiation of mesoeucrocodylian lineages in South American between the areas represented by geological unities where the fossils occurred.

MATERIAL AND METHODS

The phylogeny hypothesis was generated from a matrix with 94 taxa and 351 characters from Geroto & Bertini (2019), run in TNT v.1.1 (Goloboff *et al.*, 2008) with a *hold* 15000 and 10000 replicates using the RAS+TBR algorithm. To BPA only the “Gondwanasuchia” clade was chosen, then pruned the Neosuchia and Thallatosuchia for compressed aquatic forms non-limited by the same physical barriers than the terrestrial forms. The exclusion of *Mariliasuchus robustus* was due to my understanding that this species is a junior synonym of *Mariliasuchus amarali*. See supplementary information to the complete cladogram, taxa list and characters description used in phylogeny.

It is important to point out that the phylogenetics analysis results were divided between two main interpretations. The first one is based in the characters list by Pol (1999, 2003) which has come to be expanded and reformulated by several authors (Z. Gasparini, 2006; Nascimento & Zaher, 2011; Pol & Leardi, 2015; Pol *et al.*, 2012, 2014), these analysis always recover a monophyletic Sebecosuchia and, in the last versions, it recovered Araripesuchidae like a sister clade of Peirosauridae. The second interpretation is a series of original character lists in which analysis shared common results like a paraphyletic Sebecosuchia, Araripesuchidae sister-group to all Notosuchia, a close relationship between Peirosauridae, Sebecidae and Mahajangasuchidae, and a Peirosauridae sister-group of Notosuchia (*e.g.* (de Andrade, Edmonds, Benton, & Schouten, 2011; Geroto & Bertini, 2019; Godoy *et al.*, 2014; Larsson & Sues, 2007; Felipe C. Montefeltro, Larsson, De França, & Langer, 2013). The phylogeny I used in this BPA and BBM analysis is fixed in the second situation (see supplementary information for a complete cladogram).

Brooks Parsimony Analysis (BPA) is a *posteriori* method to test the null hypothesis: all taxa in an area shares the same biogeographic history and this reflects in their phylogeny. Being a *posteriori* method means that inferences before the analysis are not allowed. BPA is a more sensitive method to biogeographic analysis and allows identification of different forms of dispersal (Brooks & McLennan, 2001). BPA identifies vicariance events in the cladogram as synapomorphies, dispersion as parallelism and extinction as reversals (Morrone, 2008).

BBM was chosen as an auxiliary method due to a refinement and initial interpretation provided by it. BBM is a RASP (Reconstruction Ancestral State Phylogeny) (Yu, Harris, & He, 2010, 2015) mode and uses a modified code of MrBayes 3.1.2 (Ronquist

& Huelsenbeck, 2003) to run a MCMC (Markov Chain Monte Carlo Analysis) allowing reconstruction of the ancestral area to a given Node.

To BBM analysis since there are more than nineteen areas it is not possible to use the S-DIVA algorithm (Table 1). My choice was the BBM (Bayesian Binary Method for Ancestral State) algorithm, with models JC, JC+G, F81 and F81+G, not allowing Null Areas, 250000 cycles and a temperature of 0.1. As all species are endemic, but with more than one species occurring in the same area, the maximum number of areas setting was three. RASP allows to merge distinct results in a single consensus, in this case each model was run 3 times, resulting in 12 outcomes that were combined, decreasing conflicting interpretations for Nodes. To minimize the differences, the results of four BBM models were combined into a single cladogram.

The primary and secondary BPA (Fig. 1) are performed using TNT v. 1.1 (Goloboff, Farris, & Nixon, 2008) *hold* 15000 trees and implicitly enumeration search strategy. I made the divisions of the area following the strategies of Brooks *et al.* (2001), but I considered a temporal gap between the taxa to divide the areas. An example is *Amargasuchus minor*, found in outcrops from La Amarga Formation from the Barremian Age, separated from another Crocodyliforms of Neuquén Basin by two unconformities (Leanza *et al.*, 2004) and a 29 million years gap. The calibration of the nodes for the general area cladogram (GAC) is following the protocol for time calibration from Folinsbee *et al* (Folinsbee & Evans, 2012). Since BPA is a *posteriori* methodology, the interpretation of results is made in the Discussion section below, based in the works of Brooks *et al* (Brooks, Veller, & McLennan, 2001), Brooks & McLennan (2001), Liebermann (2003), and Halas *et al* (Halas, Zamparo, & Brooks, 2005). The paleobiogeography reconstruction follows the hypotheses of Sereno *et al* (2004), Sampson *et al.* (1998), Hay *et al.* (1999), Krause *et al.* (2006) and Ezcurra & Agnolin (2012). Maps used in reconstruction of dispersion routs are plotted by Ocean Drilling Stratigraphic Network ((Research Center for the Marine Geoscience at the CAU, 2014).

The secondary BPA recovered a general area cladogram (GAC) like a phylogenetic cladogram, allowing the overlapping of the nodes. Thereby a correlation between the GAC and phylogenetic nodes is made, showing that some GAC nodes represent two or three nodes of phylogenetic cladogram. For example, the node 46 of GAC is an assemble of nodes 162 and 161 of the phylogenetic cladogram, the same applies to GAC node 55, relative to nodes 142 and 141, the GAC node 60 and the phylogenetic nodes 138 and 137, and the GAC node 62 to phylogenetic nodes 136, 135 and 130. Therefore, the ancestral area reconstructions are presented and discussed here in GAC.

Both RASP and BPA found a dominance of dispersal events, opposed to vicariance, but in RASP most vicariance events are overlapping with dispersal events since the software were unable to resolve between both. In this case of overlap, each node is examined individually, and the reconstruction is chosen between the options found by BBM. To solve that I run a S-DIVA analysis to each of Notosuchia and Sebecia clade, due to the limited number of areas of S-DIVA. Vicariance is always assumed as a favorite event, however, the BPA results falsely this hypothesis and then dispersal had to be considered. The ancestral area chosen was the one that better adjusted to paleogeographical hypothesis and the events reported by the literature was preferred. No reconstructions with less than 1% of chances were used.

RESULTS

Primary BPA results (Fig. 2) in one cladogram shows strong vicariance support between areas that are not closely related, like the Araripe Basin, Chubut Group and Kem Kem Beds (Node 35). Even though, there is strong support between areas with taxa closely related, like Bauru Group and Neuquén Basin (Node 30), and Iullemmeden Basin with Mahajanga Basin (Node 20). I found a moderate support to areas with a known vicariance history, like Pab Formation with Bauru and Neuquén groups (Node 31). However, the homoplasy in cladogram pointed to a reticulated history involving the areas with strong vicariance support. These characters are found like parallelism and signalized to dispersal.

With the application of secondary BPA I found three divisions of Bauru Group, plus four divisions of Neuquén Group and Iullemmeden Basin, two divisions of Mahajanga Basin, and only one division of Araripe Basin, to resolve all homoplasies and reveal that some of the vicariance relationships are artifacts and disappear with the division of areas. The secondary BPA (Fig. 3) results in only one parsimonious tree without polytomies. A reticulated history with lots of dispersal events is found by BPA. There is strong support to vicariance events in node 62 and moderate support to nodes 46, 55, 60. Furthermore, the nodes 35, 47, 61, 63, 64 most likely represent vicariance events considering the geological history of the separation of Gondwana. Secondary BPA found these Nodes represent dispersal events assenting with JC and F81 models. Extinction events are found by BBM and S-DIVA in different nodes, BPA does not identify any extinction event.

BBM found 91 dispersal events overlapping 45 vicariance events. This means that, in any node, when BBM found a vicariance event, it happened after a dispersal event. If more than one taxa moves to a new area and is followed by an emergence of a barrier that produces a vicariance, this is called Geodispersal (Morrone, 2008). The consequence of Geodispersal is a biogeographic convergence and a reticulated history. The BBM analysis recovered a crescent consensus between the results of four models and a great occurrence of dispersal. The difference between two models is due to the application of Gamma distribution (G+), this distinction is expected since JC is a nested model of F81 (Posada, 2003). The Monte Carlo Method has proven to be sensitive to find problems in the distribution of species in areas as a result from the phylogeny. *Stolokrosuchus lapparenti* (species 11) is a problem, since in BPA analysis she is a descendant from species 75, which is a descendant from species 76, and occurs in the same area of *T. taqueti* and *M. oblita*, but at an earlier time (Aptian – Albian). I consider this is an artifact from dubious position of clade *Trematochampsia* + *Miadasuchus*, two taxa composed of fragmentary material and a questionable taxonomy validity (e.g. Larsson & Sues, 2007; Geroto & Bertini, 2019). It is possible that both *Stolokrosuchus* and the ancestral species of *Trematochampsia* and *Miadasuchus* (species 64) descend from the same ancestral (species 75 or 76) an isolated peripheral. As a test, when not separated, B3 from B area resulted in a polytomy in GAC. Considering species 75 like a missing data solve the polytomy but returned a species 74 homoplastic, showing that species 74 is artificial, in the sense that it is not a real ancestral to *Stolokrosuchus* and its sisters' clades.

The combined models result in area B (Iullemmeden Basin) reconstructed like an ancestral area to all “Gondwanasuchia”. The calibration of general area cladogram (fig.4) stipule the cladogenesis between Notosuchia and Sebecia in Valengian – Hauterivian interval, with Notosuchia dispersion to area M (Litoral Basin), with a strong distribution in South America, while Sebecia have an African centered history. The main difference between the results found by the models regards the ancestral areas

of Peirosauridae leading to Pepesuchinae and Peirosaurinae cladogenesis. Species 8 (*Amargasuchus minor*), 64, and 69 must be peripheral isolate.

DISCUSSION

BBM is a Bayesian method with some limitations. The MCMC algorithm tests how likely each informed area is an ancestral area to each node in a phylogenetic cladogram. First limitation is that only the informed areas are considered by the BBM, areas where fossils do not occur were disregarded by the MCMC. This causes a problem when all taxa are endemic to only a geographic limited area, that can be a basin, a group or a formation, even a member. Hardly an animal have been limited by the basin margins. Extant crocodile species, like *Caiman yacare* and *Caiman crocodilus* occur in Pantanal Basin and localities outside of the basin limits. In the analysis this is exemplified by the Baurusuchidae dispersion. Two problematic taxa inside Baurusuchidae are also problematically resolved by MCMC. The first case is *Pabwehshi pakistanensis*, a baurusuchian taxon recurrently found, which occur in Pab Formation in Pakistan and is closely related to a Neuquén and Bauru Group baurusuchians. Two dispersions routes can be proposed, one Baurusuchian ancestral dispersed to Pakistan via Africa, although no fossils of Baurusuchidae were found in African basins, or, which is most acceptable, a dispersion route via Antarctica, although no fossils of crocodyliforms were found in the continent yet (Wilson, Malkani, & Gingerich, 2001). The number of taxa in a chosen area is used by RASP to calculate the probability of this area to be the ancestral area. That is the principle of Bayesian Probability. *A priori* beliefs of the observer are adjusted and reinforced by the amount of evidences inserted in the analysis. I made a test and removed *Stolokrosuchus* of the analysis and resulted in a completely different outcome where Neuquén Formation is the most probable ancestral area to all nodes. Finally, whenever more taxa of a determined area were used, the greater the probability of this area being the ancestral area in most Nodes. This is a biased information, if the cladogram being used excludes taxa with large missing data (e.g. *Amaragasuchus* or *Trematochampsia*) I may end up with a cladogram of an ancestral area where determined area is more expressive (more taxa) and is chosen like an ancestral reconstructed to the Nodes. On the other hand if all taxa are included it is more likely to have problems, like more prospecting works (resulting in more species described), taphonomic problems (more fossils preserved, which does not mean that the area with less or none fossils do not contains taxa of that group) and synonyms problems (e.g. Bauru Group and its 25 crocodyliforms species against 6 dinosaurs species). To resolve that bias, I used another analysis, also by RASP, called S-DIVA, a modified algorithm from DIVA, that searches for vicariations events.

The northern of Africa (area B) is possibly an ancestral area to “gondwanasuchian” Mesoeucrocodylia. There are a few works proposing Africa as the ancestral area to Notosuchia + Sebecia clade. Dal Sasso *et al.* (2017) points that southern Gondwana is this ancestral area, based in the taxonomic position of the recently revisited taxon *Razanandrongobe sakalavae*, classified as Notosuchia from Middle Jurassic, bringing problems to the interpretation of node 39. Trying to replicate the analysis of Dal Sasso *et al.* (2017) in TNT found a well resolved clade formed by *Chimaerasuchus paradoxus* and *R. sakalavae*, sister group of all Sebecosuchia. Codifying *R. sakalavae* in the matrix used in the RASP analysis resulted in the species being a sister taxon from all other Neosuchia, and the collapse of all Shartegosuchidae. If *R. sakalavae* is considered an advanced Notosuchia, BBM analysis still found Ilummeden Basin as the ancestral area to Gondwanasuchia, but the time calibration put the node 170 in the Lower Jurassic, while the node 169 is in the Torasian — Audelevian interval, culminating with two long

ghost lineages, one to advanced Notosuchia and another to Sebecia, until the Lower Cretaceous. In this case, like *C. paradoxus*, *R. sakalavae* is an advanced Notosuchia outside Upper Cretaceous, and like *C. paradoxus*, *R. sakalavae* is found associated with Sebecosuchia in a contested clade. The material of *R. sakalavae* is extremely fragmented, the maxillary palatal bones, one of the main characters pointed to include the taxon in Mesoeucrocodylia, don't exhibit a medial contact, being dubious to point out if it really formed a true secondary palate or if it is a partial condition like the Sphenosuchia and Protosuchia condition. The presence of an extremely derived Notosuchia in middle Jurassic is a temporal challenge. In the same way, if *R. sakalavae* is a Neosuchia it bears an uncommon morphology with an absent triangular posterodorsal process of premaxilla wedging between maxilla and nasals, a short mandibular symphysis, limited to an anterior portion of rostrum in the level of posterior border of premaxilla-maxilla, deep mandibular symphysis, ziphodont dentition, heterodont dentition of premaxilla with incisiform teeth followed by caniniform teeth, frontal external nares and absent diastemic fossa between premaxilla and maxilla. The polytomy caused in Shartegosuchidae due to the inclusion of *R. sakalavae* can be a clue to a phylogenetic relationship of this taxon. Therefore, further tests must be made in order to confirm the position of *R. sakalavae*. Due to this *R. sakalavae* is not included in the analysis.

North Africa is confirmed by BBM like the ancestral area to "Gondwanasuchia" clade (Fig. 5), its reconstruction found the Iullemmeden Basin as the ancestral area with a high probability (51,92), but it was unable to determine if vicariance or dispersal occurred. The children node 52 recovered a BH area (Iullemmeden Basin + Neuquén Basin). S-DIVA found to this node an equal probability (16,67%) of an ancestral area combination between African and South American areas (e.g. ABIMN, AHIMN, BHIMN, ABHIM, ABHIN, ABHMN), more important, the Neuquén Basin (H area) is found in all six combinations, corroborating the BBM reconstruction. To children node 38 BBM it was found a high probability (63,94%) for the B area as ancestral area, but S-DIVA is unable to reconstruct any area combination as ancestral area. That first dispersion from Iullemmeden Basin (B) to several localities in Africa (A and N) and South America (H, I, M) can be an evidence of a wider distribution of an ancestral in all Gondwana (Fig. 6). I assumed a possible dispersal event from node 39 to children nodes 38 and 52 associated to the end of a main eruption stage of Paraná-Etendeka magmatism in Valangian ((Renne et al., 2013, 1992; Renne, Glen, Milner, & Duncan, 1996; D. D. E. F. Rossetti & Góes, 2003; L. M. Rossetti, Lima, Waichel, Scherer, & Barreto, 2014; Thiede & Vasconcelos, 2010) Rossetti *et al.*, 2014).

The ancestral area B is reconstructed with a probable ancestral area to Nodes 38, S-DIVA however is unable to recover any area to this node. A dispersal from area B (Node 39) to area B (Node 38) can be explained by the punctuated equilibrium (Gould, 1982), when a taxon dispersed to a peripheral area, goes through a subsequent differentiation and returns to an ancestral area. BPA found dispersion in this node as it is sustained by species 78. S-DIVA proposed a dispersal or extinction event isolated the species in the Child Nodes 37 and 41. Extinctions speciation events find patterns that are more relevant in extant taxa, however, the register may bias extinct taxa (Morrone, 2008). In this case, the dispersion explanation is more likely. BBM found 19,20% of probability of a dispersal event against the 2% of extinction probability from S-DIVA.

BBM found a combination between dispersal and vicariance events on Node 37, while BPA and S-DIVA show a dispersal of Peirosauridae (specie 77) lineage from Africa (area B) to area BH (Iullemmeden + Neuquén) to the southern portion of Gondwana (Node 37). Therefore, it is a safe assumption that the common ancestral of all Sebecia

were largely distributed in South America and Africa in Valangian/Hauterivian. BPA allowed to identify a dispersal of a peripheral isolated in Neuquén Basin (area H, species 8) originating *Amargasuchus minor*. That is the most probably, due to the occurring of *Amargasuchus minor* (species 8) in rocks of Hauterivian/Barremian age in La Amarga Formation, descending of the species 77. In this context, the Node 37 can be associated with rift processes related to the opening of Atlantic beginning in the Late Jurassic with the rift stage occurring in the Valangian/Hauterivian interval (Assine, 2007). At Node 36 no ancestral area was found by S-DIVA, but BBM reconstructed area B with 86,29%. Node 35 was found to be AB ancestral area with 100% by S-DIVA and 5,35% by BBM. The S-DIVA and BPA analysis suggest that a dispersal event have isolated the child node 35 for the child node 49.

Node 49 is reconstructed as area B alone, with 90,81% and BH with 1,20 % by BBM. S-DIVA found a combination of almost all areas (e.g. BHIK, BIK, BHK, BHIJK, BIJK, BH, all of them with 6.67%), but not for area B alone. in this situation the preferred ancestral area is the consensus (BH area) between BBM and S-DIVA. BPA found dispersal in node 36 and node 49, while BBM and S-DIVA found a combination of dispersal/vicariance events.

The interpretation of these results is the dispersion from African peirosaurids to South America in Barremian – Aptian interval. A post-dispersional vicariance event in Node 49, isolated area B (*Stolokrosuchus*) from area JK (Node 48). This event took place in the Barremian-Aptian interval and is most likely related with a second rift pulse occurred in the Barremian — Aptian boundary. The hypothesis of a punctuated equilibrium for this situation solves the weird distribution of the clade *Miadasuchus* + *Trematochampsia* (child Node 35) and *Stolokrosuchus* (child Node 49). *Stolokrosuchus* and *Trematochampsia* are taxa from Iullemeden Basin, but *Trematochampsia* age is Coniacian — Santonian (Moody & Sutcliffe, 1991) and *Stolokrosuchus* is an early taxon from Aptian-Albian (P. C. Sereno et al., 2003).

BPA, BBM and S-DIVA confirmed that a dispersal event on Node 48 (area JK) at the end of Barremian isolated the species 68 in South America (area IJ, Node 50) and species 73 in the north portion of Gondwana and south portion of South America (HK), inducing the separation between Peirosauridae subfamilies: *Pepesuchinae* and *Peirosaurinae* (Node 48) (Figure 7).

At the Node 47 the reconstruction of area HK have little confidence, BBM found 2,48% chances and S-DIVA found several combinations, all with 10%. Again, the consensus between the reconstructions is choice, viz. HK. BBM and S-DIVA found a dispersal event followed by a vicariance while BPA found a dispersal. The child Node 47 is a posterior dispersion of species 73 to area K (Kem Kem Beds) in Africa. In this scenario, *Hamadasuchus rebouli* (species 17) is a peripheral isolated as shown by BPA results. The vicariance event of Node 47 is associated with the postrift I stage in Aptian/Albian (*sensu* Assine, 2007), isolating the South American ancestral species *Peirosaurinae* (species 71 and 72) from the African species (*Hamadasuchus rebouli* species 17). Following that event there is a dispersion of species 72 and a separation between *Peirosaurinae* of Bauru Group and (Chubut Group + Neuquén Basin) in Node 46. This vicariance event took place in the end of Barremian stage. S-DIVA identified another vicariance event in Node 45 during the Aptian stage, isolating the *Peirosauridae* from Neuquén Basin from the Chubut Group and BBM found a high probability for this event (80.84).

According to Manassero et al (2000), the pyroclastic sediments from Cerro Barcino formation, Chubut Group, are correlated to the volcanic activity from Angostura Colorado Formation, its main phase occurring in the Barremian – Aptian interval)

allowing to connect the vicariations events in Nodes 46 and 45 with the main volcanic activity of Angostura Colorado Formation.

Node 50 represents a biogeographic history of *Pepesuchinae* exclusive as a south American clade. The ancestral area IJ is reconstructed by BBM with 4.68% of chances, but S-DIVA found 100% of this reconstruction. BPA found a dispersal event in this node, but S-DIVA and BBM agreed with a vicariance in a coincident time with the magmatism Pernambuco, occurred in the postrift II stage *sensu* Assine (2007). This event of dispersion characterizes a first migration wave from Araripe Basin to the southern of South America and is followed by the migration of *Araripesuchus* genus (e.g. Ortega *et al.* 2000) (Node 64). The isolation of *Caririsuchus* from *pepesuchines* from Bauru Basin can be attributed to the start of post-rift II stage from Araripe Basin (Assine, 2007). Inside Bauru Basin BPA it was found only events of sympatry speciation, confirmed by BBM and S-DIVA.

The most recent paleobiogeographical *Sebecia* history is represented by Node 35 (BA area) and is a result of dispersion from B area to BA area followed by an isolator event in Cenonian—Turonian stages. This event with isolated species 9 and 10 (Node 35) is a vicariance confirmed by all three analysis (BBM, S-DIVA and BPA) and can be associated with a moment of marine transgression in Iullemmeden Basin (Bata, 2016; Moody, 1997).

BBM analysis reconstruction found Iullemmeden Basin (area B) with a high probability (47.49%) to be the ancestral area for *Notosuchia* (Node 52, Fig. 6), the Neuquén Basin (area H) with 23.53% and a combination of both with a low probability (2.35%).

S-DIVA found a more complex combination of areas between South American and African localities (e.g. ABEFG 16.67 ACEFG 16.67 BCEFG 16.67) from that point there was a dispersion of *Notosuchia* throughout all Gondwana territories. After the end of Hauterivian the biogeographical history of *Notosuchia* was centered in South America, only with peripheral isolated lineages reaching Africa (Nodes 53 and 65). The common ancestor to all *notosuchians* (species 110) divided in two lineages (Figure 8), one represented by species 110 staying in South American and then, according to BPA results, dispersed to the south portion of Gondwana (BBM: HM area; S-DIVA: AHMN area), another lineage is a peripheral isolated ancestor of *Araripesuchus* (species 80) that reaches the north portion of Gondwana (BBM: B area, S-DIVA: BI), and then went through the vicariance event associated to postrift opening South America/Africa separation in Barremian/Aptian (Assine, 2007). That event is associated to an origin of *A. wegeneri* and a South American lineage of *Araripesuchidae* (Node 65, species 79).

The ancestor species 79 dispersed to the south portion of South America during the Aptian-Albian interval, reaching the Neuquén Basin area (H) when an isolator event separated the *A. gomesii* and *A. patagonicus* species. That is the third dispersion wave, protagonized by *Araripesuchus* genus (species 79) (Fig. 9). The direction of migration is contradictory, since BBM found a movement from Neuquén Basin to Araripe Basin, followed by a vicariance, and therefore a geodispersion event, while S-DIVA found a spreading in a IH area (Araripe Basin reunited with Neuquén Basin) followed by a vicariance event that isolated the two species during the Albian (Node 64). So, *Araripesuchus* can enter in South American by south, probably via Antarctica continental bridge or by north via the contact between South American and Africa.

A pre-Aptian dispersion to *Araripesuchus* genus was already proposed by Ortega *et al.* (2000) based in works of Kellner (1994) with no coincident similarities found between the amphiatlantic fauna of fish and reptiles. A fourth species described by Turner (Turner, 2006), *Araripesuchus tsangatsangana*, found in Mahajanga Basin in Madagascar brings one more taxon related to the dichotomy Iullemmeden

Basin/Mahajanga Basin (see GAC Nodes 61, 63, 35) all situated during the rift or post rift stage (Aptian-Campanian), time when Mozambique Channel finished the opening initialized in Barremian (Ali & Krause, 2011). However, the BPA did not found an associated history between those events, with the division of secondary BPA indicating that these are individual events. It is possible, due to the presence of this dichotomy nodes and related forms like *A. tsangatsangana* and *Malawisuchus* (Gomani & Gomani, 1997) in more southern localities of the continent, the occurrence of a dispersion event from Iullemmeden Basin to south reaching Madagascar land. The opening of Mozambique Channel not showing an effective barrier to this dispersion, due to the capacity of small terrestrial animals like araripesuchians and notosuchians to travel by island jumping or carried on by natural boats like trees. Still, *Araripesuchus tsangatsangana* was recovered closely related to *A. wegeneri* almost sister group of *A. gomesii* + *A. patagonicus* clade (Andrade et al., 2011; Montefeltro et al., 2013; Pol et al., 2014) and in this case its biogeographical history of south African dispersion is a different event of that of *A. gomesii* + *A. patagonicus* clade, that reaches South America by Araripe Basin and disperses to Neuquén Basin, pointing to a migration from north to the south of continent.

With the relation between Araripe Basin—Bauru Group, Iullemmeden Basin—Neuquén Basin and Araripe Basin—Neuquén Group, three migrations routes can be traced to northeast of South America to the southern portion. The first wave is related to the dispersion of *Pepesuchinae* ancestral (species 68) from Araripe Basin area to Bauru Group. Second dispersion wave is from ancestral species of South American *Peirosaurid* (species 71 and 72), from Africa to the south portion of this continent. The third wave is the dispersion of *Araripesuchus* (species 79) from Araripe Basin to Neuquén Basin. With three distinct clades coming from Araripe Basin and reaching Neuquén Basin and Bauru Group during the Aptian/Albian, it is possible to confirm a migration route, probably by the drain channels (Carvalho, de Gasparini, Salgado, de Vasconcellos, & Marinho, 2010; Potter, 1997), which rise in in Aptian and allowed faunistic exchanges between north, south and central areas of South American.

Uruguaysuchus speciation is given by a peripheral isolated from species 109 (Node 51), which can be considered a persistent ancestral to all advanced notosuchians from South American. Forced *Uruguaysuchus* inside *Araripesuchidae* do not invalidate this interpretation, since species 110 continued to be a common ancestor to all *Notosuchia*. The only way in which this results are not valid is the confirmation of Pol et al. (2012, 2014) hypothesis of *Araripesuchidae* like a sister clade to *Peirosauridae*.

BPA found evidence of two vicariance events in Node 55, one of them is species 107 originating species 106 and *Comahuesuchus brachibucallis*. BBM reconstructed the ancestral area as being Neuquén Basin (area H, 86.77%) while S-DIVA found 100% to this result. Since *Comahuesuchus* also occur in Neuquén Basin area, this turns out to be a within-area speciation. Halas et al (2005) suggested that in this case one of the species is a persistent ancestral while the another is a peripheral isolated. Species 107, which originated two taxa in same area (*Comahuesuchus* and specie 106), is considered the persistent ancestral, while species 106 is the peripheral isolated, since is ancestral to *Candidodon itapecuruensis*, a taxon that occurs in north of South America. Species 106 suffers a post-speciation dispersion which descendent is *Candidodon itapecuruensis*. The Node 55 is associated to the events of magmatism from Sardinha Formation (Vaz et al., 2007). The vicariance event which originated *Comahuesuchus* it is likely the same event of *Notosuchus terrestris* (Node 66), since both came from Bajo de La Carpa Formation (Martinelli, 2003; Pol & Apesteguía, 2005) in Neuquén Basin. That

hypothesis is confirmed by BPA which found the same vicariance event related with Node 66.

Node 58 is an event of separation between two advanced notosuchians lineages descendant from species 105, Baurusuchidae (Node 59) and (Notosuchidae Sphagesauridae) (Node 57). Both BBM and S-DIVA found HJ as the ancestral area for advanced Notosuchia. To the end of Aptian, the advanced notosuchians dispersed by the south portion of South America and the baurusuchian reach the Indian/Madagascar plate. In the Albian/Cenomanian the plate separates from Antarctica and begins the sliding towards Asia, bringing forth the vicariance event of Node 60 and an isolation from species 102, originating *Pabwehshi pakistanensis* in Maastrichtian (Wilson et al., 2001). That proposition supported the paleogeographical reconstruction of Hay *et al.* (1999) that prolonged the duration of the link between Indian/Madagascar plate and Antarctica until Campanian.

Node 59 is reconstructed as area HQ (Neuquén Basin + Wulong Formation) by S-DIVA (100%) and BBM (3.90%), but that hypothesis is discarded due to the biogeographical impossibility of the union between the two areas. BBM found a high probability (54.27%) of Neuquén Basin (area H) as the ancestral area to this node and is related to the isolator event leading to the speciation of *Chimaerasuchus paradoxus*, a taxon supposedly found in Wulong Formation, Lower Cretaceous of China (X.-C. Wu & Sues, 1996; X. Wu et al., 1995). *C. paradoxus* is continuously recovered in the analyses as an advanced Notosuchia closely related with Sphagesauridae or Baurusuchia (Brandalise, Andrade, & Bertini, 2008; Geroto & Bertini, 2019; Godoy et al., 2014; Felipe C. Montefeltro et al., 2013; Turner & Sertich, 2010). Hao et al. (1986) *apud* Andrade & Bertini, 2007ab) and Andrade & Bertini (2007ab; 2008) attested little confidence in the age of Wulong Formation or the proceeding of *C. paradoxus* from this stratigraphical assignment. A critical review presented by Andrade & Bertini (2007a) suggest that *C. paradoxus* is a basal Notosuchia or a sister taxon for all the other Notosuchia. That hypothesis, if recovered in a phylogenetic analysis, could better explain a dispersion of a Notosuchia in a Laurasian area happening before a broken up of Pangea. Considering all of the phylogenetic results, it is more likely that the holotype of *Chimaerasuchus paradoxus* did not come from Wulong Formation (Andrade & Bertini *op. cit.*).

Following the results here presented, *Chimaerasuchus paradoxus* represents an anomalous vicariance event between Wulong Formation and Neuquén Group, according to S-DIVA or long-range dispersion from South American follow by a vicariance event (Geodispersal), according to BBM results. BPA found *Chimaerasuchus paradoxus* emerging from a peripheral isolated from Node 59 and it agrees with BBM results, which reconstructed a dispersion from ancestral area H to area Q, followed by a vicariant event (H->QH->Q|H). Regarding the interpretation and discussion of the results, as we are talking about biogeographical relationships between a Laurasian and a gondwanan taxa for purposes of historical paleobiogeography, the age of the formations is not that relevant as their geographical ranges (Morrone, 2008). Laurasia and Gondwana begin the separation in the Jurassic, and the Pan-Gondwana and Africa First models do not admit a link between Gondwana and Laurasia after the Early Cretaceous. The Atlantogea model from Ezcurra & Agnolin (2012) considers a reapproximation and a reestablishment of a link between Africa and Eurasia in the Campanian-Maastrichtian until Eocene. Vicariance for *Chimaerasuchus* cannot be admitted unless a connection between Gondwana and Laurasia is extended until the Aptian—Albian interval. On the other hand, a geodispersal event is confirmed by two of three analyses used in this investigation (BBM and S-DIVA) and both agree with any interpretation of age for

Wulong Formation. However, these results and Atlantogea model support a different age proceeding for the *Chimaerasuchus paradoxus* material, probably from Campanian-Maastrichtian age.

Starting in HJ area in Coniacian/Santonian boundary, Baurusuchia reached the Bauru Group area and the Node 62 represents a strong supported vicariant event in BPA and S-DIVA while BBM found a geodispersal event, which divided the two subfamilies proposed by Montefeltro *et al.* (2011). More information is necessary to understand this node since it shows a complex relation of information. BPA found at least three within-area speciation events (species 101 originates species 100, which originates species 95 that originates species 93). One of the child taxa of species 101 is *Cynodontosuchus rothi*, a Baurusuchia from Santonian of Neuquén Basin, is sometimes proposed as being a senior synonym of genus *Baurusuchus*, and the specimen considered a juvenile (Gasparini, 1996). Species 95 originates two species, 93 and 94. Species 93 has two taxa children, *Wargosuchus australis* from Campanian of Neuquén Basin and *Pissarrachampsa sera* from Campanian of Bauru Basin, while species 94 originates the clade *Campinasuchus paulistanus* e *Gondwanasuchus scabrosus*. BPA found dispersal as the main event which causes the speciation in those clades. BBM found geodispersal (dispersion followed by vicariance) in the event that separated species 100 from *Cynodontosuchus rothi*, and between *Pissarrachampsa* and *Wargosuchus*. S-DIVA found vicariance for both events.

Two hypotheses can be proposed here: if *Cynodontosuchus* is a juvenile synonym of *Baurusuchus*, so the *Baurusuchus* (= *Cynodontosuchus*) genus emerge in Santonian in area HJ, and after the separation between Bauru Basin and Neuquén Group, the genus originates the species *B. rothi* and all baurusuchian taxa from Bauru Basin. This removes species 101 from GAC and reduces the within-area speciation for two (100 > 95 > 93). Species 94 and 99 will be peripheral isolated in Bauru Basin area and *Pissarrachampsa* isolated from *Wargosuchus* by dispersal rather than vicariance found by BBM and S-DIVA. Another hypothesis, *Cynodontosuchus* is a valid species and the connection between Neuquén Basin and Bauru Basin is recovered and lost more than once, probably by the drain channels of Musachio (2000). A first vicariance event isolated *Pissarrachampsinae* (species 95) from *Baurusuchinae* (species 99), and a second isolated *Pissarrachampsa sera* from *Wargosuchus australis*. Both events are found by S-DIVA. A dispersion event found by S-DIVA isolated *Gondwanasuchus* + *Campinasuchus* clade. The baurusuchian species from Bauru Group probably evolved by sympatry.

Node 57 placed in Coniacian/Santonian, BBM found the ancestral area J (Bauru Group with 89.08%) and S-DIVA found HJ or only H, both with 50% of chances to be the ancestral area. The HJ ancestral area agrees with the ancestral area of Baurusuchia found in Node 62. There is not a particular event that can be identified in this node by BBM, but S-DIVA and BPA found a dispersal event that can be associated with an inclination change from Chilean volcanism during the Aptian (*e.g.* Tunik *et al.*, 2010), it divided the advanced Notosuchia (species 92) in two lineages, Notosuchidae (area HJ) and Sphagesauridae (area J). The species 83, a common ancestral to Notosuchidae, was isolated during the Coniacian/Santonian by the vicariant event of Node 66 causing the speciation of *Notosuchus terrestris* and *Mariliasuchus amarali*. Those events are probably associated to the uplift of Bauru Group margins in Santonian (Riccomini, 1997) and support a Santonian—Campanian age proposed by Menegazzo *et al.* (2016) to Araçatuba and Adamantina formations.

Node 56 is reconstructed as JP area by S-DIVA (100%), that result is found by BBM with 1.01% and area J with 97.77%. This node represents an isolation of *Yacararani*

boliviensis from Bauru Group sphagesaurids (Fig. 10). S-DIVA found a vicariant event while BBM found a geodispersal event. Primary BPA found a dispersal event related to this node and Secondary BPA found three within-area speciation and persistent ancestors (species 88, 89, 90 and 91).

All persistent ancestor originates Bauru Group taxa with exception of species 88, ancestor for *Y. boliviensis* from Cajones Formation. This result points to a strong sympatric signal in ancestral area being probably Bauru Group (J area) and not JP area, found by S-DIVA. The Cajones Formation is interpreted with representative of marine depositional environment, possibly a shore line, but with red sandstones of fluvial origin. In this case the marine transgression cannot be a strong barrier to small animals like sphagesaurids which can be transported via tree branches and dispersed. Species 88 dispersed across this barrier and isolated originated *Y. boliviensis*. The Bauru Group sphagesaurids species also evolved by sympatry.

That's results put the origin of Gondwanasuchia in Africa portion of Gondwana while the ancestral lineages spread for all that ancient continent during the Early Cretaceous. Notosuchia ancestral appear in South America portion e dispersed for all territory, only peripheral lineages reach the Africa, while Peirosauridae ancestral appear in Africa portion and have a more strong presence in this territory. The separation of Gondwana isolated the Peirosauridae lineages with Peirosaurinae occurring in north portion of Africa, and posteriorly reach the south portion of South America and Pepesuchinae been an endemic lineage of South America. The migration between north and south portion of South American probably occurring in Early Cretaceous between the drain channels of Potter (1997), three migrations wave the first been the Pepesuchinae ancestral from Araripe Basin to Bauru Group, second the Peirosaurinae from Africa to southern South America and the third one been de Araripesuchidae ancestral between the Araripe Basin and Neuquén Basin. Pepesuchinae lineage fixed in Bauru Group become an endemic from this area, Peirosauridae become a high dispersive lineage, occurring in Neuquén Basin and Bauru Group until the Late Cretaceous. The Santonian isolation of Bauru Group originated an endemic area with a strong sympatric signal specially represented for the high richness of Notosuchia and Peirosauridae species, with some groups like Sphagesauridae are high specialized and only occurring there. The sympatry appears in other groups like Titanosauria and deserve future investigations.

CONCLUSION

Vicariance processes have little contribution to the speciation of South American Mesoeucrocodylian clades less generalist than families. Peripheral isolated occupied a larger role in speciation, especially in Notosuchia Geodispersal events (dispersion followed by vicariance) are common. Later Cretaceous species mostly appear by postdispersion speciation, especially in the Bauru Group and Neuquén Basin. Indeed, most of the Baurusuchidae and Sphagesauridae speciation events indicated paralogy. Therefore, allopatry and sympatry are the main type of speciation regarding the South American mesoeucrocodylians.

Sebecia and Notosuchia did not recover a single pattern of speciation, showing a reticulated history being product of distinct events. The history of Sebecia shows itself as more reticulated than that of Notosuchia, while the notosuchian lineage, especially the advanced forms (Notosuchidae, Baurusuchidae and Sphagesauridae), stay mainly in South America.

Furthermore, the results do not support the Africa-first or Pan-Gondwana hypothesis (SAMPSON *et al.*, 1998; HAY *et al.*, 1999; SERENO *et al.*, 2004; TURNER 2004; KRAUSE *et al.*, 2006), instead confirming a link between Gondwana and Europe (e.g.

Rabi & Sebok, 2015) until Aptian/Albian, and returned in Campanian-Eocene in the province of Atlantogea (Ezcurra & Agnolin, 2012). The fossil evidence of this faunistic exchange is the occurrence of *Chimaerasuchus paradoxus* (e.g. Wu *et al.*, 1995), a laurasian Notosuchia related to Aptian of China and Gondwanan Shartegosuchidae related from Santonian of Argentina, *Neuquensuchus australis* (e.g. Fiorelli & Calvo, 2008) and the related sebecians taxa of South America and Europe.

TABLES

Table 1: Areas used in the analyzes, the codes assigned to each one and the distribution of the taxa. Bold letters indicate change in code due to the smaller number of areas accepted by S-DIVA

Areas	Distribution		
	BBM	S-Diva	
Maevarano Formation	A	A	<i>Miadasuchus oblita</i> ; <i>Mahajangasuchus insignis</i> ; <i>Simosuchus clarki</i>
Iullemmeden Basin	B	B	<i>Kaprosuchus saharicus</i> ; <i>Stolokrosuchus lapparenti</i> ; <i>Trematochampsia taqueti</i> ; <i>Araripesuchus wegneri</i> ; <i>Anatosuchus minor</i>
Felgueira Grande Formation	C	C	<i>Iberosuchus</i>
Santa Lucia Formation	D	D	<i>Zulmasuchus querajazu</i>
Sarmiento Formation	E	E	<i>Sebecus icaeorhinus</i>
Maiz Gordo Formation	F	F	<i>Bretesuchus bonapartei</i>
Messel Formation	G	G	<i>Bergisuchus dietrichbergi</i>
Neuquén Basin	H	C	<i>Amargasuchus minor</i> ; <i>Lomasuchus palpebrosus</i> ; <i>Gasparinisuchus peirosauroides</i> ; A. <i>patagonicus</i> ; <i>Comahuesuchus brachybuccalis</i> ; <i>Notosuchus terrestris</i> ; <i>Pehuenchesuchus enderi</i> ; <i>Cynodontosuchus rothi</i> ; <i>Wargosuchus australis</i>
Araripe Basin	I	E	<i>Caririsuchus camposi</i> ; <i>Araripesuchus gomesii</i> ;
Bauru Group	J	D	<i>Itasuchus jesuinoi</i> ; <i>Barreirosuchus franciscoi</i> ; MCT 1723-R; <i>Pepesuchus deiseae</i> ; <i>Montealtosuchus arrudacamposi</i> ; <i>Uberabasuchus terrificus</i> ; <i>Peirosaurus torminni</i> ; <i>Mariliasuchus amarali</i> ; <i>Morrinhosuchus luziae</i> ;

			<i>Labidiosuchus amicum</i> ; <i>Adamantinasuchus navae</i> ; <i>Armadillosuchus arrudai</i> ; <i>Caryonosuchus pricei</i> ; <i>Sphagesaurus huenei</i> ; <i>Caipirasuchus paulistanus</i> ; <i>Caipirasuchus stenognathus</i> ; <i>Caipirasuchus montealtensis</i> ; <i>Pissarrachampsia sera</i> ; <i>Gondwanasuchus scabrosus</i> ; <i>Campinasuchus dinizi</i> ; <i>Stratiosuchus maxhecti</i> ; <i>Baurusuchus pacheco</i> ; <i>Baurusuchus salgadoensis</i> ; <i>Aplestosuchus sordidus</i> ; <i>Baurusuchus albertoi</i>
Kem Kem “Beds”	K	K	<i>Hamadasuchus rebouli</i>
Cerro Barcino Formation	L	L	<i>Barcinosuchus</i>
Litoral Basin	M	F	<i>Uruguaysuchus aznarezi</i>
Oasis Bahariya	N	G	<i>Libycosuchus brevirostris</i>
Parnaíba Basin	O	H	<i>Candidodon itapecuruensis</i>
Cajones Formation	P	I	<i>Yacarerani boliviensis</i>
Wulong Formation	Q	J	<i>Chimaerasuchus paradoxus</i>
Pab Formation	R	K	<i>Pabwehshi pakistanensis</i>

FIGURES

Figure 1: Phylogenetic cladogram for Mesoeucrocodylia without Neosuchia, with the branches numbered to BPA. The letters are codes to identify the areas.

Figure 1 is a stratigraphic chart showing the correlation of geological stages between the Juras, Cretáceo, and Paleógeno eras. The chart is divided into three main columns: Juras, Cretáceo, and Paleógeno. The vertical axis represents time in millions of years (Ma) from 163.5 to 33.9. The chart shows various geological stages and their corresponding time ranges, with some stages having multiple sub-divisions. The stages are color-coded: Juras (blue), Cretáceo (green), and Paleógeno (orange). The chart also includes a scale for the time intervals between stages, with values ranging from 0.1 to 6.2 Ma.

Era	Sub-Éra	Stage	Time Range (Ma)
Juras	Neo	Tithoniano	152.14 ± 0.9
	Kimmeridgiano	Kimmeridgiano	157.34 ± 1.0
	Oxfordiano	Oxfordiano	163.5
Cretáceo	Eo	Berriasiano	139.8
	Valanginiano	Valanginiano	132.9
	Hauterueviano	Hauterueviano	129.4
	Barremiano	Barremiano	125.0
	Aptiano	Aptiano	113.0
	Albiano	Albiano	100.5
	Cenomaniano	Cenomaniano	98.8 ± 0.0
	Coniaciano	Coniaciano	96.3 ± 0.0
	Santoniano	Santoniano	93.6 ± 0.0
	Campaniano	Campaniano	72.1 ± 0.0
	Maastrichtiano	Maastrichtiano	66.0
Paleógeno	Paleoc.	Daniano	61.6
	Selandiano	Selandiano	59.2
	Thanetiano	Thanetiano	56.0
	Ypresiano	Ypresiano	47.8
	Lutetiano	Lutetiano	41.2
	Bartoniano	Bartoniano	37.8
	Priamboniano	Priamboniano	33.9
Eoceno	Eoceno	33.9	

Figure 4: Time-calibrated General Area Cladogram from Gondwanan Mesoeucrocodylia. Grey bars represent the possible range of divergence times at each time-calibrated node. See the discussion below for node-by-node interpretations of biogeographical events.

145 Ma Reconstruction

Figure 6: Dispersion routes from Ancestral Area in Iullemmeden Basin to another African and South American localities.

Figure 7: Peirosauridae dispersion routes from Africa to South American in two distinctive moments: first from Africa to northern of South American, second to Africa to Bauru Group and then to Neuquén Group.

Figure 8: Consensus BPA/BBM/S-DIVA General Area Cladogram with node ancestral area reconstruction for Notosuchia. Thicker lines represent general nodes; thinner lines represent unique, clade-specific events. Sequential Arrows = post-speciation dispersal into the areas. Spotted circle (ancestor) + open circle (peripheral isolate) = instance of peripheral isolates speciation. Numbers accompanying slash marks refer to species.

Figure 9: Dispersion route of *Araripesuchus* from African area to South American areas.

Figure 10: Dispersion route of Notosuchidae and Sphagesauridae. The isolation of Bauru Group after de Santonian favored the endemism of this groups.

Data available statement: The tnt matrix file, the nexus file to BPA and Condensed tree to RASP analysis can be download by the link: <https://bit.ly/2KPN1Rp>

REFERENCES

- Ali, J. R., & Krause, D. W. (2011). Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: Refutation of the Gunnerus Ridge causeway hypothesis. *Journal of Biogeography*, 38(10), 1855–1872. <https://doi.org/10.1111/j.1365-2699.2011.02546.x>
- Assine, M. L. (2007). Bacia do Araripe, 371–389.
- Bata, T. (2016). Evidences of Widespread Cretaceous Deep Weathering and Its Consequences: A Review. *Earth Science Research*, 5(2), 69. <https://doi.org/10.5539/esr.v5n2p69>
- Brandalise, M., Andrade, D., & Bertini, R. J. (2008). A new Sphagesaurus (Mesoeucrocodylia : Notosuchia) from the Upper Cretaceous of Monte Alto City (Bauru Group , Brazil), and a revision of the Sphagesauridae. *Historical Biology*, 20(2), 101–136. <https://doi.org/10.1080/08912960701642949>
- Brooks, D. R., & McLennan, D. A. (2001). A comparison of a discovery-base and an event-based method in historical biogeography. *Journal of Biogeography*, 28(3), 757–767. <https://doi.org/10.1046/j.1365-2699.2001.00598.x>
- Brooks, D. R., Veller, M. G. P. Van, & McLennan, D. A. (2001). How to do BPA , really. *Journal of Biogeography*, 28, 345–358.
- Buffetaut, E., & Rage, J. (1993). Fossil amphibians and reptiles and the Africa-South America connection. In *The Africa–South America connection* (pp. 87–99).
- Calvo, J. O. (2007). The first “protosuchian” (Archosauria: Crocodyliformes) from the Cretaceous (Santonian) of Gondwana. *Arquivos Do Museu Nacional*, 65(4), 417–459.

- Carvalho, I. de S., de Gasparini, Z. B., Salgado, L., de Vasconcellos, F. M., & Marinho, T. da S. (2010). Climate's role in the distribution of the Cretaceous terrestrial Crocodyliformes throughout Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 297(2), 252–262. <https://doi.org/10.1016/j.palaeo.2010.08.003>
- Carvalho, I. de S., Ribeiro, L. C. B., & Avilla, L. dos S. (2004). *Uberabasuchus terrificus* sp. nov., a new crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. *Gondwana Research*, 7(4), 975–1002. [https://doi.org/10.1016/S1342-937X\(05\)71079-0](https://doi.org/10.1016/S1342-937X(05)71079-0)
- Colbert, E. H. (1984). Mesozoic reptiles, India and Gondwanaland. *Indian Journal of Earth Sciences*, 11, 25–37.
- Colbert, E. H. (2006). The Eustachian Tubes in the Crocodilia. *Copeia*, 1946(1), 12. <https://doi.org/10.2307/1438813>
- Dal Sasso, C., Pasini, G., Fleury, G., & Maganuco, S. (2017). Razanandrongobe sakalavae, a gigantic mesoeucrocodylian from the Middle Jurassic of Madagascar, is the oldest known notosuchian. *PeerJ*, 5, e3481. <https://doi.org/10.7717/peerj.3481>
- de Andrade, M. B., Edmonds, R., Benton, M. J., & Schouten, R. (2011). A new Berriasian species of Goniopholis (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus. *Zoological Journal of the Linnean Society*, 163(SUPPL. 1), 66–108. <https://doi.org/10.1111/j.1096-3642.2011.00709.x>
- Ezcurra, M. D., & Agnolín, F. L. (2012). A new global palaeobiogeographical model for the late mesozoic and early tertiary. *Systematic Biology*, 61(4), 553–566. <https://doi.org/10.1093/sysbio/syr115>
- Fiorelli, L., & Calvo, J. O. (2008). New remains of Notosuchus terrestris Woodward, 1896 (Crocodyliformes : Mesoeucrocodylia) from Late Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos Do Museu Nacional, Rio de Janeiro*, 66(1), 83–124.
- Folinsbee, K. E., & Evans, D. C. (2012). A protocol for temporal calibration of general area cladograms. *Journal of Biogeography*, 39(4), 688–697. <https://doi.org/10.1111/j.1365-2699.2011.02643.x>
- Gasparini, Z. (2006). An Unusual Marine Crocodyliform from the Jurassic-Cretaceous Boundary of Patagonia. *Science*, 311(5757), 70–73. <https://doi.org/10.1126/science.1120803>
- Gasparini, Zulma. (1996). Biogeographic evolution of the South American crocodilians. *Münchener Geowiss. Abh.*, 30, 159–184.
- Geroto, C. F. C., & Bertini, R. J. (2019). New material of Pepesuchus (Crocodyliformes; Mesoeucrocodylia) from the Bauru Group: Implications about its phylogeny and the age of the Adamantina Formation. *Zoological Journal of the Linnean Society*, 185(2). <https://doi.org/10.1093/zoolinnean/zly037>
- Godoy, P. L., Montefeltro, F. C., Norell, M. A., & Langer, M. C. (2014). An additional Baurusuchid from the cretaceous of Brazil with evidence of interspecific predation among crocodyliformes. *PLoS ONE*, 9(5), 1–12. <https://doi.org/10.1371/journal.pone.0097138>
- Goloboff, P. A., Farris, J. S., & Nixon, K. C. (2008). Cladistics TNT , a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.
- Gomani, E. M., & Gomani, E. M. (1997). A crocodyliform from the early cretaceous dinosaur beds, northern malawi. *Journal of Vertebrate Paleontology*, 17(2), 280–294. <https://doi.org/10.1080/02724634.1997.10010975>
- Gould, S. J. (1982). Punctuated equilibrium-a different way of seeing. *New Scientist*, 94(1301), 137–141.

- Halas, D., Zamparo, D., & Brooks, D. R. (2005). A historical biogeographical protocol for studying biotic diversification by taxon pulses. *Journal of Biogeography*, 32, 249–260.
- Hao, Y., Su, D., Yu, J., Li, P., Li, Y., Wang, N., ... Zhang, Q. (1986). Stratigraphy of the China: the Cretaceous system of China. *Beijing: Geological Publishing House*, 2, 310.
- Hay, W. W., DeConto, R. M., Wold, C. N., Wilson, K. M., Voigt, S., Schulz, M., ... Söding, E. (1999). Alternative global Cretaceous paleogeography. *Special Paper 332: Evolution of the Cretaceous Ocean-Climate System, Special Pa*, 1–47. <https://doi.org/10.1130/0-8137-2332-9.1>
- Krause, D. W., O'Connor, P. M., Rogers, K. C., Sampson, S. D., Buckley, G. A., & Rogers, R. R. (2006). Late Cretaceous Terrestrial Vertebrates From Madagascar: Implications for Latin American Biogeography 1. *Annals of the Missouri Botanical Garden*, 93(2), 178–208. [https://doi.org/10.3417/0026-6493\(2006\)93\[178:LCTVFM\]2.0.CO;2](https://doi.org/10.3417/0026-6493(2006)93[178:LCTVFM]2.0.CO;2)
- Krause, D. W., Sertich, J. J. W., Connor, P. M. O., Rogers, K. C., & Rogers, R. R. (2019). The Mesozoic Biogeographic History of Gondwanan Terrestrial Vertebrates : Insights from Madagascar's Fossil Record. *Annual Review of Earth and Planetary Sciences*, (6), 519–553. <https://doi.org/10.1146/annurev-earth-053018-060051>
- Larsson, H. C. E., & Gado, B. (2018). A new Early Cretaceous crocodyliform from Niger. *Neues Jahrbuch Für Geologie Und Paläontologie - Abhandlungen*, 217(1), 131–141. <https://doi.org/10.1127/njgpa/217/2000/131>
- Larsson, H. C. E., & Sues, H. (2007). Cranial osteology and phylogenetic relationships of Hamadasuchus rebouli (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. *Zoological Journal of the Linnean Society*, 149(4), 533–567. <https://doi.org/10.1111/j.1096-3642.2007.00271.x>
- Leanza, A. H., Apesteguía, S., Novas, F. E., & Fuente, M. S. de la. (2004). Basin Cretaceous terrestrial beds from the Neuque (Argentina) and their tetrapod assemblages, 25. <https://doi.org/10.1016/j.cretres.2003.10.005>
- Lieberman, B. S. (2003). *Unifying theory and methodology in biogeography*. (R. Macintyre & M. T. Clegg, Eds.). New York: SPRINGER SCIENCE+BUSINESS MEDIA, LLC.
- Maganuco, S., Dal Sasso, C., & Pasini, G. (2006). A new large predatory archosaur from the Middle Jurassic (Bathonian) of Madagascar. *Atti Della Societa Italiana Di Scienze Naturali e Del Museo Civico Di Storia Naturale in Milano*, 147(I), 19–51.
- Maisey, J. G. (1991). *Santana fossils illustrated atlas*. (J. G. Maisey, Ed.). Neptune: T.F.H. Publications.
- Manassero, M., Zalba, P. E., Andreis, R. R., & Morosi, M. (2000). Petrology of continental pyroclastic and epiclastic sequences in the Chubut Group (Cretaceous): Los Altares-Las Plumas area, Chubut, Patagonia Argentina. *Revista Geológica de Chile*, 27(1), 13–26. <https://doi.org/10.4067/S0716-02082000000100002>
- Martinelli, A. G. (2003). New cranial remains of the bizarre notosuchid Comahuesuchus brachybuccalis (Archosauria, Crocodyliformes) from the Late Cretaceous of Río Negro Province (Argentina). *Ameghiniana*, 40(4), 559–572. <https://doi.org/00027014>
- Menegazzo, M. C., Catuneanu, O., & Kiang, C. H. (2016). The South American retroarc foreland system: the development of the Bauru Basin in the back-bulge province. *Marine and Petroleum Geology*. <https://doi.org/10.1016/j.marpetgeo.2016.02.027>

- Meunier, L. M. V., & Larsson, H. C. E. (2017). *Trematochampsia taqueti and the crocodyliform diversity of the Late Cretaceous In Beceten Formation of Niger. Zoological Journal of the Linnean Society.*
- Montefeltro, Felipe C., Larsson, H. C. E., De França, M. A. G., & Langer, M. C. (2013). A new neosuchian with Asian affinities from the Jurassic of northeastern Brazil. *Naturwissenschaften*, 100(9), 835–841. <https://doi.org/10.1007/s00114-013-1083-9>
- Montefeltro, Felipe C., Larsson, H. C. E., & Langer, M. C. (2011). A new baurusuchid (Crocodyliformes, Mesoeucrocodylia) from the late cretaceous of Brazil and the phylogeny of Baurusuchidae. *PLoS ONE*, 6(7). <https://doi.org/10.1371/journal.pone.0021916>
- Montefeltro, Felipe Chinaglia. (2013). *Revisão filogenética de Mesoeucrocodylia: irradiação basal e principais controvérsias*. Universidade de São Paulo. Retrieved from <http://www.teses.usp.br/teses/disponiveis/59/59139/tde-12032013-092125/en.php>
- Moody, R. T. J. (1997). The Iullemmeden Basin. In R. C. Selley (Ed.), *African Basins. Sedimentary Basins of the World* (3rd ed., pp. 89–103). Amsterdam: Elsevier Science B.V.
- Moody, R. T. J., & Sutcliffe, P. J. C. (1991). The Cretaceous deposits of the Iullemmeden Basin of Niger, central West Africa. *Cretaceous Research*, 12, 137–157.
- Morrone, J. J. (2008). *Evolutionary Biogeography: An Integrative Approach with Case Studies*. Columbia University Press.
- Nascimento, P. M., & Zaher, H. (2011). The skull of the Upper Cretaceous baurusuchid crocodile Baurusuchus albertoi Nascimento & Zaher 2010, and its phylogenetic affinities. *Zoological Journal of the Linnean Society*, 163(SUPPL. 1), 116–131. <https://doi.org/10.1111/j.1096-3642.2011.00708.x>
- Ortega, F., Gasparini, Z., Buscalioni, A. D., & Calvo, J. O. (2000). A new species of Araripesuchus (Crocodylomorpha, Mesoeucrocodylia) from the lower Cretaceous of Patagonia (Argentina). *Journal of Vertebrate Paleontology*, 20(1), 57–76. [https://doi.org/10.1671/0272-4634\(2000\)020\[0057:ANSOAC\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2000)020[0057:ANSOAC]2.0.CO;2)
- Pol, D. (1999). *El esqueleto postcraneano de Notosuchus terrestris (Archosauria : Crocodyliformes) del Cretácico Superior de la Cuenca Neuquina y su información filogenética*. Universidad de Buenos Aires, Argentina.
- Pol, D. (2003). New Remains of Sphagesaurus Huenei (Crocodylomorpha: Mesoeucrocodylia) From the Late Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, 23(4), 817–831. <https://doi.org/10.2307/4524384>
- Pol, D., & Apesteguía, S. (2005). New Araripesuchus Remains from the Early Late Cretaceous (Cenomanian–Turonian) of Patagonia. *American Museum Novitates*, 3490(1), 1. [https://doi.org/10.1206/0003-0082\(2005\)490\[0001:NARFTE\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2005)490[0001:NARFTE]2.0.CO;2)
- Pol, D., & Leardi, J. M. (2015). Divertisty patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) during the Cretaceous of Gondwana. *Publicación Electrónica de La Asociación Paleontológica Argentina*, 15(1), 172–186. <https://doi.org/10.5710/PEAPA.10.06.2015.108>
- Pol, D., Leardi, J. M., Lecuona, A., & Krause, M. (2012). Postcranial anatomy of Sebecus icaeorhinus (Crocodyliformes, Sebecidae) from the Eocene of Patagonia. *Journal of Vertebrate Paleontology*, 32(2), 328–354. <https://doi.org/10.1080/02724634.2012.646833>
- Pol, D., Nascimento, P. M., Carvalho, A. B., Riccomini, C., Pires-Domingues, R. A., & Zaher, H. (2014). A new notosuchian from the late cretaceous of Brazil and the phylogeny of advanced notosuchians. *PLoS ONE*, 9(4).

- <https://doi.org/10.1371/journal.pone.0093105>
- Posada, D. (2003). Selecting models of evolution. In M. Salemi & A.-M. Vandamme (Eds.), *The phylogenetic handbook. A practical approach to DNA and protein phylogeny* (pp. 345–361). Cambridge, UK: Cambridge University Press.
<https://doi.org/10.1017/cbo9780511819049.012>
- Potter, P. E. (1997). The Mesozoic and Cenozoic paleodrainage of South America: a natural history. *Journal of South American Earth Sciences*, 10(5–6), 331–344.
[https://doi.org/10.1016/S0895-9811\(97\)00031-X](https://doi.org/10.1016/S0895-9811(97)00031-X)
- Price, L. I. (1945). A new reptil from the Cretaceous Brazil. *Divisão de Geologia e Mineralogia Notas Preliminares e Estudos*, (25), 1–9.
- Price, L. I. (1955). Novos Crocodilídeos dos Arenitos da Série Baurú, Cretáceo do Estado de Minas Gerais. *Anais Da Academia Brasileira de Ciências*, 27(4), 487–453.
- Rabi, M., & Sebok, N. (2015). A revised Eurogondwana model: Late Cretaceous notosuchian crocodyliforms and other vertebrate taxa suggest the retention of episodic faunal links between Europe and Gondwana during most of the Cretaceous. *Gondwana Research*, 28(3), 1197–1211.
<https://doi.org/10.1016/j.gr.2014.09.015>
- Renne, P. R., Deino, A. L., Hilgen, F. J., Kuiper, K. F., Mark, D. F., Mitchell, W. S., ... Smit, J. (2013). Time Scales of Critical Events Around. *Science*, 339(February), 684–687. <https://doi.org/10.1126/science.1230492>
- Renne, P. R., Ernesto, M., Pacca, G., Coe, R. S., Glen, J. M., Prevot, M., & Perrin, M. (1992). The Age of Parana Flood Volcanism, Rifting of Gondwanaland, and the Jurassic-Cretaceous Boundary. *Science*, 258, 975–979.
- Renne, P. R., Glen, J. M., Milner, S. C., & Duncan, A. R. (1996). Age of Etendeka flood volcanism and associated intrusions in southwestern Africa. *Geology*, 24(7), 659–662. [https://doi.org/10.1130/0091-7613\(1996\)024<0659:AOEFVA>2.3.CO;2](https://doi.org/10.1130/0091-7613(1996)024<0659:AOEFVA>2.3.CO;2)
- Research Center for the Marine Geoscience at the CAU, K. (2014). Ocean Drilling Stratigraphic Network. Retrieved July 30, 2017, from <http://www.odsn.de/odsn/index.html>
- Riccomini, C. (1997). Arcabouço estrutural e aspectos do tectonismo gerador e deformador da Bacia Bauru no Estado de São Paulo. *Revista Brasileira de Geociências*, 27, 153–162.
- Romer, A. S. (1997). *Osteology of the reptiles* (Reprint Ed). Berlin: Malabar Krieger Publishing Company.
- Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes3: Bayesian phylogenetic inference undermixed models. *Bioinformatics*, 19, 1572–1574.
- Rossetti, D. D. E. F., & Góes, A. N. A. M. (2003). Caracterização paleoambiental de depósitos albianos na borda sul da Bacia de São Luís-Grajaú : modelo de delta fluvial influenciado por tempestade, 33(3), 299–312.
- Rossetti, L. M., Lima, E. F., Waichel, B. L., Scherer, C. M., & Barreto, C. J. (2014). Stratigraphical framework of basaltic lavas in Torres Syncline main valley, southern Parana-Etendeka Volcanic Province. *Journal of South American Earth Sciences*, 56, 409–421. <https://doi.org/10.1016/j.jsames.2014.09.025>
- Sampson, S. D., Sampson, S. D., Witmer, L. M., Forster, C. A., Krause, D. W., Connor, P. M. O., & Dodson, P. (1998). Predatory Dinosaur Remains from Madagascar : Implications for the Cretaceous Biogeography of Gondwana. *Science*, 280, 1048–1051. <https://doi.org/10.1126/science.280.5366.1048>
- Sereno, P. C., Sidor, C. a., Larsson, H. C. E., & Gado, B. (2003). A new notosuchian from the Early Cretaceous of Niger. *Journal of Vertebrate Paleontology*, 23(June),

- 477–482. [https://doi.org/10.1671/0272-4634\(2003\)023\[0477:ANNFTE\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2003)023[0477:ANNFTE]2.0.CO;2)
- Sereno, P. C., Wilson, J. A., & Conrad, J. L. (2004). New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proceedings of the Royal Society B: Biological Sciences*, 271(1546), 1325–1330. <https://doi.org/10.1098/rspb.2004.2692>
- Sereno, P. C., Larsson, H. C., Sidor, C. a., & Gado, B. (2001). The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science*, 294(5546), 1516–1519. <https://doi.org/10.1126/science.1066521>
- Sereno, Paul C, Wilson, J. A., Conrad, J. L., Sereno, P. C., Wilson, J. A., & Conrad, J. L. (2009). New dinosaurs link southern landmasses in the Mid – Cretaceous New dinosaurs link southern landmasses in the Mid-Cretaceous, (July 2004). <https://doi.org/10.1098/rspb.2004.2692>
- Sill, W. D. (2006). The Zoogeography of the Crocodilia. *Copeia*, 1968(1), 76. <https://doi.org/10.2307/1441553>
- Simpson, G. G. (1937). An ancient eusuchian crocodile from Patagonia. *American Museum Novitates*, (965), 1–20.
- Thiede, D. S., & Vasconcelos, P. M. (2010). Paraná flood basalts: Rapid extrusion hypothesis confirmed by new ⁴⁰Ar/³⁹Ar results. *Geology*, 38(8), 747–750. <https://doi.org/10.1130/G30919.1>
- Tunik, M., Folguera, A., Naipauer, M., Pimentel, M., & Ramos, V. A. (2010). Early uplift and orogenic deformation in the Neuquén Basin: Constraints on the Andean uplift from U-Pb and Hf isotopic data of detrital zircons. *Tectonophysics*, 489(1–4), 258–273. <https://doi.org/10.1016/j.tecto.2010.04.017>
- Turner, A. H. (2004). Crocodyliform biogeography during the Cretaceous: Evidence of Gondwanan vicariance from biogeographical analysis. *Proceedings of the Royal Society B: Biological Sciences*, 271(1552), 2003–2009. <https://doi.org/10.1098/rspb.2004.2840>
- Turner, A. H. (2006). *Osteology and phylogeny of a new species of Araripesuchus (Crocodyliformes: Mesoeucrocodylia) from the Late Cretaceous of Madagascar. Historical Biology A Journal of Paleobiology* (Vol. 18). <https://doi.org/10.1080/08912960500516112>
- Turner, A. H., & Sertich, J. J. W. (2010). Phylogenetic history of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 30(sup1), 177–236. <https://doi.org/10.1080/02724634.2010.532348>
- Upchurch, P. (1995). The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 349(1330), 365–390. <https://doi.org/10.1098/rstb.1995.0125>
- Vaz, P. T., Andrade, G. De, Ribeiro, J., Filho, W., Antônio, W., & Travassos, S. (2007). Bacia do Parnaíba, 253–263.
- Wilson, J. a, Malkani, M. S., & Gingerich, P. D. (2001). New crocodyliform (Reptilia, Mesoeucrocodylia) from the Upper Cretaceous Pab Formation of Vitakri, Balochistan (Pakistan). *Contributions from the Musuem of Paleontology*, 30(12), 321–336. Retrieved from http://www-personal.umich.edu/~wilsonja/JAW/Publications_files/Wilson&al2001.pdf
- Woodward, A. S. (1896). On two Mesozoic crocodilians *Notosuchus* (Genus Novum) and *Cynodontosuchus* (Genus Novum) from the red sandstones of the territory of Neuquen. *Anales Del Museo Nacional de La Plata. Paleontologia Argentina*, 4(1–2), 1–19.
- Wu, X.-C., & Sues, H.-D. (1996). Anatomy and phylogenetic relationships of *Chimaerasuchus paradoxus*, an unusual crocodyliform reptile from the Lower

- Cretaceous of Hubei, China. *Journal of Vertebrate Paleontology*, 16(4), 688–702. <https://doi.org/10.1080/02724634.1996.10011358>
- Wu, X., Sues, H.-D., & Sun, A. (1995). A plant-eating crocodyliform reptile from the Cretaceous of China. *Nature*. <https://doi.org/10.1038/376678a0>
- Yu, Y., Harris, A. J., & He, X. (2010). S-DIVA (statistical dispersal-vicariance analysis): a tool for inferring biogeographic histories. *Molecular Phylogenetics and Evolution*, 56(2), 848–850.
- Yu, Y., Harris, A. J., & He, X. (2015). RASP (Reconstruct Ancestral State in Phylogenies): A tool for historical biogeography. *Molecular Phylogenetics and Evolution*, 87(February 2016), 46–49. <https://doi.org/10.1016/j.ympev.2015.03.008>

Biosketch: Caio Fabricio Cezar Geroto has special interests in Crocodylomorpha systematic and biogeography. The present work is a continuous of their PhD efforts to understand the complex evolutionary history of this group mainly during the Cretaceous Period.