

Late Cretaceous Notosuchians of the Maevarano Formation, Mahajanga Basin: An Ecomorphological Perspective

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ABSTRACT

The Maastrichtian Maevarano Formation of northwestern Madagascar represents deposition in a seasonal dry-wet system and hosts a rich assemblage of well-preserved fossil vertebrates. Notosuchian crocodyliforms, a diverse group of mesoeucrocodylians frequently found in Upper Cretaceous rocks of Gondwana, are well represented in this assemblage. The current study focuses on the four recognized notosuchians (*Simosuchus clarki*, *Araripesuchus tsangatsangana*, *Miadasuchus oblita* and *Mahajangasuchus insignis*), examining their morphologic diversity to provide insight into the ecology of these sympatric taxa. Here, several complete and incomplete skulls were examined, with measurements of each cranial opening acquired for quantitative analysis. Digital photographs and high-resolution renderings based on CT/ μ CT reconstructions were utilized. The size, position, and orientation of the external nares, orbits, and choanae were characterized, with the relative position and size of temporal, suborbital, and external mandibular fenestrae noted for comparisons. The dentitions (size, shape, number of teeth) of the four notosuchians were also included in this study, allowing direct insight into feeding ecology of the four taxa. From the data and approaches used herein, morphologic differences were utilized to interpret potential roles of the different species in the Maevarano ecosystem. The four notosuchians can be divided between terrestrial and semi-aquatic habits, and within these ecologies, size and tooth shape assist in determining possible feeding ecology. Of the three primarily carnivorous taxa (*Mahajangasuchus*, *Miadasuchus*, *Araripesuchus*), only *Miadasuchus* and *Araripesuchus* overlapped ecologically as terrestrial predators. Maximum adult size differences between these two forms likely contributed to differences in prey choice, thereby permitting coexistence in the terrestrial environment. *Simosuchus*, the other terrestrial notosuchian, clearly differs from the others based on both skull and dental morphology and occupied a primarily herbivorous niche. Finally, *Mahajangasuchus* is the sole semi-aquatic notosuchian in the assemblage, sharing this habitat with representative and smaller-bodied neosuchians and other aquatic vertebrates and potentially competing with the other carnivorous forms for prey. In sum, the Maevarano Formation vertebrate assemblage can be used as a case-study for comparison with other Mesozoic assemblages with multiple crocodyliforms.

Key Words: Ecomorphology, crocodyliforms, Maastrichtian, Maevarano Formation, Mahajanga Basin, Madagascar

RÉSUMÉ

La Formation Maevarano Maastrichtienne du nord-ouest de Madagascar représente un dépôt d'un système saisonnier sec-humide et abrite une richesse bien conservée d'assemblage de fossiles de vertébrés. Les crocodyliformes notosuchiens, un groupe diversifié de mésoeucrocodyliens fréquemment trouvés dans les couches du Crétacé supérieur du Gondwana, sont bien représentés dans cet assemblage. La présente étude a comme objectif de caractériser les quatre notosuchiens reconnus (*Simosuchus clarki*, *Araripesuchus tsangatsangana*, *Miadasuchus oblita* et *Mahajangasuchus insignis*), en examinant leur diversité morphologique pour donner un aperçu de l'écologie de leur taxons sympatriques. Pour ce faire, des mensurations

en vue d'une analyse quantitative de plusieurs crânes complets et incomplets ont été prises et particulièrement au niveau de chaque ouverture crânienne. Des photographies numériques et des images à haute résolution basées sur des reconstructions CT/ μ CT ont été utilisées. La taille, la position et l'orientation des narines externes, des orbites et des choanes ont été caractérisées, la position et la taille relatives des fenêtres temporales, sous-orbitaires et mandibulaires externes étant notées à des fins de comparaison. Les résultats mettent en lumière plusieurs aspects significatifs. Tout d'abord, à partir des données et des méthodes utilisées, les différences morphologiques ont été utilisées pour interpréter l'écosystème potentiels de Maevarano. Les quatre notosuchiens peuvent être divisés entre habitats terrestres ou semi-aquatiques, avec leurs écologies. La taille et la forme des dents s'avèrent des indicateurs importants pour déterminer les aspects possible du type de mode d'alimentation. Parmi les trois taxons principalement carnivores (*Mahajangasuchus*, *Miadasuchus*, *Araripesuchus*), seuls *Miadasuchus* et *Araripesuchus* se chevauchaient écologiquement en tant que prédateurs terrestres, en raison de leur taille adulte maximale qui contribue aux différences dans le choix des proies and permettent ainsi la coexistence. Par ailleurs, *Simosuchus*, étant un notosuchien terrestre, se distingue clairement des autres en termes de la morphologie crânienne et dentaire, occupant une niche principalement herbivore. Enfin, *Mahajangasuchus* est le seul notosuchien semi-aquatique dans cet l'assemblage, partageant cet habitat avec des néosuchiens représentatifs et de plus petit corps et d'autres vertébrés aquatiques et potentiellement en compétition avec les autres formes carnivores pour les proies. En résumé, l'ensemble des vertébrés de la Formation de Maevarano peut être utilisé comme étude de cas pour la comparaison avec d'autres assemblages du Mésozoïque comprenant plusieurs crocodyliformes.

Mots-clés: Ecomorphologie, Crocodyliformes, Maastrichtien, Formation de Maevarano, Bassin de Mahajanga, Madagascar

I. Introduction

The Upper Cretaceous Maevarano Formation (Fm), Mahajanga Basin, northwestern Madagascar abounds with a rich vertebrate fauna (Krause et al., 1999, 2006, 2019, 2022). Much of the recent (1990s to the present) research on the Maevarano Formation faunal assemblage, stratigraphy, and paleoenvironments has been conducted under the framework of the Mahajanga Basin Project (MBP), a long-term collaborative effort between the University of Antananarivo (Madagascar), Ohio University (USA), Stony Brook University (USA), Macalester College (USA), and the Denver Museum of Nature & Science (USA). Fourteen field expeditions have been carried out as part of the MBP, with numerous contributions describing a range of taxa

and their paleoenvironmental and geochronological context (see Krause et al., 2006, 2022; Rogers et al., 2000, 2013, and references therein for reviews). To date, the discovery and descriptions of representatives from nine groups of intriguing fossil vertebrates have sought to characterize the biodiversity of the landmass at the end of the Cretaceous Period (Krause et al., 2022). Regarding reptiles, and crocodyliforms specifically, there are currently six distinct taxa known from the Maevarano Formation, with two still undergoing primary description and awaiting formal names. The remaining four are notosuchians, and include two small terrestrial forms, *Simosuchus clarki* (Buckley et al., 2000) and *Araripesuchus tsangatsangana* (Turner, 2006), one medium-sized terrestrial form represented by *Miadasuchus oblita* (Buffetaut and Taquet, 1979; Simons and Buckley, 2009); and the large, semi-aquatic, *Mahajangasuchus insignis* (Buckley and Brochu, 1999; Turner and Buckley, 2008). These four species and their associated fauna are remarkably well preserved and represented in the Maevarano Formation.

Previous research on Maevarano Fm notosuchians have addressed a range of topics, including evolution of the secondary palate (Turner and Buckley, 2008) and a preliminary ontogenetic study of the skull of *Mahajangasuchus insignis* (Rakotozafy, 2016). A redescription of *Miadasuchus* (= *Trematochampsia*) *oblita* was made by Simons and Buckley (2009), highlighting the various species among taxa included in Trematochampsidae. Finally, *Simosuchus clarki* has received the most detailed attention, with a thorough accounting of its general background and paleoenvironmental context (Krause et al., 2010), a monographic treatment of both its cranial/dental (Kley et al. 2010) and postcranial (Raveloson, 2007; Georgi and Krause, 2010; Hill, 2010; Sertich and Groenke, 2010) anatomy, and a comprehensive phylogenetic assessment (Turner and Sertich, 2010). Finally, *Simosuchus* has also featured more recently in considerations of the evolution of crocodyliform dentitions (Ősi, 2013; Melstrom and Irmis, 2019).

Considering such detailed research on many aspects of the Maevarano Formation notosuchian assemblage, none to date have sought to provide a formation-level overview of the ecomorphology of these species in the context of their

environment. The basic questions addressed in this contribution highlight how morphology reflects ecology of four notosuchian crocodyliforms within this single formation. As an ecomorphological analysis, the current work focuses on the general architecture, position, and anatomical relationships of openings (e.g., fenestrae) in different regions of the craniomandibular skeleton, an overview of dental morphology, and a consideration of body size disparity within the Maevarano Formation notosuchian fauna. The specific objectives are to characterize the morphology of the cranial openings and dentition in the four crocodyliform taxa to develop hypotheses regarding their ecological roles.

Setting of the Maevarano Formation

The basic geomorphology of the Mahajanga Basin in which the Maevarano Formation is exposed consists of a landform with extensive erosion that dissects the Cretaceous surface into complex valleys and hills, giving this region an open and rugged appearance ; much of it is vegetated with fire throughout the year (Rogers et al., 2000; Rahantarisoa, 2007). There are four main field areas in which crocodyliforms have been recovered (Fig. 1), with the Berivotra field Area being the most intensely surveyed to date. It is characterized by a steppe embellished by palm trees while other areas (e.g., Kinkony, Masikakoho) are represented by more extensive dry forests (see Rogers et al., 2013 for an overview of the landform characteristics).

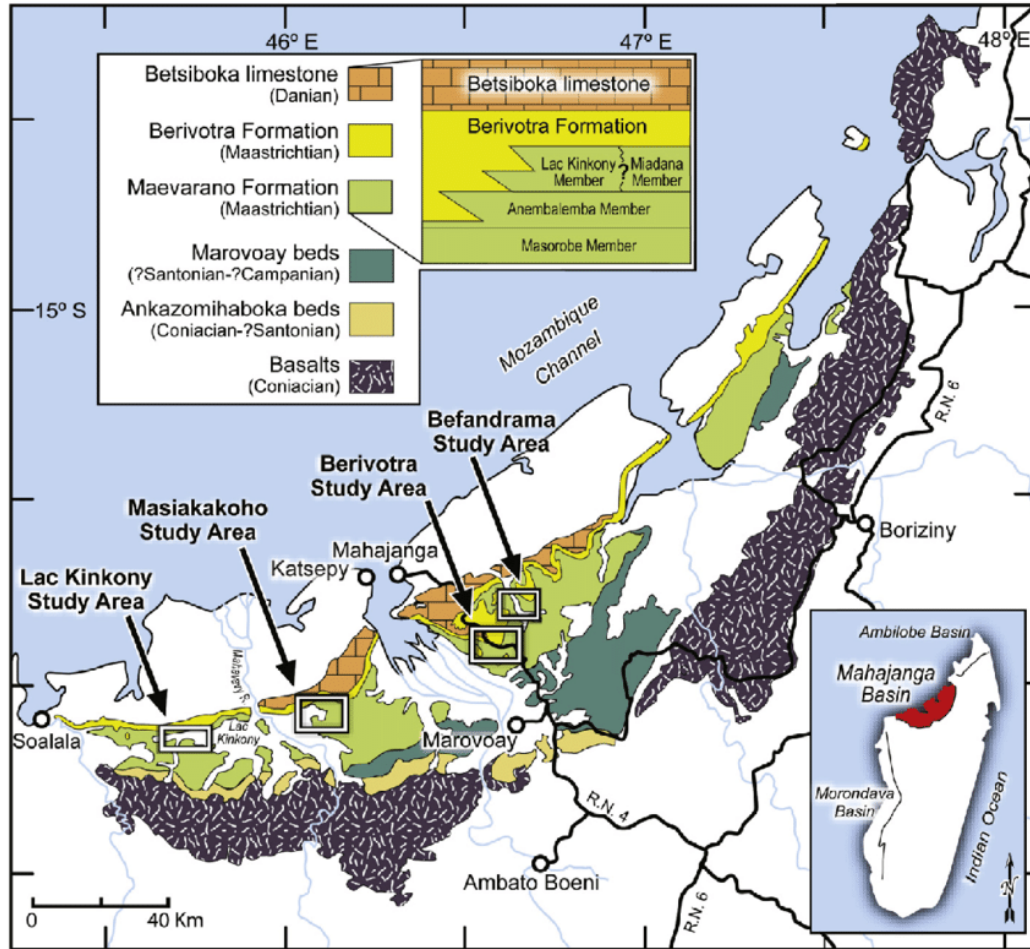


Figure 1: Geological context and main field areas of the Mahajanga Basin Project (modified from Rogers et al., 2013).

Lithological Characteristics of the Maevarano Formation

The sedimentology and stratigraphy of the Maevarano Formation was thoroughly characterized by Rogers and colleagues (2000, 2013). It is typically continental in nature, deposited during a mix of rainy and dry seasons during the Maastrichtian. The basic lithology consists of coarse-to-fine grained sandstone with intercalations of clayey or silty sandstone. The Maevarano Formation overlies the Marovoay beds (?Santonian-?Campanian); however, the nature of their contact remains unknown due to a lack of outcrop and extensive vegetation cover. By contrast, the overlying marine Maastrichtian Berivotra Formation, characterized predominantly by siltstones and claystones, provides a clear upper boundary with

extensive outcrop contacts with the Maevarano Formation (Rogers et al., 2000, 2013 Fig. 2).

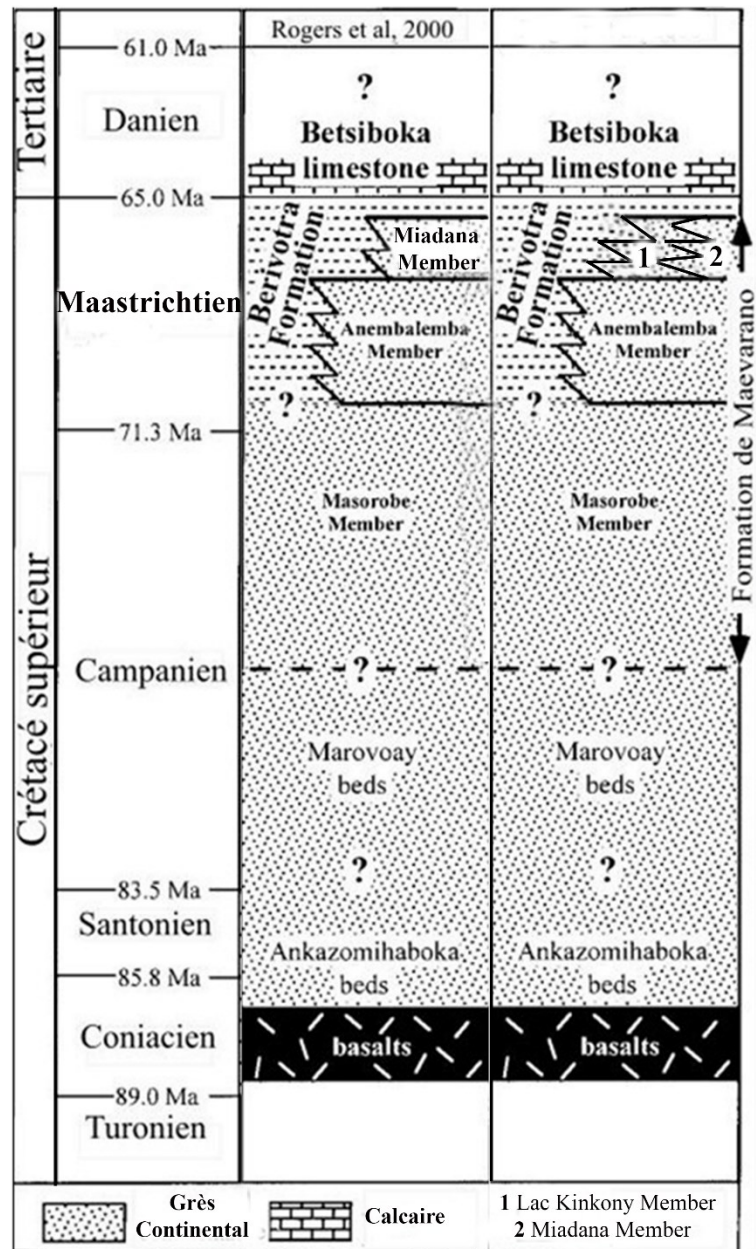


Figure 2: Lithostratigraphy of Upper Cretaceous strata in the Mahajanga Basin with (1) Lac Kinkony Member and (2) Miadana Member highlighted and overlying the Anembalemba Member (modified from Rogers et al., 2000, 2013).

The Maevarano Formation is composed of a succession of stratigraphically distinct layers that have been formalized as four members (see Rogers et al., 2000, 2013). The four subunits from the base upwards are the Masorobe, Anembalemba, Miadana, and Kinkony members (Fig. 2). The precise relationships of the latter two subunits are

ambiguous due to non-overlapping geographic exposure; nonetheless, both Kinkony and Miadana members overlie the Anembalemba Member. Each member presents different lithological and sedimentological characteristics, as follows:

- Masorobe Member: This presents well exposed outcrops in the vicinity of Berivotra, Lake Kinkony, and Masiakakoho. It is generally formed by green mottled red sandstone horizons of indurated clays and paleosols with root traces. Originally deposited by a sandy fluvial system, overprinting by paleosol development and roots indicate that much of the Masorobe Member represents long-term floodplain accumulations (Rogers et al., 2000).
- Anembalemba Member: This is best exposed near the Village of Berivotra, with more limited exposures at Kinkony and Masiakakoho (Rogers et al., 2000, 2013). This unit shows a massive texture composed of two distinct facies, representing different depositional mechanisms that lead to different fossil preservation (Rogers et al., 2000; Rogers, 2005). Facies 1 is white in color with cross bedded structure and limited fossils of high-quality preservation. Facies 2 is olive green in color and consists of a massive deposit (without structure) that is relatively dense in fossils of variable preservation quality.
- Miadana Member: Outcrops are best visible on the small hills of Miadana in the Berivotra Study Area and near Befandrama (Marshall and Rogers, 2012). This is usually difficult to recognize, as the stratification consists of only faint, localized cross-bedding (Rogers et al., 2000). In general, however, it can be identified by the variation of white color into greenish and deep red at the base with a mix of fine-to coarse-grained lithologies. Vertebrate fossils are relatively sparse in the Miadana Member, but when present can be well preserved.
- Kinkony Member: This subunit has only been located in the vicinity of Lake Kinkony, where it lies directly overlies Anembalemba Member. It is white in color and massive, sometimes with weakly interwoven structure. The Kinkony Member was deposited in a coastal, estuarine setting, exhibiting bi-directional cross-bedding, and bioturbation by invertebrates (e.g., *Ophiomorpha*), and includes chalky limestone and dolomitic mud (Rogers et al., 2013).

All subunits of the Maevarano Formation contain fossil material of variable preservation and that represent of all major continental vertebrate groups.

Crocodyliforms of the Maevarano Formation

***Mahajangasuchus insignis* (Buckley and Brochu, 1999)**

Mahajangasuchus insignis, the largest crocodyliform in the Maevarano Fm fauna (up to ~5 m estimated length), is remarkable for its enormous, platyrostral skull indicative of a semi-aquatic lifestyle (Buckley and Brochu, 1999; Turner and Buckley, 2008). Its overall skull morphology has been deemed as a 'hippopotamus-like' and it has been characterized among hypercarnivorous crocodyliforms (Pol and Larsson, 2011). It exhibits interesting secondary palate morphology (e.g., choanae enclosed by the pterygoid bone) that is reminiscent of Eusuchia (Turner and Buckley, 2008), while its remaining features indicate affinities with non-neosuchian mesoeucrocodylians. It has been interpreted as closely related to Peirosauridae (Carvalho et al., 2004; Sertich and O'Connor, 2014), and a strong relationship has been established with *Kaprosuchus saharicus* (Sereno and Larsson, 2009; Pol and Leardi, 2015; Nicholl et al. 2021). The strong affinities with *Kaprosuchus* have prompted the formalization of Mahajangasuchidae (Sereno and Larssen, 2009), a relationship that has been strongly supported by most recent analyses (e.g., Wilberg et al., 2019; Lamanna et al., 2019; Nicholl et al., 2021).

***Miadanasuchus oblita* (Buffetaut and Taquet, 1979; Simons and Buckley, 2009)**

Trematochampsia oblita was the first crocodyliform described from the Maevarano Formation (Buffetaut and Taquet, 1979). Originally assigned to Trematochampsidae (Buffetaut, 1991), it is now recognized as a member of Peirosauridae, a diverse family of crocodyliforms with anteriorly facing external nares, a small antorbital opening, a maxilla with wavy ventral margins, and enlarged dentary teeth at the 4th and 10th positions with circular, spaced alveoli. Simons and Buckley (2009) reinterpreted *Trematochampsia oblita* using new material recovered by the MBP. This work resulted in re-evaluation the genus *Trematochampsia*, revealing that *T. oblita* and *T. taqueti* do not share characters to support the congeneric association, not to mention that the two have significantly different mandibular morphologies.

Simons and Buckley (2009) retained the species designation but established the new genus *Miadasuchus*. The following characters were used in support of this designation: presence of a median ridge on the dorsal surface of the fused frontal bones, snout with a sinusoidal lateral margin in dorsal view, and a tooth structure proportionally larger and deeper than those of its sister taxa. Its estimated size is ~3 m long based on the dentary size (Buffetaut and Taquet, 1979; Simons and Buckley, 2009). The peirosaurid affinities of Trematochampsidae have been further discussed (Larsson and Sues, 2007; Simons and Buckley, 2009; Sertich and O'Connor, 2014), with *Miadasuchus* currently undergoing a detailed redescription and revised phylogenetic treatment (Sertich, in prep).

***Simosuchus clarki* (Buckley et al., 2000; Krause and Kley, 2010)**

Simosuchus clarki is a small, robust terrestrial crocodyliform that is approximately ~0.75 m in body length. This species was established on a specimen with a complete skull (Brochu et al., 2000), and is now known from several other partial skulls and skeletons (Kley et al. 2010). This is among the most unique crocodyliforms yet discovered, having small foliiform teeth with multicuspid crowns similar to those of ankylosaur dinosaurs and herbivorous iguanids (Kley et al., 2010; Krause et al., 2010). The brevirostral skull is dorsally flattened, with a quadrangular snout and a short mandibular symphysis. The tooth morphology suggests an herbivorous diet for this terrestrial form (Brochu et al., 2000; Kley et al., 2010; Melstrom and Irmis, 2019). This species is the most studied among of the four notosuchian crocodyliforms from the Maevarano Formation, with publications focusing on most parts of the postcranial skeleton (Georgi and Krause, 2010; Hill et al., 2010; Sertich and Groenke, 2010).

***Araripesuchus tsangatsangana* (Turner, 2006)**

Araripesuchus tsangatsangana is another small-bodied, terrestrial notosuchian from the Maevarano Formation. It is less than ~0.5 m long, with an upright posture, and has a rather weakly pointed, conical skull that is moderately elongate (Turner, 2006; Sereno and Larsson, 2009). The absolute size of *Araripesuchus* is considerably smaller than *Simosuchus*. It has numerous conical, pointed teeth that are slightly flattened labio-lingually (Turner, 2006). The lower tooth row varies in size, with a slight

hypertrophy at the level of the 8th tooth position and slightly smaller one at the level of the 10th tooth position. The skull also presents an ornamentation in the form of small pits and crenellations marked on the external surfaces of the skull elements.

II. Materials and Methods

The materials used in this study are complete or near-complete skulls of the four notosuchian crocodyliforms from the Maevarano Formation. They are repositied at the following institutions: **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **UA**, University of Antananarivo, Antananarivo, Madagascar; **DMNH**, Denver Museum of Nature & Science, Denver, Colorado, USA.

The primary specimens used in this study include:

Mahajangasuchus insignis

- **FMNH PR 2448**, partial cranium
- **DMNH EPV.138293**, tooth
- **UA 9737**, complete mandible

Miadasuchus oblita

- **DMNH EPV.136311**, rostrum and partially preserved braincase
- **DMNH EPV. 142185**, tooth

Simosuchus clarki

- **UA 8679**, holotype cranium and mandible
- **UA 9759**, tooth

Araripesuchus tsangatsangana

- **UA 8720**, holotype
- **FMNH PR 2297**, incomplete skull (Turner, 2006)
- **FMNH PR 2299**, incomplete braincase
- **FMNH PR 2317**, dentary

Systematic Paleontology

ARCHOSAURIA (Cope 1869)

CROCODYLOMORPHA (Walker 1970)

CROCODYLIFORMES Hay 1930 (sensu, Benton and Clark 1988)

MESOEUCROCODYLIA (Whetstone and Whybrow 1983)

NOTOSUCHIA (Gasparini 1971)

Simosuchus clarki (Buckley 2000)

PEIROSURIDAE (Gasparini 1982)

Miadasuchus (Simons and Buckley 2009)

Miadasuchus oblita (Buffetaut and Taquet 1979)

MAHAJANGASUCHIDAE (Serenio and Larsson 2009)

Mahajangasuchus insignis (Buckley and Brochu 1999)

URUGUAYSUCHIDAE (Gasparini 1971)

Araripesuchus tsangatsangana (Turner 2006)

The anatomical organization of craniomandibular openings (e.g., fenestrae) often contains essential information for inferring broad ecological characteristics in Crocodyliformes, with the four Maevarano Formation taxa exhibiting significant variation in these features. As such, the main cranial openings were assessed and measured on (1) physical specimens, (2) digital photographs of fossils, (3) high-resolution research casts, and (4) digital renderings based on computed tomography/micro-computed tomography (CT/ μ CT) scans. Scaled stipple drawings based on composite skulls reconstructed from multiple specimens were also used for this work. ImageJ (1.53t) was used to derive linear measurements for both standard metrics and derived measures useful for capturing morphological variation in craniomandibular anatomy. For all digital renderings, only orthographic projections were used to capture high-resolution images.

Length and width measurements of major craniomandibular openings were collected for all taxa. These included the external naris, antorbital fenestra, orbital fenestra, supra- and infratemporal fenestrae, mandibular fenestra, suborbital fenestra, and the choana. These measures were used to characterize general skull morphology in the four taxa and for general comparisons with other crocodyliforms. For this purpose, the total length and width of the skull are considered to evaluate the relative size of the openings (Fig. 3). Then, ratios between cranium length and width, mandible size, and the various craniomandibular openings allowed the quantitative assessment

of morphological variation in the four taxa. Additional consideration was given to other ecomorphological traits (e.g., tooth shape) of the four taxa and contextualized within the paleoenvironmental reconstruction of the Maevarano Formation in which the four taxa lived.

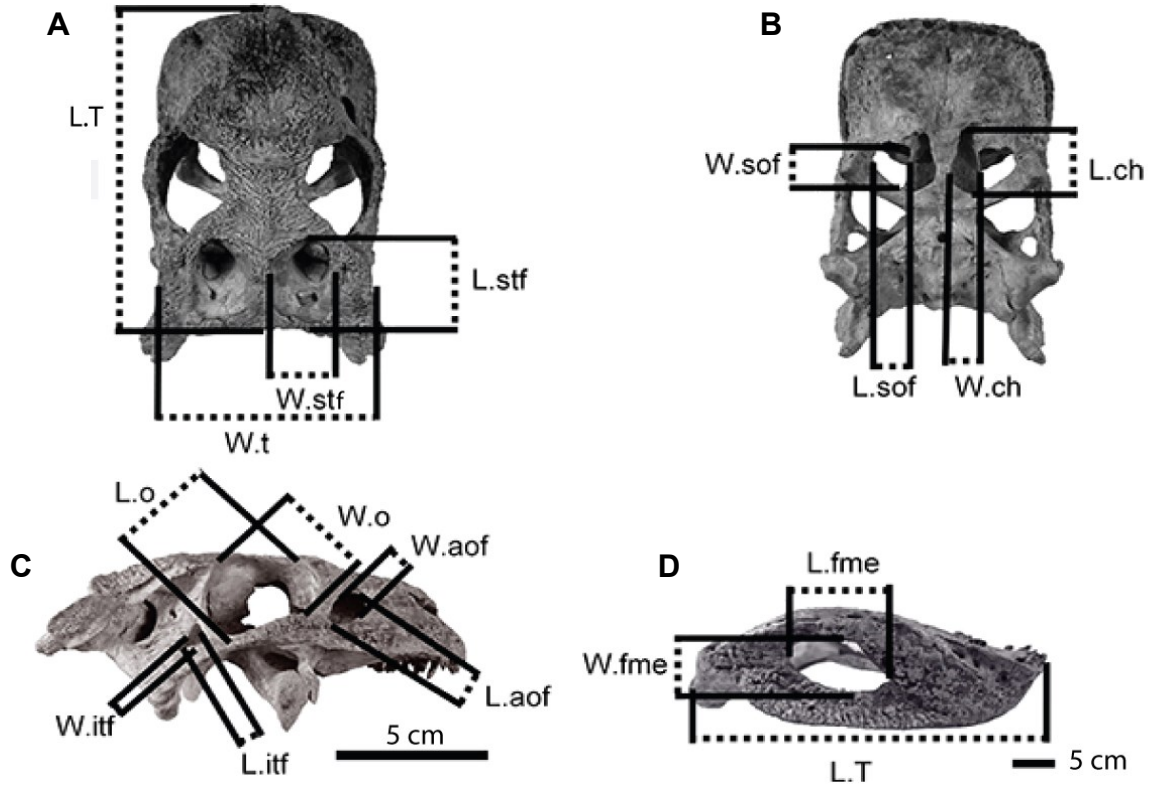


Figure 3: Standard measurements of the cranium and mandible used in this study. Dorsal (A), ventral (B), and right lateral (C) views of skull; right lateral (D) view of mandible. *Simosuchus clarki* used as example. **Abbreviations:** L.T., total length of the skull; W.t., total width of the skull; L.stf, supratemporal fenestra length; W.stf, supratemporal fenestra width; L.aof, antorbital fenestra length; W.oaf, antorbital fenestra width; L.ch, choana length; W.ch, choana width; L.sof, suborbital fenestra length; W.sof, suborbital fenestra length width; L.o, orbit length; W.o, orbit width; L.itf, infratemporal fenestra length; W.itf, infratemporal fenestra width; L.fme, external mandibular fenestra length; W.fme, external mandibular fenestra width.

III. Results

Below we describe and compare craniomandibular and dental morphology, and in particular, the major openings in the skull in four Maevarano Formation notosuchian crocodyliforms. When possible, multiple specimens of each species have been

assessed to increase our general knowledge of the representative groups, while also providing preliminary perspectives on intraspecific variation.

III-1. Cranial fenestrae and other openings

External narial fenestra

The external nares in crocodyliforms are typically bounded anteromedially, anteriorly, and laterally by the premaxilla and dorsomedially (or posteriorly in platyrostral forms) by the premaxillary process of the nasal. The latter feature spans longitudinally through the external nares to reach its anterior margin in most notosuchian crocodyliforms, including those of the Maevarano Fm. (Figs. 4A, 4C, 4E). In *Simosuchus clarki*, due to the morphology of its quadrangular rostrum, this opening is more widely developed while the aperture faces in the anterolateral direction. It is separated by the large premaxillo-nasal process medially (Fig. 4E). Both *Araripesuchus tsangatsangana* and *Miadasuchus oblita* exhibit anteriorly facing external nares that are clearly separated by a median premaxillo-nasal process (Fig. 4A). This opening is bounded mainly by the premaxilla and a small contribution from the nasal, the latter of which borders the fenestra posteriorly/posteromedially. With this configuration, the aperture opens more anteriorly in those species (e.g., Fig. 4A). Thus, for *Simosuchus*, *Araripesuchus*, and *Miadasuchus*, this opening is oriented anteriorly or anterolaterally, as is typical in terrestrial (i.e., non-aquatic) forms (Fig. 4A, 4D–4E). By contrast, *Mahajangasuchus insignis* exhibits a relatively small, dorsally positioned external nares (Fig. 4C), a positioning that is generally present in semi- to fully-aquatic taxa. This basic attribute of external narial anatomy provides key insight into how an animal accommodates itself in its habitat. An anteriorly positioned external narial opening indicates a terrestrial form whereas a dorsally directed external naris is indicative of an aquatic or semi-aquatic form. The latter position facilitates breathing while mostly submerged in water. Thus, the size, position, and most importantly, orientation of the external nares remain important for constraining ecological attributes related to these aspects of habitat utilization.

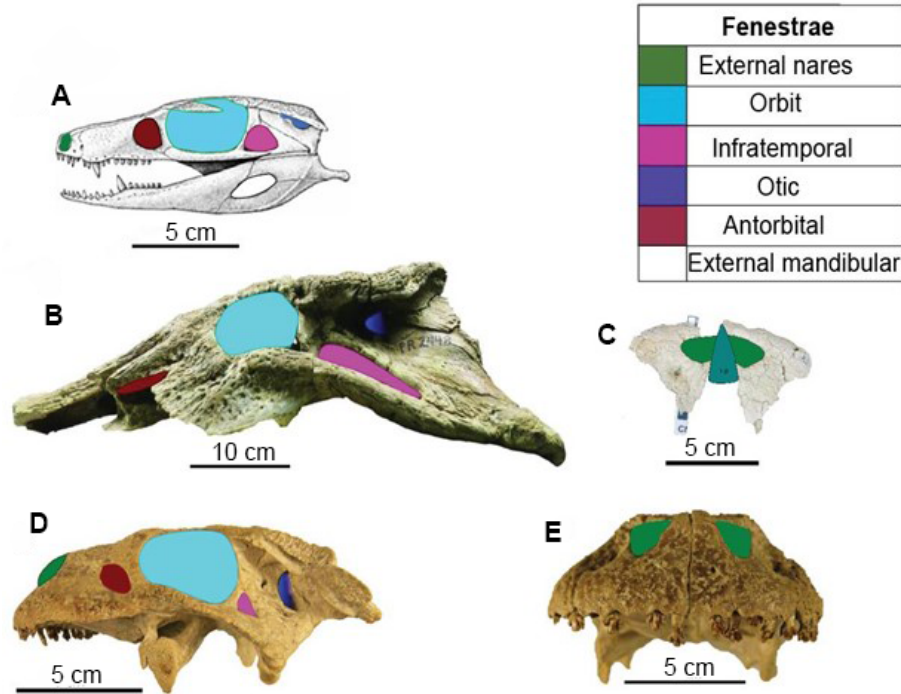


Figure 4: Position and orientation of cranial openings in the Maevarano Formation crocodyliforms. (A) Stipple reconstruction of *Araripesuchus tsangatsangana* (based on UA 8720 and FMNH PR 2297) in left lateral view; (B) cranium of *Mahajangasuchus insignis* (missing anterior rostrum) (FMNH PR 2448) in left lateral view; (C) terminal rostrum of *Mahajangasuchus insignis* juvenile (FMNH PR 2449) in dorsal view; (D, E) cranium of *Simosuchus clarki* (holotype, UA 8679) in left lateral (D) and anterior (E) views.

Antorbital fenestra

The antorbital fenestra is located posterolaterally on the rostrum (Fig. 4). It is a shared feature (synapomorphy) among archosaurs (Leardi et al., 2012). The fenestra is generally bounded by the maxilla anteriorly, the maxilla and sometimes the jugal ventrally, and the lacrimal posteriorly and dorsomedially or medially. The nasal does not participate in the contour in most species, including *Simosuchus*, *Araripesuchus* and *Mahajangasuchus* (Brochu and Buckley, 2000; Turner, 2006; Turner and Buckley, 2008). The antorbital fenestra is reduced in many taxa (e.g., *Miadanasuchus* among the Maevarano Fm. forms (Fig. 5; Table 1), becoming completely closed as in most neosuchians and some mesoeucrocodylians (e.g., *Iharkutosuchus*, *Marillasuchus*, *Adamantinasuchus*, *Pakasuchus*). The opening is relatively large in other crocodyliforms such as *Simosuchus clarki* and *Araripesuchus tsangatsangana* (Fig.

5; Table 1). By contrast, it is relatively small in some extinct aquatic and/or semi-aquatic forms like *Mahajangasuchus* and it is completely absent in extant crocodylians (Witmer, 1997). The variable expression of this opening in crocodyliforms likely relates to trade-offs between structural demands (i.e., biomechanics) of the bony cranium/rostrum, cranial pneumaticity, and size/placement of adductor (e.g., m. pterygoideus) musculature (Witmer, 1997; Sellers et al., 2022). Complete closure of the antorbital fenestra in neosuchians/crocodylians has been interpreted as necessary for stabilization of the platyrostral snout during prey capture and feeding, along with the rostral expansion of pterygoideus musculature (Witmer, 1997; Bona and Desojo, 2011; Sellers et al., 2022).

Taxon	Relations	aof	fO	stf	itf	fme	Sob	ch
<i>Simosuchus</i>	L/LT	0.12	0.30	0.27	0.11	0.30	0.19	0.26
	W/ LT	0.10	0.30	0.25	0.08	0.16	0.18	0.12
<i>Miadasuchus</i>	L/ LT	-	-	0.23	-	0.18	0.36	0.11
	W/ LT	-	-	0.15	-	0.08	0.18	0.04
<i>Mahajangasuchus</i>	L/ LT	0.06	0.12	0.14	0.14	0.11	0.16	0.03
	W/ LT	0.04	0.11	0.10	0.07	0.05	0.10	0.04
<i>Araripesuchus</i>	L/ LT	0.15	0.30	0.28	0.14	0.33	0.49	0.30
	W/ LT	0.13	0.29	0.25	0.13	0.22	0.35	0.26

Table 1: Relationship between length and width of openings in the skull relative to the total skull length. Abbreviations: aof, antorbital fenestra; **fO**, orbital fenestra; **stf**, supratemporal fenestra; **itf**, infratemporal fenestra; **fme**, mandibular external fenestra; **ch**, choana; **sof**, suborbital fenestra and **LT**, total length of the mandible and cranium; **L**, length and **W**, width of the opening.

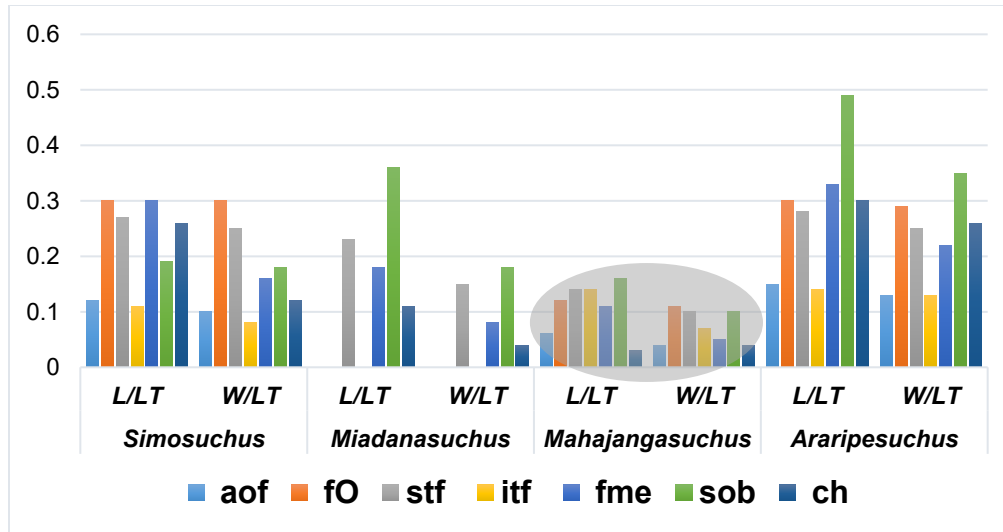


Figure 5: Relationship between length of the fenestrae (L)/total length of skull (LT) and width of the fenestrae (W)/total length of skull in Maevarano Formation notosuchians. Abbreviations: aof, antorbital fenestra; fO, orbital fenestra; stf, supratemporal fenestra; itf, infratemporal fenestra; fme, external mandibular fenestra; sob, suborbital fenestra; ch, choana. Grey oval highlights the relatively small openings of *Mahajangasuchus*.

Orbital fenestra

The orbital margin is generally bounded by the lacrimal anteriorly, jugal ventrally, postorbital bar (jugal and postorbital) posteriorly, and frontal and prefrontal dorsomedially. In notosuchians, there is often a pair of palpebrals enclosing the dorsal border of the functional orbit. The palpebral can be absent or reduced or very well developed in some crocodyliforms, ultimately influencing the orientation or direction of the fenestra. For this, the mode of life of the group is often indicated by the orientation of the opening. Specifically, the direction (Fig. 4) and size (Fig. 5) of the orbital opening differs in crocodyliforms with different lifestyles. For example, the opening is directed laterally and typically large in early branching terrestrial crocodyliforms (Fig. 5; Table 1). This is also the situation in *Miadanasuchus*, *Simosuchus*, and *Araripesuchus*. In contrast, the opening assumes a dorsal or dorsolateral orientation and medium size in semi-aquatic forms (e.g., crocodylians and selected mesoeucrocodylians like *Mahajangasuchus* (Fig. 4)). Cerio and Witmer (2023) noted that the development of the eyeball, other orbital soft tissues, and functional demands of the visual system together play a dominant role in shaping

orbital morphology; a situation that applies to archosaurs (and amniotes) more generally). As such, the orientation of the opening, as with the external nares, provides some insight on the mode of life of the taxon. Importantly, a laterally directed opening restricts the visual system to monocular field of view in certain forms (e.g., terrestrial crocodyliforms and some mammalian carnivores), a trait adapted to a terrestrial more than an aquatic lifestyle. For those with a fully aquatic lifestyle, the orbital opening may either be well developed in size and oriented laterally (e.g., *Tyrannoneustes lythrodectikos*) when the prefrontal bone is large or dorsolateral (e.g., *Dyrosaurus maghribensis*) with minimal involvement of the prefrontal or palpebrals at its margin. Indeed, in semi-aquatic species (e.g., *Mahajangasuchus insignis*), this opening is usually quite large and opens directly dorsally (Fig. 5; Table 1). A dorsally directed orbit of moderately large size and lacking large palpebral ossifications presents a panoramic view that allows the species to better receive visual input from its environment when floating and while partially or mostly submerged during hunting.

Temporal fenestrae

The temporal fenestrae are composed of two pair of openings: the supratemporal (dorsotemporal fenestra of Holliday et al., 2019) fenestra and the infratemporal fenestra. The supratemporal fenestra (Fig. 6) is positioned between the frontal and postorbital anteriorly, the postorbital and squamosal laterally, the squamosal posterolaterally, and the parietal posteromedially and medially. The infratemporal fenestra (Fig. 4) is delimited by the postorbital and squamosal dorsally, the ventral postorbital process and the ascending process of the jugal anteriorly, the quadratojugal/quadrato posteriorly, and the posterior process of the jugal ventrally. These openings are associated with musculature and exhibit substantial variation in different groups, with this variation hypothesized to relate to biomechanical and ecological adaptations (Holliday et al., 2019). The supratemporal fenestra, and specifically, the ventrally continuous supratemporal (=dorsotemporal) fossa, is occupied by the deep external adductor mandibulae musculature. The supratemporal fenestra/fossa is generally better defined than that of the infratemporal opening that serves as the location of the medial external adductor mandibulae muscle (Holliday et

al., 2013) (Fig. 6). See Holliday et al. (2019) for an enhanced discussion of both nomenclatural and specific soft-tissue associations for the supratemporal fenestra/fossa in archosaurs more generally. For our purposes, we will focus on the size and position of the supratemporal fossa and fenestra as general proxies for interpreting muscular volume and shape of the dorsal cranial table, respectively.

The supratemporal fenestrae/fossae (Fig. 6) in the four Maevarano Fm notosuchians, although differing in shape and slightly in relative size, seem unremarkable regarding inferred differences in adductor musculature among the taxa. By general comparison, the Maevarano Fm crocodyliforms exhibit a supratemporal fenestra/fossa that is generally large (Table 1), meaning that it likely supported substantial musculature (e.g., *M. adductor mandibulae externus profundus*; MAMEP) involved in mandibular adduction. A future study examining the volume of the supratemporal fossa (i.e., the volume specifically related to housing the dorsal portions of the mandibular adductor musculature; Holliday et al., 2019) would be a necessary next step more refined interpretations of adductor force generation in these taxa. The infratemporal fenestra (Fig. 4) is generally unremarkable in three of the four taxa, but is substantially reduced in *Simosuchus*, a state that is likely related to its apomorphically abbreviated skull and inferred unique, mostly herbivorous feeding ecology (Kley et al., 2010).

As in the case of the antorbital fenestra, a reduction in size or closure of the supratemporal fenestra/fossa may serve to increase stabilization of the skull table, but also implies an increase in dependence on musculature situated in infratemporal fenestra and/or the palatal region in such forms. More broadly, the supratemporal fenestra exhibits a size reduction in extant crocodylians and is completely closed in the early branching eusuchian *Iharkutosuchus* (Ősi et al., 2007; Ősi and Weishampel, 2009; Ősi, 2017), requiring additional consideration (e.g., does this represent a specialized feature/ecological adaptation) in those taxa.

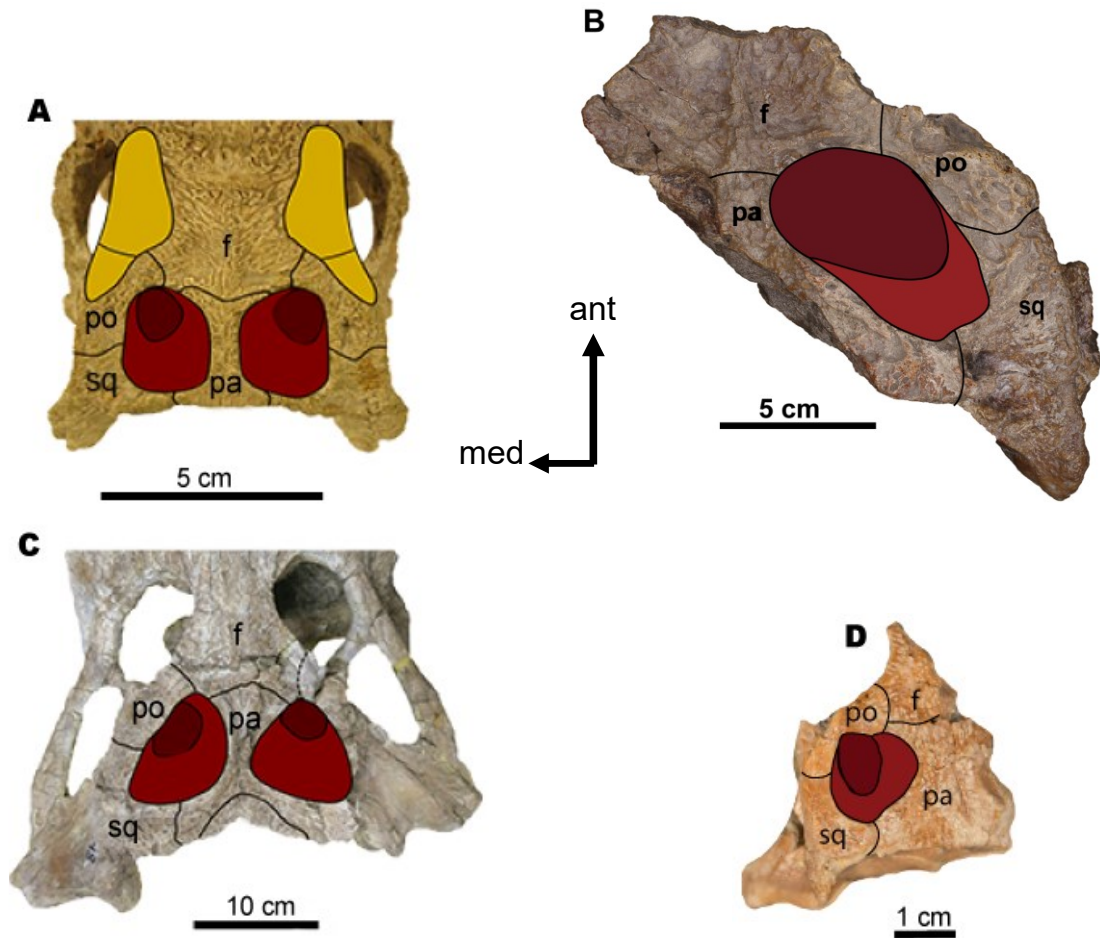


Figure 6: Supratemporal fenestra morphology. (A) *Simosuchus clarki* (UA 8679), (B) *Miadasuchus oblita* (DMNS EPV. 136311), (C) *Mahajangasuchus insignis* (FMNH PR 2448) and (D) *Araripesuchus tsangatsangana* (FMNH PR 2299); all images in dorsal view, anterior to the top of image; Color overlie indicates position of supratemporal fenestra (light red) and supratemporal fossa (dark red).

Abbreviations: **stf**, supratemporal fenestra (in red color); **itfo**, supratemporal fossa (in brown color); **sq**, squamosal; **pa**, parietal; **f**, frontal; **po**, postorbital and **ant**, anterior; **med**, medial.

Choanae

Historically, the position, size, and bony borders (e.g., maxilla vs. palatine vs. pterygoid) of the choana have been important for tracing the evolutionary history, if not defining the phylogenetic relationships, of Crocodylomorpha (e.g., Adrade et al., 2006; Turner and Buckley, 2008; Dollman and Choiniere, 2022). In earlier branching forms (non-mesoeucrocodylian crocodylomorphs) with a complete secondary palate, choanae are placed anteriorly and variably bordered by the maxillae and palatines

and completely unrelated to the pterygoid (although representative shartegosuchoids present a complex level of choanal variation in this regard—see Dollman and Choiniere, 2022). In later branching forms (e.g., mesoeucrocodylians), the choana is supported anteriorly by the palatine (i.e., excluding the maxilla) and variably include the pterygoid at/near the posterior border. For example, the choana is located medially between the pterygo-palatine in certain forms (as in *Sarcosuchus* and *Araripesuchus*). Yet, the choana is located posteriorly and completely enclosed within the pterygoid in eusuchians (Crocodylia; Fig. 7E) and convergently in selected non-eusuchians (e.g., *Mahajangasuchus*; Sereno and Larsson, 2009; Turner and Buckley, 2008; Pol et al., 2009; Leite and Fortier, 2018; Dollman and Choiniere, 2022) (Fig. 7). More generally, the size of the choana/choanal groove is reduced and assumes a more posterior position over the course of crocodylomorph evolution.

In the case of the Maevarano Fm crocodyliforms, choanae are anatomically positioned in accordance with the phylogenetic placement of these taxa among non-eusuchian mesoeucrocodylians, with *Mahajangasuchus* exhibiting a uniquely derived, pterygoid-enclosed condition unlike the one in eusuchians. For example, in *Araripesuchus tsangatsangana* (Fig. 7D), the choana is bounded mostly by the palatine anteriorly and enclosed by the pterygoid posteriorly; note that preservation makes high-resolution delimitation of the choanal borders difficult. Nonetheless, it appears large, elongate (see Tab. 1) and anteriorly positioned. There is a thin median septum separating the right and left choana.

In *Miadanasuchus* (Fig. 7B), the choana is reduced in size, slightly elongate, and similar in position to that of *A. tsangatsangana*. This opening is enclosed by the palatine anteriorly and anterior process of the pterygoid medially (forming a relatively thick median choanal septum) and posteriorly.

In *Simosuchus* (Fig. 7A), the choana is large, subrectangular in shape, and anteriorly positioned. The opening is bounded anteriorly by a small portion of palatine, medially by the ventral lamina of the anterior process of the pterygoid, and posteriorly by the transverse process of the pterygoid (Kley et al., 2010). The lateral edge of the choana is formed by the thin roofing lamina of the pterygoid, with little contribution from the transverse process of the pterygoid.

Finally, in *Mahajangasuchus* (Fig. 7C), the choana is small, subtriangular in shape, and posteriorly positioned. It is surrounded by the pterygoid and the two choanae are separated by a thick septum that expands anteriorly to exclude the palatine from contact with the opening (Turner and Buckley, 2008). This has been noted to represent convergence in the development of a eusuchian-like, pterygoid-enclosed choana (Turner and Buckley, 2008). Its construction is unique relative to eusuchians in which the pterygoids meet along the midline anterior to the choana. Turner and Buckley (Turner and Buckley, 2008) provide resolution on the topic about the position of the choana, offering the hypothesis that the eusuchian-style palate (i.e., posteriorly positioned choanae completely enclosed within the pterygoids) is best interpreted as a strain resisting mechanism related to feeding with a platyrostral snout.

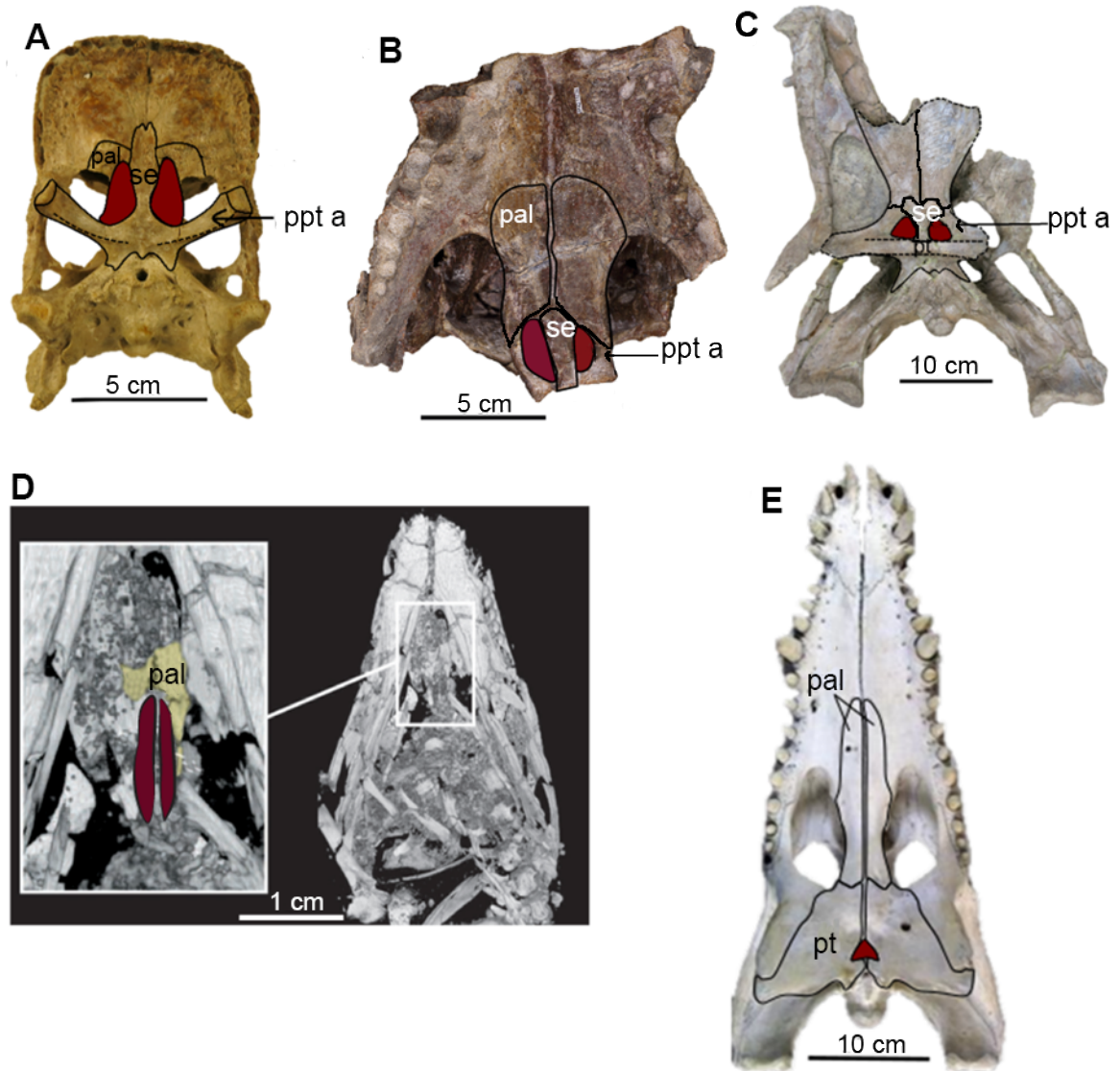


Figure 7: Choanal morphology of crocodyliforms from Maevarano compared to Crocodylia. (A) *Simosuchus clarki* (UA 8679), (B) *Miadasuchus oblita* (DMNH EPV. 136311), (C) *Mahajangasuchus insignis* (FMNH PR 2448), (D) *Araripesuchus tsangatsangana* (FMNH PR 2297; Turner, 2006), and (E) *Crocodylus rhombifer* (from Morgan et al., 2018), all images in ventral view, anterior to the top of each image. Red color overlay indicates position of the choana. **Abbreviations:** **pal**, palatine ; **pt**, pterygoid ; **ppt t**, transverse pterygoid process ; **ppt a**, anterior pterygoid process.

Suborbital fenestra

The suborbital fenestra exhibits variability in size and shape in crocodyliforms (extinct and/or extant). It extends anteriorly as far as the 5th maxillary tooth (i.e., from the posterior end of the tooth row; Fig. 8) in Mesoeucrocodylia but to the 7th tooth position in Crocodylia (e.g., Fig. 7E). In the Maevarano Fm crocodyliforms, it is broadly

developed and extends to the 8th position in *Miadasuchus* (Fig. 8B) and *Mahajangasuchus* (Fig. 8C). It is more challenging to delimit the opening in *Araripesuchus* due to preservation (Fig. 7D). Concerning *Simosuchus*, it exhibits an apomorphically developed suborbital fenestra compared to the other three taxa (Figs. 5 & 8A). For this species, the suborbital fenestra extends anteriorly only to the last tooth position of the maxilla (Fig. 8A), likely related to the extreme cranial modification exhibited by this form. It is positioned directly ventral relative to the orbital fenestra (Kley et al., 2010) and is laterally positioned with the relatively large choana opening dorsal to the medial 1/3 of the suborbital fenestra. The suborbital fenestra allows for passage of pterygoideus musculature that typically accounts for a large proportion of the force generated during the mandibular adduction (Sellers et al., 2022). Thus, its reduction in size in *Simosuchus* may suggest relatively weak muscle force generation compared to that in the other three species (*Mahajangasuchus*, *Miadasuchus*, and *Araripesuchus*) (Figs. 5, 8), and in crocodyliforms more generally.

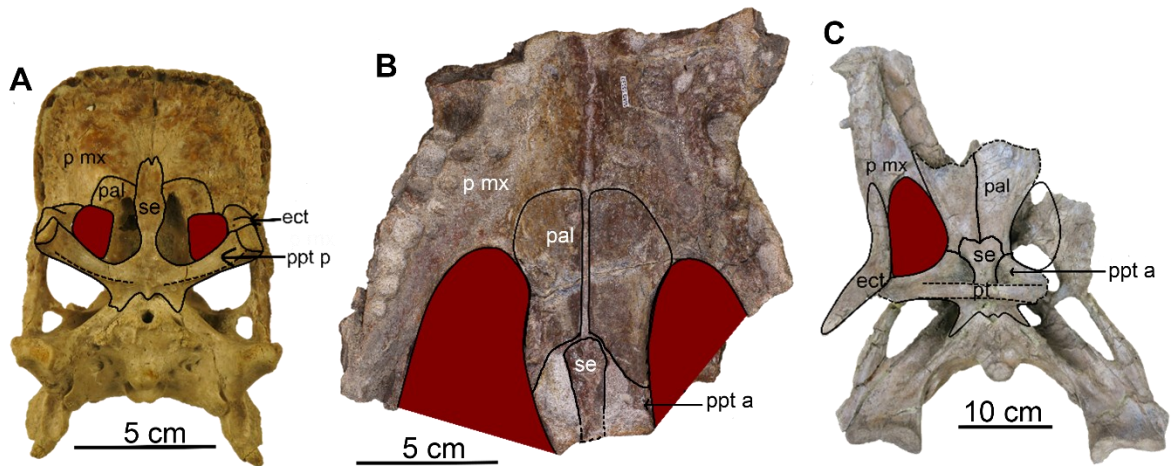


Figure 8: Morphology of the suborbital fenestra: (A) *Simosuchus clarki* (UA 8679), (B) *Miadasuchus oblita* (DMNH EPV.136311), (C) *Mahajangasuchus insignis* (FMNH PR 2448); all images in ventral view, anterior to the top of image. Red color overlay indicates of suborbital fenestra. **Abbreviations:** p mx, palatal process of maxilla; pal, palatine; pt, pterygoid; ppt a, anterior pterygoid process; ppt t, traverse pterygoid process; se, choanal septum; ect, ectopterygoid.

External mandibular fenestra

Like the supratemporal and antorbital openings that exhibit reduction or closure and with some relation to changes in adductor musculature, the external mandibular fenestra also exhibits variation in crocodyliforms. For example, it is completely closed in some members of the pelagic "thalatosuchians" (Leardi et al., 2012) and some neosuchians, but exhibits substantial variability in both size and shape in most semi-aquatic and terrestrial forms. It is relatively large (compared to total mandible size) and sub-oval in *Simosuchus* (Figs. 9A; Table 1), small and oval in *Miadasuchus* (Fig. 9B), small and teardrop shaped in *Mahajangasuchus* (Fig. 9C), and relatively elongate in *Araripesuchus* (Fig. 4A and 9D).

The region around this opening and the medial surface of the lateral mandibular wall (i.e., the medial surface of the surangular, angular, and dentary) plays an important role for the adductor muscle insertion responsible for generating power during jaw adduction. The general configuration of the elements bordering the fenestra (Fig. 9), including the surangular, angular, and dentary are generally different in the four Maevarano Formation taxa. In *Mahajangasuchus*, they are relatively robust, particularly the surangular, to support the musculature that attaches near the opening. It appears as though the robusticity of the bones surrounding the external mandibular fenestra decreases with decreasing body size for the generally carnivorous species in this ecosystem. By contrast, *Simosuchus* exhibits a robust angular relative to the surangular, likely related to a different mandibular stabilizing mechanism in a crocodyliform taxon with a vastly different feeding ecology (i.e., being among the exceedingly rare herbivorous crocodyliforms) (Kley et al., 2011).

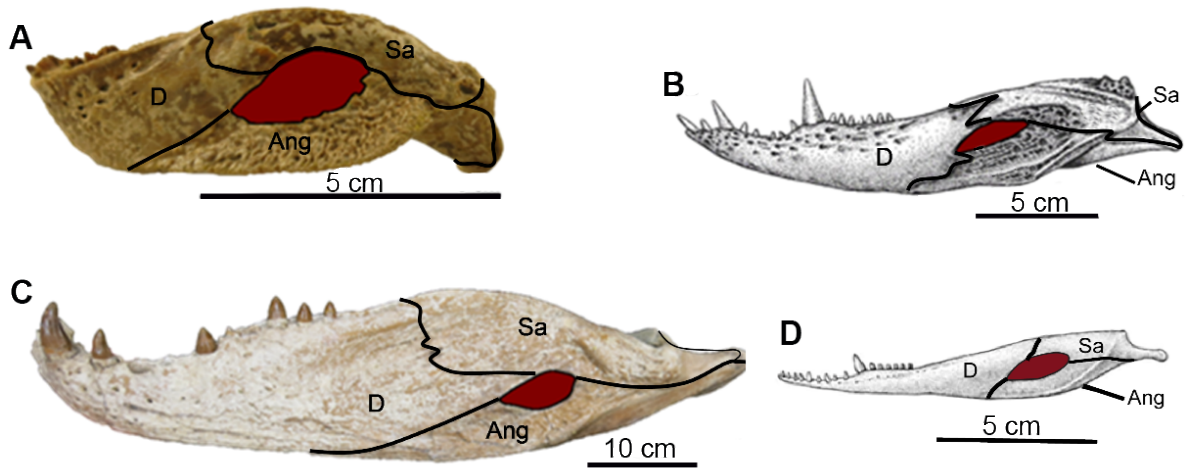


Figure 9: Morphology of the external mandibular fenestra. (A) *Simosuchus clarki* (UA 8679), (B) *Miadanasuchus oblita* (based on FMNH PR 2343 and FMNH PR 2837), (C) *Mahajangasuchus insignis* (UA 9737), and (D) *Araripesuchus tsangatsangana* (based on UA 8720 and FMNH PR 2297; Turner, 2006); all images are in left lateral view. Red color overlay indicates position of the external mandibular fenestra. **Abbreviations:** D, dentary; ang, angular; sa, surangular.

III-2. Variation in tooth count and general characteristics of tooth shape

Few aspects of skeletal-dental morphology are as distinctive among the four Maevarano Formation notosuchians as their dentition. Although three of the four taxa (i.e., *Mahajangasuchus*, *Araripesuchus*, *Miadanasuchus*) exhibit teeth that fall within the expected range of variation for crocodyliforms, *Simosuchus* presents foliiform teeth that are unique among crocodyliforms (Buckley et al., 2000; Kley et al., 2010). Regarding the latter, *Simosuchus clarki* exhibits 16 teeth in the upper jaw, with five in the premaxilla and 11 in the maxilla. There are 15 teeth in the lower jaw. The foliiform teeth are specialized among crocodyliforms, with multicuspid crowns. The number of cusps increases from three in front to six or more in the posterior region of the dental series; individual cusp size also decreases moving posteriorly through the tooth row (Fig. 10B). The teeth are small but have a thick root and exhibit a distinct constriction between the root and crown. Tooth crowns become more labiolingually compressed in more posterior sections of the dental series. Although there is some variation (e.g., number of cusps, arrangement and size of a cusp series on a given tooth) in crown shape along the tooth row, it is not apparent that the upper and lower dentition worked together to process food (Kley et al., 2010). Small multicuspid teeth are typical among

specialized, primarily herbivorous reptiles (although unique among crocodyliforms). The best comparison for teeth with this morphology is among a range of herbivorous reptiles such as ankylosaur, stegosaur, and some ornithomimid dinosaurs, and omnivorous to mostly herbivorous iguanids (Sander et al., 2010; Kley et al., 2010; Christensen and Melstrom, 2021).

Araripesuchus tsangatsangana possessed 16 teeth on the upper jaw (like *Simosuchus* in the number of teeth in premaxilla and maxilla), with 18 in the lower jaw (Fig. 10A). These teeth are quite small and similar in overall shape to that of many crocodylians in being conical and flattened labiolingually. The dentition is moderately heterodont because the teeth in positions one through eight are spatulate, with an increasing conical shape moving posteriorly. The 9th tooth is the largest and tallest and is conical, with the 10th to 18th-teeth becoming small and spatulate (Fig. 10A). The size and shape of these teeth are suggestive of an animal specialized for feeding on insects and other invertebrates, with the possibility of including small vertebrates in its diet (Turner 2006). Placing this dental morphology in the context of its small body size, fusiform snout shape, and anteriorly directed external nares, *Araripesuchus* likely existed as a terrestrial animal adapted for active predation on a range of invertebrates and small-bodied vertebrates.

The dentition of *Miadasuchus oblita* consists of 16 teeth in the upper jaw (four in the premaxilla and 12 in the maxilla) and 17 teeth in the lower jaw. These are all large and conical-to-sub oval due to being flattened lingually. The third tooth in the maxilla is the largest in the upper tooth row, with the 4th position, followed the 10th, being largest in the lower tooth row. These teeth present denticles along the mesial and distal carinae (Buffetaut and Taquet, 1979; Simons and Buckley, 2009). The large size and shape of the teeth in *Miadasuchus*, along with the presence of denticles, paints a view of this taxon as typically carnivorous in its feeding ecology. Given the inferred terrestrial nature and body size of *Miadasuchus*, adults would have likely specialized on the medium to large vertebrate components of the fauna (e.g., dinosaurs, mammals, other crocodyliforms).

Finally, *Mahajangasuchus insignis* has 15 teeth in the upper tooth row, four the premaxilla and 11 in the maxilla, and 13 in the lower tooth row. These are generally large compared to *Miadasuchus*. The largest teeth in the series are in position three in the maxilla and at positions four and eight in the lower dental series. The rest of the teeth are modest in size and decrease in size posteriorly. Tooth crowns in *Mahajangasuchus* are generally laterally compressed and with notable crenulations (Fig. 10D) (Buckley and Brochu, 1999; Turner and Buckley, 2008). From tooth and skull shape, this taxon is the largest crocodyliform from the Maevarano Formation. The semi-compressed teeth reflect its carnivorous feeding and given its adult body size and inferred semi-aquatic habit, implies that it was able to take large aquatic prey (e.g., turtles, fish) and many terrestrial animals (e.g., small to medium dinosaurs, mammals, terrestrial crocodyliforms) at or near the water's edge.

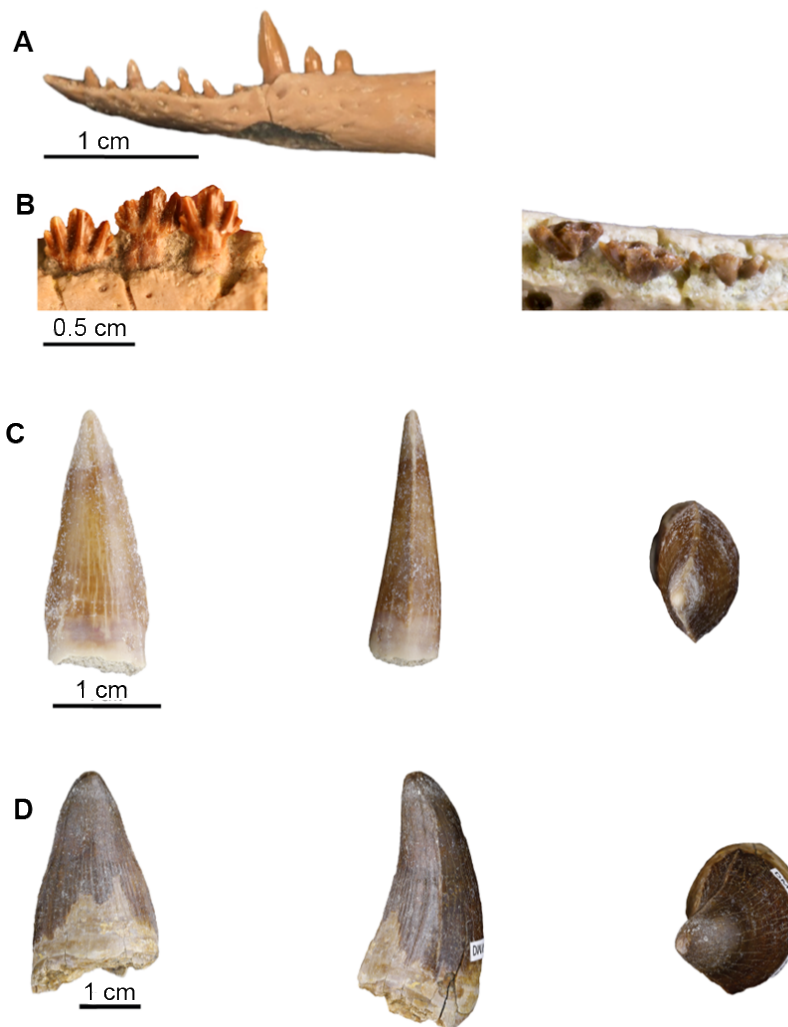


Figure 10: Dental morphology of the four notosuchian crocodyliforms from the Maevarano Formation. (A) *Araripesuchus tsangatsangana* (FMNH PR 2318), left dentary in lateral view; (B) *Simosuchus clarki* (UA 8679), portion of left dentary in lingual (left image) and dorsal (right image) views; (C) *Miadanasuchus oblita* (DMNH EPV. 142185) and (D) *Mahajangasuchus insignis* (DMNH EPV.138293). Images in C–D arranged as follows from left to right: lateral view, mesial view, and occlusal view.

IV. DISCUSSION

IV.A. Overview of the four notosuchians from the Maevarano Formation

The four Maevarano Formation crocodyliforms represent an ideal case study with which to develop an ecomorphological perspective during the Maastrichtian in this region of Gondwana. The four taxa vary significantly in both body size and other key morphologies related to feeding ecology yet are all representatives of Notosuchia. One large (~5 m), carnivorous, semi-aquatic form, along with a range of terrestrial, medium (~3 m) to small (~0.5 m) body-sized taxa existed in this ecosystem. Importantly, the terrestrial species occupied distinct niches, including mega-carnivorous, small-bodied herbivorous and insectivorous forms (Buckley et al., 2000; Turner, 2006; Turner and Buckley, 2008; Rasmusson Simons and Buckley, 2009; Kley et al., 2010). This ecomorphological analysis indicates that the position of the external nares and orbit provide the key information for inferring general ecological characteristics (e.g., terrestrial vs. semi-aquatic habits) of the Maevarano Fm crocodyliforms. Other openings on the external surface of the skull (e.g., temporal fenestrae, external mandibular fenestra) or on the palate (e.g., choanae, suborbital fenestra) provide taxon-specific character information useful for better considering phylogenetic affinities and/or general biological attributes related to feeding mechanics, skull development, etc. Taken together with the dentition, itself perhaps the single best indicator of feeding ecology in the four taxa, we can now place the four notosuchian crocodyliforms of the Maevarano Formation amongst the broader paleobiological environment in which they existed.

For example, a large, laterally facing orbit (e.g., as in *Simosuchus*, *Miadanasuchus*, and *Araripesuchus*) is consistent with a terrestrial mode of life when compared to a dorsal or dorsolaterally facing orbit (e.g., as in *Mahajangasaurus*) in

semi-aquatic forms (Ősi et al., 2018; Wilberg et al., 2019). Orbit orientation, and its proxy for visual field overlap, can inform hypotheses on the presence of species-specific monocular vs binocular visual ability, with this being tied to foraging style and predator-prey dynamics. Although a higher mean orbital convergence has been shown to exist in mammalian predators/faunivores (e.g., Heesey, 2008), additional work is necessary to assess such relationships in crocodyliforms in general and in the Maevarano Fm taxa and notosuchians more specifically. As another example, the size, position, and shape of antorbital fenestra has been extensively considered in archosaurs (Witmer, 1997), with current hypotheses supporting a balance of functional trade-offs among paranasal air sinus pneumatization, jaw musculature, and cranial skeletal biomechanics. Moreover, the sub-orbital, temporal and mandibular fenestrae variably relate to adductor musculature (and other soft tissue systems) (Busbey, 1989; Stubbs et al., 2013). The variation in these features (i.e., antorbital, temporal, external mandibular, and antorbital fenestrae) among the four Maevarano Fm crocodyliforms is consistent with species-specific functional and clade-specific characteristics, as discussed in primary descriptive contributions (e.g., Buckley and Brochu, 1999; Turner 2006; Turner and Buckley, 2008; Kley et al., 2010). For the remainder of this section, we will focus on the external nares and the dentition for their utility in further considering ecological attributes of the Maevarano Fm crocodyliforms.

External nares

The anteriorly oriented external narial opening represents the plesiomorphic condition for Crocodylomorpha and Crocodyliformes, and is present in many mesoeucrocodylians, including *Simosuchus clarki*, *Miadanasuchus oblita*, and *Araripesuchus tsangatsangana* among the Maevarano Fm taxa. This character indicates a terrestrial rather than aquatic mode of life (e.g., Nobre and Carvalho, 2006). Such an orientation allows a given species to breathe easily on land like those of many tetrapods (extant and extinct). With an anteriorly positioned external nares, inhaled and exhaled air travels into and through the nasal cavity and nasopharynx to facilitate air exchange for respiration. By contrast, dorsally positioned external nares like those in semi-aquatic and aquatic species (e.g., *Mahajangasuchus* among the

Maevarano Fm taxa) allow an animal to float and/or to remain partially-to-mostly submerged (but still able to exchange air) while awaiting opportunities for prey capture. We can thus conclude that the Maevarano Fm ecosystem supported both terrestrial and sub-aquatic notosuchian crocodyliform ecomorphs based on this singular attribute.

Dentition

The dentition of the four notosuchians in terms of tooth number is generally consistent with the clade, with a slight reduction being more important on the premaxilla (4 vs. 5) and dentary (13 vs. 15/18) between the large-bodied (*Mahajangasuchus* and *Miadasuchus*) and small-bodied (*Simosuchus* and *Araripesuchus*) forms. Such variation may be related to capture of large prey and general feeding mechanics (e.g., Ösi et al., 2013; Iori and Carvalho, 2018), but may also represent interspecific variation, with either possibility being outside the scope of the current work. All three faunivorous taxa, *Araripesuchus*, *Miadasuchus*, and *Mahajangasuchus*, display some degree of heterodonty and regionalization, with enlarged caniniform teeth present at different positions. The posterior dentitions of all three are relatively uniform within each taxon.

In contrast, the variation in shape and size of the teeth in these four crocodyliforms offers more insight into feeding ecology. For example, the existence of hypertrophied, ziphodont teeth in *Miadasuchus* and *Araripesuchus* suggests that these species are best characterized as faunivores, albeit with the larger-bodied *Miadasuchus* hypothesized to have focused on medium-sized vertebrate prey and the small-bodied *Araripesuchus* likely to have specialized on small vertebrates and invertebrates (e.g., insects). Laterally compressed and serrated teeth in other archosaurs (e.g., theropod dinosaurs, rauisuchians) are hypothesized to slice, suggesting some utility for both prey acquisition and processing. The more robust, conical to semi-conical teeth of *Mahajangasuchus* are like those of large extant crocodylians that specialize in ambush predation. These teeth are ideal for seizing, holding, and crushing rather than for cutting. Much like extant crocodylians, *Mahajangasuchus* may have swallowed prey whole, or processed large prey items by

twisting in an aquatic setting to break down carcasses prior to consuming in large pieces. Finally, the multicuspid dentition in *Simosuchus* is unusual among crocodyliforms, but similar in general to the flattened foliform teeth like those in presumably herbivorous ankylosaurs among dinosaurs. The thick root, along with the small but multi-cusped crown, suggests specialization for plant-eating (Buckley et al., 2000; Ósi and Weishampel, 2009; Ósi et al., 2013; Mallon and Anderson, 2014; Benson et Godoy, 2019). Taken as a group then, dental morphology in the Maevarano Fm crocodyliforms clearly indicates ecological partitioning among both traditional faunivory (albeit among a range of body sizes) and a uniquely expressed form of archosaurian herbivory.

A composite analysis of different regions of the skull (e.g., skull roof, palatal region), individual openings in the cranium (e.g., external nares, choanae), and the suite of individuals bones that hold teeth are required to wholistically characterize potential ecological ‘adaptations’ in crocodyliforms. The Maevarano Fm notosuchians present a diverse assemblage of crocodyliforms that seemingly span an array of ecologies and filled disparate niche space in this ancient ecosystem.

IV.B. Paleoenvironments of the Maevarano Formation and Crocodyliform Ecomorphology

The Maastrichtian Maevarano Formation, and the Anembalemba Member specifically, includes a diverse assemblage of crocodyliforms among a vast array of other terrestrial and freshwater vertebrates. The Maevarano Fm accumulated in an alluvial plain setting, with some peripheral marine influence, and records a seasonal, semiarid environment during this time (Rogers et al., 2000, 2013). This sediment package was deposited in a highly seasonal context, with examples of both dry/semi-arid and wet climatic influences during deposition. Of particular interest for this study, the diversity of crocodyliforms is best known from Facies 2 (Rogers, 2005) of the Anembalemba Member. Interpreted as debris flows with characteristic exceptional fossil preservation, Facies 2 is a massive, poorly sorted, muddy sandstone that represents mobilization of loosely consolidated soils during periods of intensified rain following the dry season. The unique circumstances of Facies 2 deposition therefore

do not reflect paleoenvironmental preference of preserved taxa, but instead represents chance preservation of many faunal components not typically preserved in the normal depositional regime of the Maevarano Fm. The underlying Masorobe Member, known to preserve only limited vertebrate material, is characterized by coarse-grained, poorly sorted red (dominantly) sandstone. Paleosol development and especially carbonate accumulation (e.g., caliche) within the Masorobe Member is indicative of seasonality in the system (Rogers et al., 2000). Taken together, these interpretations paint an environment in which the biota/crocodyliforms existed on a broad alluvial plain in a semi-arid context, with evidence for seasonality that would have significantly influenced feeding ecology and lifestyles more generally in the context of heterogeneous resource availability. To date, there is little direct information for either macrofloral or palynological data from the Maevarano Formation, with the relatively abundant root traces preserved in the Masorobe Member as the lone evidence for plant material (Rogers et al., 2000) and indicating relatively dense vegetation with deep root systems. Generally, the highest likelihood of preservation among the Maevarano crocodyliforms are in those that live within primary depositional environments. In this case, *Mahajangasuchus* and two undescribed neosuchians are the most abundant crocodyliforms recovered, all three favored aquatic and semiaquatic environments. In contrast, the other three notosuchian taxa (*Araripesuchus*, *Simosuchus*, and *Miadanasuchus*) preferred terrestrial habitats and are rarely preserved outside of Anembalemba Facies 2 accumulations, especially in comparison with those species from aquatic habitats. This situation complicates paleoecological analysis of the terrestrial species.

The species richness ($n = 4$) and large morphological disparity exhibited by the Maevarano Fm notosuchians are remarkable in this paleoenvironmental context, particularly when considering the range of body sizes and morphological variability in craniodental anatomy that no doubt reflects adaptations to diverse ecologies. *Simosuchus* with specialized teeth indicating a unique plant-dominated diet, also exhibits morphology consistent with a completely terrestrial habit. The three others notosuchian taxa, each of different adult size, are grouped as predators in the

ecosystem. The dentition of the small and agile, and mostly terrestrial form, *Araripesuchus* indicates a carnivorous diet. Currently known only from exceptional chance preservation in Facies 2 of the Anembalemba Member, as with many other small-bodied vertebrates, *Araripesuchus* may have specialized as a predator of invertebrates (e.g., arthropods, mollusks) and small vertebrates (e.g., hatchlings, squamates, amphibians) present in terrestrial and marginal aquatic setting. The larger, terrestrial *Miadasuchus*, best represented in the marginal marine Miadana and Kinkony members, is also known from the Anembalemba Member. Like *Araripesuchus*, *Miadasuchus* was mostly predatory, with adults likely capable of feeding on juvenile dinosaurs and most of the other vertebrates in the Maevarano Fm assemblage. Competition driven by ontogenetic size and general feeding ecology overlap between the terrestrial predators *Miadasuchus* and *Araripesuchus* may have been mitigated by habitat segregation or prey specialization. Evidence of the former is suggested by the relative abundance of *Miadasuchus* in the Miadana Member, with diagnostic *Araripesuchus* remains are virtually unknown outside Anembalemba Member Facies 2 deposits. However, given the heterogeneous nature of locality- and/or member-specific fossil occurrences, we are cautious in establishing hypothesis related to local habitat preference at this time.

By contrast, the large-bodied *Mahajangasuchus* occupied the aquatic/semi-aquatic realm as the largest crocodyliform in the paleoenvironment (Turner and Buckley, 2008; Krause et al., 2022), perhaps hunting medium to larger prey items in both the aquatic and near-aquatic environments (see Gutherz et al., 2020). Due to extreme seasonality of the system, these aquatic habitats may have fluctuated dramatically, influencing prey type and availability throughout the year. For example, during wet seasons, when rivers became deeper and faster, and aquatic vertebrates became more active and thus available, such animals may have comprised the bulk of the diet for *Mahajangasuchus*. During dry seasons, as water sources reduced in size, terrestrial prey may have concentrated around aquatic environments making them more susceptible to ambush predation.

The unnamed Maevarano Fm crocodyliforms, both neosuchians, represent smaller, semi-aquatic forms, providing more balance to the terrestrial-aquatic split of crocodyliforms than might be expected in Late Cretaceous ecosystems (Krause et al., 2022). Ontogenetic overlap between *Mahajangasuchus* and the two neosuchian taxa may have driven prey specialization and habitat segregation as well, in addition to patterns of intraspecific competition/niche separation. Thus, the Maevarano Fm crocodyliforms, taken together with the diversity of other vertebrates known from the formation, provide an opportunity to explore the ecological range exploited by different groups during the latest Cretaceous in what is today Madagascar. Future work examining the entire crocodyliform fauna (i.e., all six taxa) within the broader context of the Maevarano Fm biota awaits ongoing primary descriptive, phylogenetic, and functional analyses of the two neosuchians.

IV.C. Crocodyliforms and a comparison of ecomorph diversity during the Late Cretaceous

The Mesozoic Era was a time in which terrestrial reptiles greatly diversified, with crocodylomorphs being one of the more ecologically diverse groups over this span. There are examples of different subclades exploiting a range of continental (fully terrestrial to semi-aquatic freshwater) and marine (near-shore to pelagic) environments. Such ecological diversification is perhaps most notable during the Cretaceous when crocodyliforms (one subgroup of Crocodylomorpha) radiated into environments and ecosystems around the planet, represented by an enormous diversity in body size and a range of ecomorphs (Benson and Godoy, 2019; Godoy and Turner, 2020; Marinho et al., 2022). The most abundant and greatest diversity of this group is known from South America among the continents making up the former supercontinent of Gondwana (Andrade and Bertini, 2008; Marinho et al., 2022; Pinheiro et al., 2023). Indeed, fragmentation of the supercontinent Gondwana may have provided an opportunity for further habitat diversification to support the concomitant morphological experimentation by crocodyliforms during the middle and Late Cretaceous (Turner, 2004; Nicholl et al., 2021).

The fossil record of Gondwanan crocodyliforms during the Cretaceous derives primarily from alluvial, fluvial and lacustrine deposits (Carvalho et al., 2010; Marinho et al., 2022). In this, notosuchian mesoeucrocodylians are the most diverse and best known from units throughout South America, although the crocodyliform fossil record from Cretaceous units in Madagascar (this contribution) and continental Africa (e.g., see (e.g., see Sereno and Larsson, 2009; O'Connor et al., 2010; Sertich and O'Connor, 2014; Saber et al., 2018; Nicholl et al., 2021) has expanded in recent years with increased efforts in field collection. Nonetheless, ~70% of named notosuchians have been recovered from South America to date (Nicholl et al., 2021). For example, the Adamantina and Serra da Galga formations from Brazil and the Bajo de la Carpia formation(s) from Argentina preserve diverse assemblages of crocodyliforms (Table 2), with multiple species (e.g., at least three species each) known from each rock unit. However, it should be noted that each unit may represent significantly more time than is preserved in the Maevarano Fm, implying that at least some of the apparent diversity is a result of lumping more than one distinct sympatric/contemporaneous faunal zone. Nonetheless, these examples suggest that it was relatively common for individual middle/Late Cretaceous continental ecosystems to support a diversity of crocodyliforms.

The Maevarano Formation crocodyliforms add to the evolving story of continental ecosystems in Gondwana, with high species richness and a broad range of ecomorphological disparity for a given paleoecosystem. This disparity, however, appears generally well matched with that observed in selected other Cretaceous Gondwanan ecosystems. For example, *Araripesuchus tsangatsangana*, a form that appears morphological similar in size and shape (e.g., similar dentition, etc.) to *A. gomesii* from Brazil and other members of the genus, is currently sitting as the earliest branching member of Uruguaysuchidae, a clade that also includes representatives from other regions of South America and continental Africa. Members of this group occupy the small bodied, terrestrial faunivore niche from a variety of locales during the middle-Late Cretaceous, a niche also commonly occupied by large squamates in some assemblages. At the other end of the body size and habitat spectrum, *Mahajangasuchus insignis*, a form that appears closely related to *Kaprosuchus*

saharicus from the middle Cretaceous of northern Africa, provides a view on the semi-aquatic mega-faunivore role in the Maevarano ecosystem. At a slightly smaller body size, the peirosaurid *Miadasuchus oblita* occupied the terrestrial mega-faunivore niche in the Maevarano Fm, mirroring many other Late Cretaceous ecosystems from which peirosaurids are represented (Table 2). Lastly, *Simosuchus clarki* rounds out the ecomorphological disparity among the Maevarano Fm notosuchians in occupying the small-bodied, terrestrial herbivore niche, a biological unicorn among crocodyliforms more generally with its palmate, multicuspid dentition (Kley et al., 2010; Ósi et al., 2013; Krause et al., 2022).

Compared with the Maevarano Formation, other Cretaceous Gondwanan ecosystems appear similar but relatively less species rich (Table 2). The Maevarano Fm, along with its accompanying diversity of vertebrates (Krause et al., 2019, 2022), may ultimately reflect an optimal sampling regime to date, one that includes a deposition model (e.g., quick burial via debris flows, with minimal transport) primed to capture both large- and small-bodied taxa (Rogers 2005, 2013). Thus, the relatively less diverse assemblages from other parts of Gondwana may currently reflect sampling rather than true crocodyliform diversity.

Formation (Age)	Location	Estimated # taxa	Taxon/Taxa	References
Maevarano (Maastrichtian)	Madagascar	4	1. <i>Mahajangasuchus insignis</i> 2. <i>Simosuchus clarki</i> 3. <i>Araripesuchus tsangatsangana</i> 4. <i>Miadasuchus oblita</i>	Brochu and Buckley, 1999; Buckley et al., 2000; Turner, 2006; Buffetaut and Taquet, 1979
Cerro Fortaleza (Campanian-Maastrichtian)	Argentina	1	1. Peirosauridae	Carabajal et al., 2021
Cajones (Turonian-Santonian)	Bolivia	1	1. <i>Yacarareni boliviensis</i>	Novas et al., 2009

Marília (Late Maastrichtian)	Brazil	4	1. <i>Uberabasuchus terrificus</i> 2. <i>Peirosaurus torminni</i> 3. <i>Itasuchus jesuinoi</i>	Candeiro, 2009
			4. <i>Labidiosuchus amicum</i>	Kellner et al., 2012
Bajo de la Carpa (Campanian- ?Maastrichtian)	Argentina		1. <i>Notosuchus terrestris</i> 2. <i>Wargosuchus australis</i> 3. <i>Microsuchus schilleri</i> 4. <i>Comahuesuchus brachybuccalis</i> 5. <i>Gasparinisuchus peirosauroides</i>	Lecuona and Pol, 2008; Martinelli and Pais, 2008; Leardi et al., 2015a; Pol et al., 2014; Martinelli et al., 2012
Adamantina (Turonian- Santonian)	Brazil		1. <i>Baurusuchus salgadoensis</i> 2. <i>Marillasuchus robustus</i> 3. <i>Marillasuchus amarali</i> 4. <i>Montealtosuchus arrudacamposi</i> 5. <i>Adamantinasuchus navae</i> 6. <i>Baurusuchids</i>	Carvalho et al., 2005; Nobre et al., 2007; Vasconcellos and Carvalo, 2005; Carvalho et al., 2007; Nobre and Carvalho, 2006; Marchetti et al., 2022; Carvalho and Teixeira, 2011
Serra da Galga (Late Maastrichtian)	Brazil		1. <i>Itasuchus jesuinoi</i> 2. <i>Neuquensuchus universitas</i> 3. <i>Peirosaurus tormini</i>	Candeiro and Martinelli, 2006; Lio et al., 2018; Martinelli et al., 2012

Candeleros (lower Cenomanian)	Argentina	2	1. <i>Araripesuchus</i> <i>patagonicus</i> 2. <i>Araripesuchus</i> <i>buitreraensis</i>	Candeiro and Martinelli, 2006
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Table. 2: Comparison of crocodyliform diversity in Late Cretaceous continental ecosystems.

CONCLUSIONS

The Maastrichtian Maevarano Formation in northwestern Madagascar and its incredible vertebrate fauna provide a view into end-Mesozoic continental ecosystems in this region of the former Gondwanan supercontinent. Among the known vertebrates from the Maevarano Fm, the diversity of crocodyliforms exceeds that of other contemporaneous faunas in terms of both preservational quality and morphological disparity. Here, the description of cranial anatomy and dentition of *Mahajangasuchus insignis*, *Miadasuchus oblita*, *Simosuchus clarki*, and *Araripesuchus tsangatsangana* provides important insight for understanding the morpho-functional ecosystem partitioning among four notosuchian species.

The shape, size, position, and orientation of the skull openings have been used to characterize the mode of life of each species. For example, the anterior orientation of the external nares in *Araripesuchus*, *Simosuchus*, and *Miadasuchus* indicates a terrestrial (rather than semi-aquatic) lifestyle for these taxa, with the dorsolaterally oriented external nares in *Mahajangasuchus* suggesting a semi-aquatic or aquatic lifestyle. Likewise, laterally oriented orbits indicate a terrestrial existence, whereas smaller and dorsally oriented orbits suggest an aquatic lifestyle. The specialized dentition of *Simosuchus* distinguishes it from the other known Maevarano crocodyliforms and indicates a primarily herbivorous diet. Overlap in the predatory terrestrial taxa *Araripesuchus* and *Miadasuchus* can be explained broadly by the considerable difference in adult size, though ontogenetic overlap may have required further partitioning of habitat or preferred prey at certain ontogenetic stages. Similarly, ecological overlap and competition between aquatic taxa, including *Mahajangasuchus*

and the two undescribed, aquatic neosuchians, may be resolved by the extreme disparity in adult size, local habitat segregation, and/or prey specialization. Analyses of habitat and prey partitioning are complicated by taphonomic and depositional constraints of the Maevarano Fm system and are beyond the scope of this project. Overall, combining analyses of cranial anatomy and tooth morphology can improve precision of inferring habitat use and lifestyle in extinct crocodyliforms, with the Maevarano Fm providing a strong case study for considering ecomorphological diversity and disparity measures in other ecosystems (past and present).

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