THE FEEDING HABITS OF THE STRANGE CROCODYLIAN
*MOURASUCHUS* (ALLIGATOROIDEA, CAIMANINAE): A REVIEW, NEW HYPOTHESES AND PERSPECTIVES

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*ABSTRACT* – The caimanine crocodilian *Mourasuchus* from the Miocene of South America is one of the most peculiar crocodylomorphs of all time. It exhibits an unusual long, wide and dorsoventrally flattened rostrum, long, slender mandibles, and relatively short cervical vertebrae. These features have led previous authors to propose that the feeding habits of *Mourasuchus* were very different from those of most crocodylomorphs. In order to significantly improve the knowledge on the feeding habits of *Mourasuchus*, we performed a comprehensive review on this issue in order to offer the most complete assessment on the question to date, and to propose new hypotheses coherent with our current knowledge on *Mourasuchus* and on the feeding habits of crocodylomorphs. As a result, this study proposes that *Mourasuchus* was likely incapable of capturing and consuming large preys and specialized in eating small ones, such as mollusks, crustaceans and small fishes. The rostrum of *Mourasuchus* possibly evolved to cover the largest possible area, in order to be more efficient in the capture of large amounts of small preys. Whether *Mourasuchus* was capable to “select” the food from other material ingested with it is not yet known. In consequence, we suggest “gulp-feeding” to describe the proposed feeding habits of these animals. *Mourasuchus* was probably an inhabitant of quiet, shallow water bodies, where there were a broad range of habitats in which the preferred preys of this taxon dwelled. It is also proposed that the habit of *Mourasuchus* evolved from the durophagous habit proposed for many fossil caimanines. This hypothesis, however, has to be addressed by future studies.

*Keywords*: *Mourasuchus*, paleoecology, paleobiology, feeding habits, Caimaninae, Crocodylia.

*RESUMO* – O crocodiliano caimaníneo do Mioceno da América do Sul *Mourasuchus* é um dos crocódilomorfos mais peculiares de todos os tempos. Ele possui um incomum rostro longo, largo e dorsoventralmente achatado, mandíbulas longas e esguias e vértebras cervicais relativamente curtas. Tais características levaram estudos prévios a propor que os hábitos alimentares de *Mourasuchus* eram muito diferentes da maioria dos crocódilomorfos. Com o objetivo de melhorar significativamente o conhecimento sobre os hábitos alimentares de *Mourasuchus*, realizamos a revisão mais abrangente acerca desta questão para oferecer uma análise mais completa sobre ela até o momento e propor novas hipóteses que sejam coerentes com o conhecimento atual sobre *Mourasuchus*, bem como com os hábitos alimentares dos crocódilomorfos como um todo. Como resultados, este estudo propõe que *Mourasuchus* era provavelmente incapaz de capturar e consumir grandes presas e se especializou em consumir presas pequenas, tais como moluscos, crustáceos e pequenos peixes. O rostro de *Mourasuchus* possivelmente evoluiu para abranger a maior área possível para permitir maior eficiência na captura de grandes quantidades de pequenas presas. Não se sabe ainda se *Mourasuchus* seria ou não capaz de “selecionar” a comida do material que ele ingeriria junto com ela. Assim, sugerimos “engolimento” como o melhor nome para os hábitos alimentares propostos para o táxon. *Mourasuchus* habitava provavelmente corpos d’água quietos e rasos, que possuíriam em maior quantidade os habitats em que viviam suas presas preferenciais. Também se propõe que o hábito de *Mourasuchus* evoluiu do hábito durofago proposto para muitos caimaníneos fósseis. Esta hipótese, porém, precisa ser avaliada por estudos posteriores.

*Palavras-chave*: *Mourasuchus*, paleoecologia, paleobiologia, hábito alimentar, Caimaninae, Crocodylia.
INTRODUCTION

The fossil crocodylomorphs of the Miocene of South America comprise one of the largest, most taxonomically diverse and morphologically disparate faunas of the Crocodylomorpha clade (Langston, 1965; Gasparini, 1996; Langston & Gasparini, 1997; Paolillo & Linares, 2007; Salas-Gismondi et al., 2007, 2015; Riff et al., 2010; Scheyer & Moreno-Bernal, 2010; Bona et al., 2013a; Scheyer et al., 2013; Bona & Barrios, 2015; Moreno-Bernal et al., 2016; Scheyer & Delfino, 2016; Souza et al., 2013; Cidade et al., 2017, 2019). This includes not only records of the extant genera Paleosuchus (Salas-Gismondi et al., 2007), Melanosuchus (Medina, 1976; Bona et al., 2017; Foth et al., 2017) and Caiman (Souza-Filho, 1987; Fortier et al., 2009; Bona & Carabajal, 2013; Bona et al., 2013a, 2014; Fortier et al., 2014; Salas-Gismondi et al., 2015), but perhaps the most impressive examples of such diversity are the crocodylomorphs whose morphology, ecological niche and feeding habits differ substantially from those of the extant crocodylians.

These include the terrestrial predators sebecids (Langston, 1965; Paolillo & Linares, 2007; Salas-Gismondi et al., 2007), the giant, semi-aquatic top predator Purussaurus (Barbosa-Rodrigues, 1892; Mook, 1941; Langston, 1965; Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006; Aureliano et al., 2015), the durophagous caimanes Gnatusuchus, Kuttanacaiman, Globidentosuchus and Caiman wannlangstoni (Langston, 1965; Salas-Gismondi et al., 2015), and the predominantly piscivorous, longirostre taxa represented by crocodyloids such as Characostusuchus and Brasilosuchus (Langston, 1965; Souza-Filho & Bocquentin-Villanueva, 1989; Souza-Filho, 1991, 1993; Souza-Filho et al., 1993), and gryposuchine gavialoids (Gürich, 1912; Langston, 1965; Gasparini, 1968; Sill, 1970; Bocquentin-Villanueva & Buffetaut, 1981; Kraus, 1998; Brochu & Rincón, 2004; Riff & Aguilera, 2008; Salas-Gismondi et al., 2016).

One of the most strikingly disparate forms of the Miocene of South America is Mourasuchus, a caimanine crocodylian that exhibits a long, wide, dorsoventrally flattened rostrum (a “platyrostral-broad” rostrum according to the classification of Busbey, 1994) with a relatively small skull table (Figure 1), slender, long mandibles (Figures 2 and 3) and cervical vertebrae relatively short anteroposteriorly (Figure 4) (see Price, 1964; Langston, 1965, 2008; Bocquentin-Villanueva, 1984; Bona et al., 2013a, 2013b; Cidade et al., 2017). The genus comprises four species: M. atopus (Langston, 1965), from the middle Miocene Honda Group of Colombia and Pebas Formation of Peru (Langston, 1965; Salas-Gismondi et al., 2015); M. amazonensis Price, 1964, from the upper Miocene Solimões Formation of Brazil (Price, 1964; Souza-Filho & Guilherme, 2011a); M. arenstdi Bocquentin-Villanueva, 1984 from the upper Miocene Urumaco Formation of Venezuela, Solimões Formation of Brazil and Ituzaingó of Argentina (Bocquentin-Villanueva, 1984; Gasparini, 1985; Souza-Filho & Guilherme, 2011b; Scheyer & Delfino, 2016); and M. pattersoni Cidade et al., 2017, also from the Urumaco Formation (Cidade et al., 2017).

There are also records of Mourasuchus for the lower/middle Miocene Castilletes Formation of Colombia (Moreno-Bernal et al., 2016), for the middle Miocene units Fitzcarrald Arch and Pebas Formation of Peru (Salas-Gismondi et al., 2007, 2015) and Socorro Formation of Venezuela (Scheyer et al., 2013), and for the upper Miocene Solimões Formation, of Brazil (Souza-Filho & Kischtal, 1995; Oliveira & Souza-Filho, 2001; Scheyer & Moreno-Bernal, 2010), Urumaco, of Venezuela (Scheyer & Delfino, 2016) and Yecua of Bolivia (Tineo et al., 2014).

Ever since the first descriptions, the unusual morphology of Mourasuchus has sparked a debate about how these animals captured their preys, and about what exactly would comprise such preys. Many hypotheses have been put forward: the first ones were proposed by Langston (1965), which would later be called “filter-feeding” by other authors (Riff et al., 2010; Bona et al., 2013b), while a second hypothesis, briefly discussed by Cidade et al. (2017), is that Mourasuchus would perform a feeding behaviour named as “gulp-feeding”. Additionally, different studies have proposed many distinct possible prey items for Mourasuchus, including fish, crustaceans, gastropod and bivalve molluscs and even herbivory (Langston, 1965, 2008; Cidade et al., 2017).

Langston (1965) proposed three different foraging strategies for this taxon: (i) Mourasuchus could stay stopped in the water surface with an open mouth, waiting that fish and arthropods ended up entering into the mouth unawary – a strategy that had been observed in living caimanes according to the author; (ii) it could swim slowly through the water surface scooping up (presumably with a “gular sac”, see below) small animals; (iii) it could forage among the mud (“mud-grubbing”), either on the margins or on the floor of the water bodies, somewhat similarly to the behavior seen in modern-day ducks, and according to Langston (1965) in extant caimanes too. In addition, Langston (1965), arguing that the teeth of Mourasuchus were too small to have a large role in food capture, stated that they would only aid in “food straining”. This expression was apparently considered by later authors (Riff et al., 2010; Bona et al., 2013b) to mean the same as “filter-feeding”. However, neither Langston (1965) nor later authors explained what “straining” and “filter-feeding” would specifically mean.

The first feeding strategy could certainly be performed by Mourasuchus, but we consider unlikely that such a behavior by itself would provide all the food necessary for the animal due to the relative level of randomness in food capture that arises in this process; additionally, it would not explain the peculiar cranial morphology developed by the taxon. The second behavior could also be performed, but most likely, in very quiet water bodies in order to diminish the resistance the animal would face to close the jaws under the water. The perspective of this study is that a similar behavior to the third one proposed by Langston (1965) better fits the known morphology of Mourasuchus and thus is here considered the most likely to be performed by the taxon (see an illustration in Figure 5), as will be discussed below.
of *Mourasuchus* for obtaining food would be foraging through bottoms and margins of shallow water-bodies, but also emphasized briefly the role of the platyrostral-broad (see Busbey, 1994) shape of the rostrum in capturing large amounts of small preys, with the ventral portion of the rostrum serving as a “fishing net” or “gular sac”. Additionally, Cidade *et al.* (2017) name this behavior proposed for *Mourasuchus* as “gulp-feeding”, which would be more accurate than “filter-feeding” in describing the behavior, as the latter could imply the idea that *Mourasuchus* would perform techniques akin to those of baleen whales, for example. Regarding the foraging strategies and methods of ingestion of the food in *Mourasuchus*, this work develops on the perspectives put forward by Cidade *et al.* (2017) but also reviews thoroughly the hypothesis of those authors as well as those of Langston (1965, 2008).

![Figure 1. The platyrostral-broad skull morphology of *Mourasuchus*: skull of the holotypes of *M. arendsi*, CIAAP-1297 (A); and *M. pattersoni*, MCNC-PAL-110-72V (B) in dorsal view. B is taken from Cidade *et al.* (2017, fig. 2). Scale bars = 10 cm.](image)

Another interesting scenario is the notable anatomical convergence between *Mourasuchus* and the Cretaceous crocodyliforms from the north of Africa *Stomatosuchus*, *Laganosuchus*, *Aegyptosuchus* and *Aegisuchus*, especially in the morphology of the skull, which is also platyrostral-broad in the first two taxa, and is inferred to have the same morphology in the other two (Stromer, 1925; Sereno & Larsson, 2009; Holliday & Gardner, 2012). This fact meant that some similar hypotheses have been proposed regarding the feeding habits of *Mourasuchus* and the taxa from the African Cretaceous, most notably that the ventral portion of the rostrum serving as a “fishing net” or “gular sac” for collecting and swallowing preys (see Nopcsa, 1926; Langston, 1965; Sereno & Larsson, 2009).
Figure 2. The long, slender mandibles of *Mourasuchus*: articulated right and left hemimandibles of the holotype of *M. pattersoni* MCNC-PAL-110-72V (A) in dorsal view and right hemimandible of the holotype of *M. arendsi* CIAAP-1297 (B) in dorsolateral view. A is taken from Cidade et al. (2017, fig. 4). Scale bars: A = 20 cm; B = 10 cm.

Figure 3. A right hemimandible (UFAC-2283) and a left hemimandible (UFAC-1669) of *Mourasuchus* (A) in dorsal view and the articulated mandibles of the holotype of *Laganotushcus thaumastos* (MNN IGU13; Niger; (B) in dorsal view, evidencing the similarities of the mandibular morphology of the two taxa. Scale bars: A = 5 cm; B = 10 cm.
Given these different hypotheses and scenarios, the goal of this paper is to present a comprehensive revision on the studies about the feeding habits of *Mourasuchus* and to discuss which hypothesis is more congruent with our current knowledge of the taxon, the paleoenvironment in which it lived and the biota with which it co-existed during the Miocene. Specifically, the three questions this study addresses are the following: how *Mourasuchus* captured its food?; what exactly *Mourasuchus* ate?; and how its unusual morphology and feeding strategy evolved, diverging from more “traditional” caimanine morphology and foraging habits.

In accordance with these objectives, comprehensive revisions were performed on the *Mourasuchus* anatomy related to feeding habits, the convergence between *Mourasuchus* and the Cretaceous crocodyliforms from northern Africa, and the antecedents on the research on *Mourasuchus* feeding habits. As a result of these revisions, the hypothesis defended by this work on the feeding habits of *Mourasuchus* is presented, along with perspectives regarding the paleoecology of this peculiar taxon.

**RESULTS**

*Mourasuchus* unusual anatomy related to feeding habits

Both the cranial and the postcranial anatomy of *Mourasuchus* exhibit remarkable differences with most crocodyliforms, even if the unusual morphological disparity exhibited by the group in the Miocene of South America is considered. Many of these peculiarities were linked by previous studies to the feeding behaviour (see Langston, 1965, 2008; Bona *et al*., 2013b; Tineo *et al*., 2014; Cidade *et al*., 2017), which are reviewed by this study.

**Institutional abbreviations.** CIAAP, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela; MCNC-PAL, Museo de Ciencias Naturales de Caracas, Caracas, Venezuela; MNN IGU, Muséum National du Niger, Niamey, Niger; UFAC, Universidade Federal do Acre, Rio Branco, Brazil.
The *Mourasuchus* skull has a remarkably long, wide, dorsoventrally flattened, “duck-like” platyrostral-broad rostrum (Figure 1). In accordance with the shape of the rostrum, the mandibles are long, but also lateromedially slender, with a short mandibular symphysis that does not extend beyond the level of the first mandibular alveolus (Cidade et al., 2017; Figures 2 and 3). Such skull most likely precluded *Mourasuchus* to capture, hold or ingest large preys in the way that many of the current crocodylians do, especially those of large size (e.g. Busbey, 1994), as it would not provide the bite force required for such activity (Langston, 1965). In addition, the shape of the rostrum would disturb the movement of the skull in water bodies with swift currents, while being met with great resistance if the animal tried to close the “duck-like” rostrum under water (Langston, 1965).

Most of the teeth of *Mourasuchus* are very small relative to the size of the skull. The first to the fourth alveoli are the biggest in the mandibulary tooth row and are comparable to the extant *Crocodylus acutus*, but from the fifth alveolous on the alveolar size of *Mourasuchus* tends to be smaller than those of other crocodylians (see Langston, 1965, fig. 29). This suggests that the teeth did not have a prominent role in the capture or handling of the prey in the mouth. As such, the morphologies of the skull and the teeth indicate that *Mourasuchus* was not capable of capturing or handling large or middle-sized prey, which are a prominent diet item in the adult individuals of current large crocodylians whose body length approaches that of *Mourasuchus* (estimated in 6.6m by Langston, 2008), such as *Crocodylus porosus*, *C. niloticus*, *Alligator mississippiensis* and *Melanosuchus niger*, among others.

The postcranial anatomy features of *Mourasuchus* that have relation to the feeding behavior corroborate these hypotheses. The cervical vertebrae of *Mourasuchus arendsi* and *M. pattersoni* are relatively anteroposteriorly shorter than those of extant crocodylians (Bocquentin-Villanueva, 1984; Langston, 2008; Figure 4), while Tineo et al. (2014) described a cervical vertebra of “*Mourasuchus sp.*” with a short vertebral centrum from the upper Miocene of Bolivia. This suggests that the neck of *Mourasuchus* was “relatively weak and less motile” than that of extant crocodylians, as proposed by Langston (2008).

Langston (2008) also linked some postcranial features to biomechanical consequences related to the feeding behavior of *Mourasuchus*. These are the “nearly vertical” trochlear surfaces on the odontoid bone, which would indicate a shorter vertical excursion of the head than that of extant crocodylians; the small, non-hooked hypapophyses of the cervical vertebrae suggest less development of the muscle *M. longus colli*, which is involved with flexing and lateral movement of the neck; and the low cervical neural spines suggest that the epaxial antagonist muscles would be less powerful that in extant taxa (see Langston, 2008, p. 139). These features, associated with the proportionally small size of the cervical vertebrae as
whole, led the same author to propose that the cervical area (“neck”) of *Mourasuchus* would be relatively weaker and less motile than that of extant crocodylians.

All these suggestions still require proper biomechanical analyses to be thoroughly tested, but this work considers that the features noted by Langston (2008) indicate at least that *Mourasuchus* was not capable of accentuated head movements, as pointed out the same author. Thus, the vertebral anatomy agrees with the skull anatomy in indicating that this taxon was very probably not capable of holding and dismembering large prey in the way many modern crocodylians do, with behaviors such as the “death roll” (see Blanco et al., 2015) being unlikely to be performed by *Mourasuchus*.

Furthermore, Tineo et al. (2014) also propose that *Mourasuchus* would have a reduced length of the vertebral column in comparison with extant crocodylians, which would result in a skull-length-to-body ratio hydrodynamically adverse to a typical aquatic crocodylian. This would be in agreement with the known features of vertebral anatomy of the taxon, but as no complete vertebral column of *Mourasuchus* has been found so far, this hypothesis needs to be seen with caution. Nevertheless, Tineo et al. (2014) also proposed that *Mourasuchus* would be a preferential inhabitant of “lentic, shallow aquatic habitats” (Tineo et al., 2014), such as swamps and quiet lakes. This agrees with the aforementioned proposition of Langston (1965) about the shape of the rostrum of *Mourasuchus* disturbing the movement of the skull in swift waters and the great resistance the animal would face to close the rostrum under water. These proposals are in agreement with the feeding habits and lifestyle proposed for *Mourasuchus* in this study, which is detailed below. Additionally, swamps and lakes were known to exist in the paleoenvironments *Mourasuchus* lived in during the Miocene (e.g., Latrubesse et al., 2010; Scheyer & Moreno-Bernal, 2010).

**Convergence with North African forms of the Cretaceous**

The unusual skull morphology of *Mourasuchus* is convergently shared with five species of four genera from the Upper Cretaceous of north Africa: *Stomatosuchus inermis* Stromer, 1925, from the Baharyia Formation of Egypt; *Laganosuchus thaumastos* Sereno & Larsson, 2009, from the Echkar Formation of Niger (Figure 3) and *L. maghrebensis* Sereno & Larsson, 2009 from the Upper Cretaceous Kem Kem Formation of Morocco; *Aegisuchus witmeri* Holliday & Gardner, 2012, also from the Kem Kem Formation; *Aegyptosuchus peyeri* Stromer, 1933, also from the Baharyia Formation. *Stomatosuchus* and *Laganosuchus* have been grouped together in Stomatosuchidae Stromer, 1925, whereas *Aegyptosuchus* and *Aegisuchus* have been grouped within Aegyptosuchidae Kuhn, 1936 (Holliday & Gardner, 2012). *Stomatosuchus* and *Laganosuchus* share with *Mourasuchus* a long, wide, dorsoventrally flattened skull and slender mandibles with short symphyses (see Stromer, 1925; Nopcsa, 1926; Sereno & Larsson, 2009). While skull and mandibles were described for *Stomatosuchus* (Stromer, 1925; Nopcsa, 1926), only mandibles were described for *Laganosuchus*, but a platyrostral-broad rostrum can be safely inferred for this taxon due to the long, slender mandibles that strongly resemble those of *Stomatosuchus* (Sereno & Larsson, 2009; Figure 3). *Aegisuchus* and *Aegyptosuchus* do not have complete skulls or mandibles preserved, but estimations made for *Aegisuchus* by Holliday & Gardner (2012) indicate that this taxon likely had a long, wide rostrum similar to that of stomatosuchids, and the phylogenetic proximity and morphological similarities between *Aegyptosuchus* and *Aegisuchus* suggest that the former possessed a similar platyrostral-broad rostrum (see Holliday & Gardner, 2012), but further specimens of *Aegyptosuchus* are required for this issue to be settled.

The convergent nature of these similarities is evident for the fact that Stomatosuchidae (represented only by *Laganosuchus* in phylogenetic analysis, since the holotype of *Stomatosuchus* was destroyed during the Second World War, see Holliday & Gardner, 2012) is phylogenetically placed as a neosuchian basal to Eusuchia (Sereno & Larsson, 2009; Holliday & Gardner, 2012), and Aegyptosuchidae is placed either as a sister-taxon of Crocodylia or as a clade within Crocodylia but unrelated to Alligatoroidea, the clade within *Mourasuchus* is situated (Holliday & Gardner, 2012).

The morphological similarities between *Mourasuchus* and the Cretaceous taxa explain that similar paleoecological hypotheses have been proposed for both. Sereno & Larsson (2009) proposed that the mandibles of *Laganosuchus* could not be adducted or abducted with great force. Langston (1965) had also described the mandibles of *Mourasuchus* as “mechanically inefficient”. Consistent with this, Sereno & Larsson (2009) suggested that *Laganosuchus* was a low-lying, sit-and-wait predator, while Langston (2008) described *Mourasuchus* as a “lie in wait” predator that inhabited quiet waters. Additionally, Langston (1965) had already suggested that *Mourasuchus* could have an ambush behaviour of staying immobile in the water with the mouth opened, waiting for small fish and other animals to enter it, a behaviour that has been observed in extant taxa (Langston, 1965), and that can also be proposed for *Laganosuchus*. Most remarkable, however, is the proposal that the musculature of the ventral part of the rostrum that could act as a “fishing net” that would allow these taxa to “collect” the prey for subsequent swallowing, presumably without any large participation of the teeth in the process. The suggestion was first made for *Stomatosuchus* by Nopcsa (1926), and later proposed for *Mourasuchus* as well (Langston, 1965; Cidade et al., 2017). Upon suggesting this mechanism for *Stomatosuchus*, Nopcsa (1926) proposed that the ventral portion of the rostrum of that taxon could be a contractible structure analogous to the gular sac found in pelicans, based on features such as the length and slenderness of the mandible, the presence of a “wing-like” process ventral to the posterior portion of the same element (that would serve as attachment area for the ligaments of the “gular sac”), and the fact that the “post-articular process” (interpreted here as the retroarticular process) is bent inwards relative to the mandible. In the available figures of *Stomatosuchus*, the inward bending of the retroarticular process is not evident, but a ventral expansion in
the posterior portion of the mandible that may be what Nopcsa
names “wing-like” process is (see Stromer, 1925, figs. 1–1a; 
Sereno & Larsson, 2009, figs. 2B–2C). None of these two
features, however, are present in Laganosuchus (see Sereno
& Larsson, 2009) or in Mourasuchus (see Langston, 1965; 
Cidade et al., 2017, 2018), but the long, slender mandibles are
shared between the three taxa. However, no specific studies
to determine how contractible the ventral portion of the skull
was in these taxa have ever been performed. In addition, the
exact role that such contraction ability could perform in the
feeding process of Mourasuchus has never been thoroughly
reviewed and discussed, for example through comparison
with observations made in extant crocodylians about the
musculature of the ventral portion of the rostrum. The latter
issue is also one of the objectives of this study.

Hypotheses defended in this work for the feeding habits
of Mourasuchus

The anatomy of both the skull and the cervical vertebrae
makes it very unlikely that Mourasuchus was able to hold,
dismember and ingest larger prey, especially if these were
able of fast movements. The only large prey Mourasuchus
could eat would be those not capable of fast movements,
such as the aforementioned Lepidosiren fish, but even these
slow-moving prey was likely to require some strength of
the skull and mandibles, as well as large and sharp teeth to
be properly manipulated; all characteristics that Mourasuchus
lacks. As such, it is here considered more likely that the prey
of Mourasuchus would be mostly comprised of small animals.

The most consumed small animals were most likely small
fish and crustaceans (e.g. fresh water crabs and shrimps),
as proposed by Langston (1965, 2008) and Cidade et al.
(2017), but also gastropod and bivalve mollusks (Cidade et al., 2017; Figure 5) which are also found in the Miocene
formations of South America and which comprise the main
diet items of several durophagous caimaines (see Salas-
Gismondi et al., 2015), whose possible relation to the feeding
habits of Mourasuchus will be discussed posteriorly. Insects
could also make part of the diet of Mourasuchus, although
presumably to a lesser extent than the prominently aquatic
gastropods, bivalves and crustaceans. The consumption of
these groups of invertebrates by extant crocodylians has been
continuously recorded, including in living caimaines (e.g.
Carvalho, 1951; Medem, 1981, 1983; Monteiro et al., 1997),
especially in juvenile stages (e.g. Monteiro et al., 1997), whilst
Caiman latirostris is considered to rely mainly on ampullarid
gastropods also during adulthood (Diefenbach, 1979, 1987;
Vanzolini & Gomes, 1979; Ayarzagüena, 1983; Monteiro, et
al., 1997; Ösi & Barrett, 2011).

The possibility that Mourasuchus could be an herbivore
is not considered here as likely, but further evidence may
point to an opposite direction. Consumption of vegetal matter
has been observed in living crocodylians, being it either of
foliage, seeds or fruits (e.g. Brito et al., 2002; see Platt et al.,
2013 for a revision); additionally, some capacity of digestion
of plant carbohydrates, proteins and lipids has been detected
in Alligator mississippiensis (Coulson et al., 1987; Staton,
1988; Platt et al., 2013). Herbivory has also been suggested
for other fossil crocodyliforms, such as Chimaerasuchus
paradoxus from Lower Cretaceous of China (Wu et al.,
1995), and Simosuchus clarki, from the Upper Cretaceous
of Madagascar (Buckley et al., 2000). As far as it concerns
Mourasuchus, however, there are no evidences yet to support
an herbivorous habit for this taxon, such as those that could
be obtained through the finding and analysis of stomach or
coprolite contents, for example.

The extinct caimaines Kuttanacaiman, Caiman wamlangstoni, Globidentosuchus and Gnatusuchus are
considered to be durophagous taxa, feeding mainly on hard-
shedded invertebrates such as bivalves and gastropods (Salas-
Gismondi et al., 2015). They are described as durophagous
mainly due to the presence of posterior globular teeth and
large mandibular symphyses, among other cranial features.
Gnatusuchus, specifically, is considered by Salas-Gismondi
et al. (2015) to have a foraging strategy of a “head burrowing”
activity in which the animal predated infaunal bivalves of
unconsolidated bottoms of lakes and rivers. Even though
Gnatusuchus was a very specialized form for this kind of
behavior, having a unique “shovel-like” structure in the lower
jaws that helped to “scrape” the bottom of the water bodies
(Salas-Gismondi et al., 2015), it is possible that such a strategy
could be performed by all the other extinct durophagous
Caimainae taxa. The bivalve infauna in the water bodies of
the Miocene of South America, where all of the aforementioned
extinct taxa lived, was very rich (Wesselingh et al., 2002;
Wesselingh, 2006; Salas-Gismondi et al., 2015), providing
and abundant diet source for durophagous crocodylians.
Given the possibility that the main prey of Mourasuchus
would be the same as that of durophagous caimaines such as
Gnatusuchus, we consider that the foraging behavior of
Mourasuchus could be somewhat similar to that of those taxa,
although exhibiting a specialization toward the swallowing
of large quantities of prey without the necessity to crunch
them with the teeth.

If durophagous Caimainae such as Gnatusuchus fed
burrowing the margins and floors of the water-bodies to collect
their prey (especially bivalve mollusks but also gastropods, as
well as crustaceans and other arthropods) and subsequently
churn them with their posterior globular teeth (a derivation
from the plesiomorphic condition in crocodyliformes, which
is to capture prey with the teeth and ingest without elaborate
mastication), Mourasuchus could use of a similar way to
capture the prey mainly in margins and bottoms of water
bodies but would not churn them with its teeth, since most
of those are not only very small but also lack the globular
shape seen in the typical durophagous crocodylians. Instead,
Mourasuchus would swallow the prey entirely, preferably in
large quantities that could be captured with the inferior part
of the rostrum and then ingested all together. Such behavior
would explain not only the small size of most of the teeth in
Mourasuchus (Langston, 1965), as it would also explain the
long, wide, dorsoventrally flattened, platyrostral-broad rostrum
of this taxon, as such morphology significantly increases the
area occupied by the rostrum, consequently increasing the
efficiency and the probability of capturing large amounts of the invertebrate prey on which *Mourasuchus* preferably fed on (Cidade et al., 2017). It explains, furthermore, the not very efficient musculature involved in the opening of the mouth as inferred in previous works (Langston, 1965, 2008; Tineo et al., 2014). Additionally, the use of the inferior part of the rostrum to collect preys would allow the taxon to capture large amounts of preys in a more efficient way than if the capture of the prey relied more on the use of the teeth, as it is frequently observed in extant crocodylians. For these reasons, this method of prey capturing, which developed on the third proposal by Langston (1965, see above) and Cidade et al. (2017) is preferred as the main foraging technique of *Mourasuchus* over the other two proposed by Langston (1965, see above). The other two could also be performed by *Mourasuchus*, but are considered as unlikely to be the main foraging techniques: in the first (that *Mourasuchus* stopped in the water surface with an open mouth, waiting that fish and arthropods ended up entering into the mouth unwary), such a behavior by itself is unlikely to provide all the food necessary for the animal due to the relative level of randomness in food capture that arises in this process and it would not explain the peculiar cranial morphology developed by the taxon. The second (that *Mourasuchus* could swim slowly through the water surface scooping up small animals) is unlikely to be the main foraging technique due to the slenderness of the mandibles, which are thus a morphology not adapted to a foraging technique based largely on underwater dorsoventral movements of the mandible to capture prey, and thus was most likely performed occasionally and on very quiet waters.

The use of the inferior part of the rostrum to collect preys is directly linked with some capacity of contraction of the ventral portion of the rostrum. Such capacity has been observed in the extant *Alligator mississippiensis*, which is achieved probably by the activation of the muscles *M. genioglossus* and *M. hyoglossus*, located underneath the tongue (Busbey, 1989). As such, this contraction can also be present in *Mourasuchus* – pending biomechanical studies that may confirm or not its existence in this taxon – and would aid in the “gulping” of the prey in the fashion proposed above. Such contraction is reminiscent of the idea of the presence of a “gular sac”, as proposed by Langston (1965). Although the expression “gular sac” could be used to denote only a contractible inferior part of the rostrum being presumably involved in the capture of the prey by *Mourasuchus*, we recommend that this expression should not be used to describe this structure for this taxon unless future studies eventually show the inferior part of the rostrum of *Mourasuchus* to have striking similarities with the gular skins found in birds like pelicans, for example. However, the role of the ventral portion of the rostrum as a contractile collecting tool for food (as a “fishing net”), regardless of the fact that it may be called a “gular sac” or not, is proposed here as a likely possibility given the inferred foraging behavior and diet items of *Mourasuchus*, as well as the presence of contraction of the musculature of this area seen in *A. mississippiensis*.

Walmsley et al. (2013) state that the crocodylian skull exhibited a “trade-off” along its evolutionary history between a long, slender rostrum that provided speed, and a shorter, yet more robust rostrum that provide strength in biting and consequently in the capture of prey. In this context, as argued by Cidade et al. (2017), *Mourasuchus* presents an interesting case in which the rostrum does not provide either speed or strength to the biting of the living individual; instead, an increase in area to optimize the capture of preferentially a large amount of small prey seems to be the great advantage this rostral morphology provided to the individuals of *Mourasuchus*.

This foraging strategy aforementioned described for *Mourasuchus* has been named as “gulp-feeding” (Cidade et al., 2017) to emphasize the process of collecting and swallowing the food that were performed by the taxon, instead of the term “filter-feeding”, which denotes the performing of a selection process on the food for which there is no evidence yet in *Mourasuchus*. However, the small invertebrate animals on which *Mourasuchus* would mainly feed would not be found separate from the microenvironment in which they live in, with these being either biotic – plants, algae – or abiotic – water, mud, sand, etc (Cidade et al., 2017). As such, *Mourasuchus* could rarely obtain its food in the aforementioned described way without also carrying into its mouth a certain amount of any of these materials, and thus it would be useful for the animal to develop a selection procedure to separate the edible matter from the non-edible matter (mud, water, etc.) that came with the former (Cidade et al., 2017). Such selection procedure may be what Langston (1965) described as “straining technique”, which later authors (e.g. Riff et al., 2010; Bona et al., 2013b) would refer to as a filtering or “filter-feeding” technique, even though none of this works give a detailed description of how these techniques would function.

Nevertheless, the possibility that *Mourasuchus* performed a procedure akin to a “selection” of the material put in the mouth before swallowing is considered here as plausible. Langston (1965) suggested that the tongue could be used to perform this procedure, as it could be elevated pressuring the water against the upper palate until the water could be expelled between the teeth, leaving the edible material concentrated for swallowing. Another possibility is that this movement proposed for the tongue by Langston (1965) could be performed by the muscles positioned between both mandibular rami in the inferior part of the rostrum. Living crocodylians have been observed to use such behavior exactly to expel water from the mouth between the teeth (Daniel C. Fortier, pers. com.). Nevertheless, our current knowledge on *Mourasuchus* does not allow inferring whether this taxon was really capable of performing such selection or not (Cidade et al., 2017), and as such we favorable “gulp-feeding” as a better name to the proposed feeding habits of *Mourasuchus*.

The proposed similarities allow the suggestion that the feeding behavior of *Mourasuchus* would have evolved from the durophagous feeding habit of cainanines such as *Gnatusuchus*. However, Cainaninae phylogenetic analyses
that include the durophagous taxa and *Mourasuchus* (Salas-Gismondi *et al*., 2015; Cidade *et al*., 2017) do not recover the latter as closely related to any of the former. These topologies indicate that the feeding habits of *Mourasuchus* have evolved independently from that of the durophagous Caimaninae. Future analyses, however, may reveal different scenarios.

Nevertheless, a durophagous habit is already known to have arisen more than once in the Alligatoroidea clade, with basal alligatoroids such as *Brachychampsa* and alligatorines such as *Allognathosuchus* also being described as having been durophagous (see Carpenter & Lindsay, 1980; Brochu, 2004; Salas-Gismondi *et al*., 2015). As such, a possible scenario for the independent evolution of the “gulp-feeding” habit of *Mourasuchus* within Caimaninae is that it may have evolved from the habit of swallowing prey without masticating (which is plesiomorphic within crocodyliformes), which gradually evolved with the enlargement of the rostrum to allow a large number of small prey to be captured simultaneously, whereas the durophagy of the other Caimaninae could be seen as a specialization of the use of the posterior globular teeth against hard-bodied prey, having evolved probably from an ancestor that exhibit a feeding behavior similar to the extant *Caiman latirostris* (see Monteiro *et al*., 1997; Ösi & Barrett, 2011).

**DISCUSSION**

**Perspectives**

The comprehensive revision and the detailed hypotheses presented in this study comprise the most complete assessment on the feeding habits of *Mourasuchus* published to date. However, both the hypotheses presented in this study and those presented by previous ones still need to be properly tested and assessed empirically.

The proposed reduced capacity of movement of the neck by *Mourasuchus* inferred by Langston (2008) still needs to be properly assessed in a biomechanical analysis. Similarly, even if the slender mandibles of *Mourasuchus* have low mechanical capacities in all likelihood, a quantitative measurement of such mechanical capacities is also still in need to be done by proper biomechanical studies. Additionally, biomechanical studies in addition with muscular reconstructions may examine how elastic the musculature of the inferior part of the rostrum of *Mourasuchus* could be so to test whether (or to which level) it could act as analogous to a “gular sac”. The same studies are necessary to investigate whether (and if yes, how) *Mourasuchus* could select the edible from the edible-matter that it introduced into its mouth in order not to ingest a significant amount of water, mud, sand, plants or other materials.

Additionally, more fossil findings and further phylogenetic analyses are required to clarify where *Mourasuchus* exactly fits in the phylogeny of Caimaninae. This is fundamental to understand how the unusual feeding habits of the taxon evolved. The hypothesis that the habit of *Mourasuchus* evolved from a durophagous one exhibited by several caimanine taxa has been put forward by this study, but further phylogenetic studies must find a close relationship between *Mourasuchus* and those taxa (which has not been recovered in the analyses performed to date; see Salas-Gismondi *et al*., 2015; Cidade *et al*., 2017) in order for this hypothesis to be more plausible. Additionally, new fossils may bring some direct evidence of the dietary items of *Mourasuchus*, such as stomach contents or remains of food in coprolites, any of which have not been found to date.

**The historical paleoecology of South American crocodylomorphs**

The evolution of the peculiar feeding of *Mourasuchus* is another consequence of the environmental conditions that allowed the establishment of an especially rich, morphologically diverse community of crocodylomorphs in the Miocene of South America. In this context, it is interesting to notice that from the four lineages that comprised such Miocene diversity (Sebecidae, Caimaninae, Gavialoidea and Crocodyloidea), two of them were already inhabiting South America by the Paleocene (Sebecidae and Caimaninae; see Bova, 2007; Riff *et al*., 2010; Brochu, 2011; Pol & Powell, 2011; Kellner *et al*., 2014; Cidade *et al*., 2019), while the first record of Gavialoidea for the continent is from the upper Oligocene/lower Miocene (Moraes-Santos *et al*., 2011) and the first records of Crocodyloidea (the putative tomitomine genera *Charactosuchus* and *Brasilosuchus*) are from the Miocene (see Riff *et al*., 2010), whereas the genus *Crocodylus* that currently inhabits the continent has its record beginning only in the Pliocene (Scheyer *et al*., 2013).

Of all these four lineages, Caimaninae is the one that exhibits the largest and most conspicuous morphological disparity in the Miocene, possessing morphotypes ranging from generalist predators (*Melanosuchus, Paleosuchus*), predominately durophagous (*Gnatusuchus, Kuttanacaimain, Globidentosuchus, Caiman brevirostris*), the giant generalist predator *Purussaurus* and the gulp-feeding *Mourasuchus* (Cidade *et al*., 2019). These two taxa were also especially large crocodylians, with *Mourasuchus* reaching up to 6.6 m (Langston, 2008) and *Purussaurus* up to 12.5 m. (Aureliano *et al*., 2015). Some gavialoids and sebecids also reached large sizes, with *Gryposuchus croizati* estimated to have reached between 9 and 10 m (Riff & Aguilera, 2008) and *Barinariosuchus arveloi* between 6.3 and over 10 m (Molnar & Vasconcellos, 2016). However, Gavialoidea, putative tomistomines and *Crocodylus* exhibited basically the same bauplan along their evolutionary history in the South American Cenozoic, including the Miocene. Sebecidae is an exception, in which the species *Lorosuchus nodosus* exhibits a platyrostral skull that denotes a semi-aquatic habit, different from the terrestrial habit possessed by the other members of the taxa (Pol & Powell, 2011). Nevertheless, this still contrasts deeply with the large morphological disparity exhibited among the Caimaninae taxa.

Compared to caimanines and sebecids, Gavialoids and crocodylids probably did not develop a similar morphological disparity in the Miocene of South America due to having arrived later in the continent. Additionally, not only the gavialoids but also the crocodylids that inhabited the South American Miocene were longirostrine, and it is possible that such skull shape would be less “plastic” than a brevirostrine one, thus precluding these taxa of exhibiting a...
larger morphological disparity. These hypotheses, however, require further, detailed research to be properly addressed.

The differences in morphological disparity between caimanines and sebecids may be related to the semi-aquatic habits of the former and the terrestrial habits of the latter. The northern part of the South America, equivalent to the area of the current Amazon rainforest and which houses the largest crocodylomorph diversity during the Cenozoic of the continent, including the Miocene, underwent gradual geomorphological changes during the Paleogene and the Neogene that gradually increased the size of the water-bodies from a series of rivers to systems of mega-lakes (see Hoorn et al., 2010).

As such, semi-aquatic crocodylomorphs had not only an ever-growing habitable space but also had ever-growing different kinds of habitats in the aquatic systems of the Cenozoic of South America which, together with the generally hot climate and high biodiversity (which generated a vast array of prey items), were the factors that allowed the Caimaninae clade to evolve the distinctly different morphotypes it exhibited in the Miocene, including the “gulp-feeding” habit of Mourasuchus. In this context, it is interesting to notice that the reduction in the size of the water systems of the Amazon area during and after the late Miocene are coincident with the extinction of all the large and specialized crocodylomorphs, such as Mourasuchus, Purussaurus, durophagous caimanines, gavialoids and the longirostrine crocodyloids Charactosuchus and Brasiliosuchus (see Riff et al., 2010; Scheyer et al., 2013; Cidade et al., 2019), which reinforces the importance of large water systems for the survival and evolution of large, specialized semi-aquatic crocodylomorphs. Additionally, it is also possible that the sebecid terrestrial-oriented morphology was also less “plastic” that that of the semi-aquatic, brevirostrine caimanines, but this issue must also be addressed by future, detailed studies.

CONCLUSIONS

As a result of the comprehensive revision and reassessment of the literature and morphological characters relevant to the understanding of the feeding habits of Mourasuchus, this study concludes that the taxon was likely unable of capturing and consuming large prey, especially those capable of fast movements such as mammals. As such, Mourasuchus was likely specialized in eating small preys, such as crustaceans, bivalves, gastropods, and small fish. Large preys would only be consumed if they were slow-moving, like the Lepidosiren fish, and likely only occasionally. There are no evidences that Mourasuchus was herbivorous.

We propose that the long, wide, dorsoventrally flattened rostrum of Mourasuchus evolved as to make the rostrum cover the largest possible area to allow a maximum efficiency in the capture of large amounts of small prey. The use of the inferior part of the rostrum would be more efficient in the capture of large amounts of prey than relying on teeth to capture and handle the small animals that likely comprised the diet items of Mourasuchus. In spite of the inferred prominent role that the inferior part of the rostrum played in the foraging of Mourasuchus, it is recommended that the term “gular sac” should not be used to describe this structure for this taxon until eventual further studies determine whether it functioned in an analogous manner to the gular skin present in extant birds, for example.

As the small animals proposed to have comprised the main diet items of Mourasuchus would nearly always be found immersed into the micro-habitat they lived in (water, mud, sand or plants, among others), it is probable that Mourasuchus also captured quantities of these materials together with the prey. As such, some sort of “selection” of the edible from the non-edible matter somewhat akin to the “filtering” mentioned by previous authors (Langston, 1965; Riff et al., 2010; Bona et al., 2013b) would be advantageous to Mourasuchus, but with our current knowledge there are no evidences that such a selection could be performed by this taxon. As such, we follow Cidade et al. (2017) in naming the presumable feeding habits of Mourasuchus as “gulp-feeding”, and not “straining” or “filtering” feeding as in those previous studies. Mourasuchus was most probably a inhabitant of quiet, shallow water bodies, not only due to the presumable mechanical inefficiency of its jaws, skull and cervical vertebrae, but also because water bodies such as those possessed the largest quantity of habitats in which the preferred prey of the taxon – mollusks, crustaceans and small fish – dwelled.

This study proposed the hypothesis that the “gulp-feeding” habit of Mourasuchus evolved from the durophagous habit proposed for many fossils caimanines, particularly the highly adapted Gnatusuchus. This hypothesis, however, needs to be properly addressed by future studies, and no phylogenetic analysis performed to date showed a close relationship between Mourasuchus and any durophagous taxa, which means a hindrance to the acceptance of this hypothesis. Additionally, many hypothesis of this and previous studies about the inferred limited movements and lack of strength of the bones, osseous structures and muscles of the mandibles, skull and the cervical vertebrae still need to be properly assessed by biomechanical and muscular reconstruction studies so a thorough and more empirically-based understanding of the feeding habits of Mourasuchus can be reached.

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