An Acad Bras Cienc (2021) 93(Suppl. 2): e20201594 DOI 10.1590/0001-3765202120201594
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

PALEONTOLOGY

Morphological variation in the dentition of Uruguaysuchidae (Crocodyliformes: Notosuchia)

RODRIGO G. FIGUEIREDO & ALEXANDER W.A. KELLNER

Abstract: Uruguaysuchidae was a diverse group of crocodyliforms with widespread Gondwanan distribution. Recent phylogenies recover a clade comprising six species of *Araripesuchus* and one *Uruguaysuchus*. We reviewed the morphological variation in the dentition of uruguaysuchid specimens, including unpublished fossils from the Crato (SMNK PAL 6404) and Romualdo (MN 7061-V) formations of the Araripe Basin. Dental patterns are clearly distinct between species, with important taxonomic and possible ecological implications. Neither *Araripesuchus* nor *Uruguaysuchus* have characters suggesting exclusive herbivory, even for species in which tooth-tooth occlusion is observed. New data on *A. gomesii* shows differences in teeth number between the new specimen MN 7061-V and the holotype, probably due to preservation. The specimen SMNK PAL 6404 has a unique combination of dental characters, which reinforces the hypothesis that it might belong to a new *Araripesuchus* species. The alveoli pattern of *A. rattoides* is very distinctive in comparison to other araripesuchids, what also suggests different taxonomic affinities. One interpretation for the morphological variation in the dentition of Uruguaysuchidae is foraging specializations for different life habits. Niche partitioning and ecological specialization could have been an important process in explaining the high taxonomic diversity and widespread spatial distribution of these animals in the Cretaceous of Gondwana.

Key words: Tooth, Heterodonty, *Araripesuchus*, *Uruguaysuchus*, Cretaceous, Gondwana.

INTRODUCTION

The evolutionary history of Crocodyliformes is characterized by high ecological diversity, which can be traced to several episodes of radiation along the Jurassic and Cretaceous (Stubbs et al. 2013, Toljagic & Butler 2013). In the last years, several new specimens were discovered particularly in South America (e.g., Souza & Campos 2019), increasing the scope of studies about these reptiles (e.g., Wilberg 2017, Cardia et al. 2019). An extensive fossil record reveals different body plans and a wide range of variation in skull morphology, notably in the shape of the rostrum, and in patterns of dentition (Riff & Kellner 2001, Ösi 2013, Wilberg 2017). Such disparity is often linked with distinct feeding habits and lifestyles, however establishing a clear correlation between form and function, and their influence on the ecological roles displayed by extinct crocodyliforms is not a straightforward task (Drumheller & Wilberg 2020).

Terrestrial Cretaceous crocodyliforms developed extraordinarily specialized dentitions, repeatedly showing one or more of such features: i. complex tooth morphology (e.g., multicuspidate teeth); ii. regionalization (i.e. incisiform, caniniform, postcaniniform, and molariform morphotypes); iii. enamel macro and micro ornamentation (e.g., ziphodont, micro-ziphodont, false-ziphodont); iv. tooth-to-tooth occlusion; v. reduction in number (Prasad & de Lapparent de Broin 2002, Andrade et al. 2010, Ösi 2013, Melstrom & Irmis 2019). Cranial-mandibular joint anatomy and dental wear facets indicate that, at least some species with specialized dentition, were capable of active oral food processing, i.e. chewing (Ösi 2013).

Notosuchia (sensu Pol et al. 2014) is the most notable group of heterodont crocodyliforms, since most of its lineages have features related to a specialized dentition, and thus a wide variety of feeding behaviors has been inferred for them, from carnivory (e.g., Riff & Kellner 2011), to insectivory (e.g., Martin & de Lapparent de Broin 2016), omnivory (e.g., Nobre et al. 2008), and herbivory (e.g., Melstrom & Irmis 2019). Nevertheless, some groups that have relatively simple dentition, at least in comparison to more highly specialized notosuchians, show considerable morphological disparity between species, which is the case of Uruguaysuchidae. This clade unites the six species of *Araripesuchus*, i.e. *A. gomesii*, *A. wegeneri*, *A. patagonicus*, *A. buitreraensis*, *A. tsangatsangana*, and *A. rattoides* (Figure 1) and *Uruguaysuchus azanarezi* (Gasparini 1971, Soto

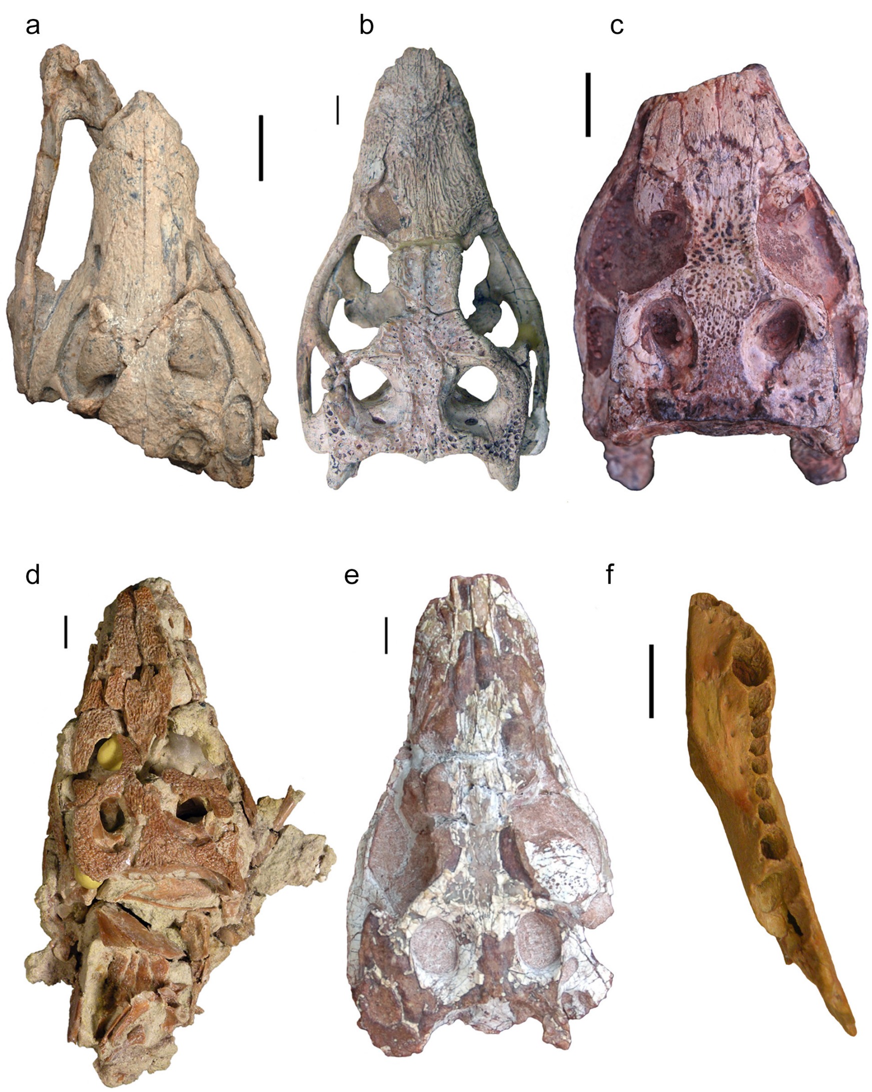

Figure 1. **Taxonomic diversity of the genus *Araripesuchus*. Skulls in dorsal view in a: *Araripesuchus gomesii* (DGM 423-R); b: *Araripesuchus wegeneri* (MNN GAD 19); c: *Araripesuchus patagonicus* (MUC PV 269); d: *Araripesuchus tsangatsangana* (FMNH PR 2297); e: *Araripesuchus buitreraensis* (MPCA-PV 235); dentary in dorsal view in f: *Araripesuchus rattoides* (CMN 41893). Scale bars 10 mm.**

et al. 2011, Fernández Dumont et al. 2020). Some authors also recovered *Anatosuchus minor* as a uruguaysuchid (e.g., Pol et al. 2014) or at least related to some *Araripesuchus* species (Sereno & Larsson 2009). Rusconi (1933) described a second species of *Uruguaysuchus*, named *U. terrai*, based on differences in the dental formula of the specimens. However, it is likely that specimens assigned to *U. terrai* represents juveniles of *U. azanarezi* (Soto et al. 2011).

Uruguaysuchids consist of one of the most interesting clades from the point of view of the evolution of Notosuchia, since this clade has the longest temporal range in the fossil record (i.e. 59 million years), spanning from Aptian to Maastrichtian (Turner 2006, Frey & Salisbury 2007). It also shows one of the widest geographic distributions in Gondwana, with fossils being found in Argentinian Patagonia and Uruguay in the southwest (Ortega et al. 2000, Soto et al. 2011); Brazil, Cameroon and Niger, in central Gondwana (Price 1959, Buffetaut 1981, Frey & Salisbury 2007); Morocco and Tunisia in the north (Sereno & Larsson 2009); and Malawi and Madagascar in southeast (Jacobs et al. 1990, Turner 2006). However, several specimens of *Araripesuchus* were only briefly mentioned in the literature (e.g., Jacobs et al. 1990, Buffetaut 1981, Frey & Salisbury 2007) and new fossils have yet to be described from the Crato Formation (SMNK PAL 6404) and Romualdo Formation (MN 7061-V) of the Araripe Basin, that have also yielded other crocodylomorphs (e.g., Kellner 1987). A further discussion on tooth morphotypes and its definitions is necessary, and here we addressed some of these issues. We analyzed many uruguaysuchid specimens to review the morphological variation in the dentition of these animals and compared them to other notosuchians, which are significant for the taxonomy of the Notosuchia.

SYSTEMATIC PALEONTOLOGY

Crocodyliformes Hay, 1930
Notosuchia Gasparini, 1971 (sensu Pol et al. 2014)
Uruguaysuchidae Gasparini, 1971
†*Uruguaysuchus* Rusconi, 1933
†*Uruguaysuchus aznarezi* Rusconi, 1933
†*Araripesuchus* Price, 1959
†*Araripesuchus gomesii* Price, 1959
†*Araripesuchus wegeneri* Buffetaut, 1981
†*Araripesuchus patagonicus* Ortega, Gasparini, Buscalioni & Calvo, 2000.
†*Araripesuchus buitreraensis* Pol & Apesteguia, 2005
†*Araripesuchus tsangatsangana* Turner, 2006
†*Araripesuchus rattoides* Sereno & Larsson, 2009

MATERIALS AND METHODS

A wide sample of fossils were first hand analyzed for this study, consisting in the following species and specimens: *Araripesuchus buitreraensis* (MPCA-PV 235); *Araripesuchus gomesii* (DGM 423-R, AMNH 24450, MN 7061-V); *Araripesuchus patagonicus* (MUCPV 269, MUCPV 267, MUCPV 268, MUCPV 268b, MUCPV 270); *Araripesuchus rattoides* (CMN 41893, UCRC PV3); *Araripesuchus* sp. (MPCA-PV 236); *Araripesuchus* sp. (“Crato Form” SMNK PAL 6404); *Araripesuchus tsangatsangana* (FMNH PR 2297-2299, FMNH PR 2318, FMNH PR 2334, UA 8750, UA 8751, UA 8756, UA 8760, UA 8761, UA 8762, UA 8763); *Araripesuchus wegeneri* (MNN GAD 19-23, MNN GAD 26); *Uruguaysuchus aznarezi* (FC-DPV 2320). So far the specimen MN 7061-V was not recovered from the fire that affected the Museu Nacional in 2018, although we still hope to recover this material as has been the case of others (e.g., Kellner et al. 2019).

Anatomical abbreviations: **alv**, alveolus/alveoli; **be**, buccal emargination; **cte**, caniniform tooth/teeth; **d**, dentary; **ect**, ectopterygoid; **exna**, external nares; **for**, foramen/foramina; **ite**, incisiform tooth/teeth; **m**, maxilla; **pcte**, postcaniniform tooth/teeth; **pl**, palatine; **pm**, premaxilla; **pmte**, premaxillary tooth/teeth; **pty**, pterygoid; **ptyf**, pterygoig flange; **sn**, slit-like notch; **tte**, transitional tooth/teeth.

Institutional abbreviations: **AMNH**, American Museum of Natural History (New York City, USA); **CMN**, Canadian Museum of Nature (Ottawa, Canada); **DGM**, Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Serviço Geológico de Brasil (Rio de Janeiro, Brazil); **FC-DPV**, Facultad de Ciencias, Universidad de la República (Montevideo, Uruguay); **FMNH**, Field Museum of Natural History (Chicago, USA); **MN**, Setor de Paleovertebrados, Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro (Rio de Janeiro, Brazil); **MNN**, Muséum National du Niger (Niamey, Republic of Niger); **MPCA**, Museo Provincial Carlos Ameghino (Cipolletti, Argentina); **MUCPV**, Museo de la Universidad Nacional del Comahue (Neuquén, Argentina); **SMNK**, Staatliches Museum für Naturkunde Karlsruhe (Karlsruhe, Germany); **UA**, University of Antananarivo (Antananarivo, Madagascar); **UCRC**, University of Chicago Research Collection (Chicago, USA).

RESULTS AND DISCUSSION

The heterodont dentition of the Crocodyliformes includes three basic morphotypes: incisiform (or incisiviform sensu Lecuona & Pol 2008), caniniform, and molariform. The nomenclature is based on mammalian dentition, but up to date there are no formal descriptions for each category, with shape, size and position being often used to distinguish each of them. A fourth morphotype is the ziphodont, composed of labiolingually compressed serrated teeth. Here we adopted the nomenclature proposed by Sereno & Larsson (2009), which use postcaniniforms for teeth located distally to the longer and/or enlarged elements of the series. Molariforms are usually also postcaniniform teeth, but this morphotype is absent in uruguaysuchids. We also follow Sereno & Larsson (2009) describing the ornamentation of the carina with the presence of denticles (observed in *A. wegeneri*), rather using ziphodont dentition, which better suits the teeth of Sebecosuchia and Theropoda dinosaurs.

Uruguaysuchidae species have heterodont dentition comprising incisiform, caniniform and postcaniniform teeth. All incisiforms and caniniforms have conical to subconial crowns that varies in size, the former are smaller and the latter are larger. The postcaniniforms show either a “spatulate” morphology (i.e. apically rounded with a constriction at the base of the crown), “lanceolate” morphology (apically pointed crowns with symmetrical carinae), or “leaf shape” morphology (apically pointed crowns with asymmetrical carinae). Other notosuchians show highly specialized morphology and dental function (Clark et al. 1989, Riff & Kellner 2001, O’Connor et al. 2010, Ösi 2013, Melstrom & Irmis 2019) in comparison with *Araripesuchus* and *Uruguaysuchus*. However, there is still considerable disparity between uruguaysuchids (Figure 2 and 3), especially regarding number of teeth, variation in size, and ornamentation, including the presence or absence of true denticles.

Premaxillary teeth

The premaxillary dentition of *Araripesuchus* species is composed by either four teeth, as in *A. patagonicus* (Ortega et al. 2000) and *A.*

Figure 2. Schematic chart showing the variation of premaxillary and maxillary dentition in *Araripesuchus* and *Uruguaysuchus* species.

gomesii (at least in the holotype DGM 423-R), or five teeth like in *A. wegeneri*, *A. tsangatsangana*, *A. buitreraensis* and the Crato Form SMNK 6404 (Figure 4). The new specimen SMNK PAL 6404 (*Araripesuchus* sp.) has a transitional tooth located at the suture between premaxilla and maxilla, which alveolus is made by both bones (Figure 4). Price (1959) described four teeth in the holotype of *A. gomesii* (DGM 423-R), but five teeth are clearly present in MN 7061-V (Figure 5), what raises the possibility that in the holotype one tooth was not preserved. There are three preserved premaxillary alveoli in *Uruguaysuchus aznarezi* (FC-DPV 2320) but is highly probable that the total number of premaxillary teeth in this species is four, giving the tip of the snout of FC-DPV 2320 is missing (Soto et al. 2011). Tooth count is extremely variable among crocodylomorphs, with notosuchians showing greater numerical range. Some species, like *Anatosuchus minor*, has six premaxillary teeth, whereas other taxa such as sphagesaurids have only two (Pol 2003, Marinho & Carvalho 2009, Sereno & Larsson 2009, Kellner et al. 2011b). However, the presence of four teeth is the most common condition observed in mesoeucrocodylians, including baurusuchids and some “advanced notosuchians” (Riff & Kellner 2001, Andrade & Bertini 2008, Lecuona & Pol 2008).

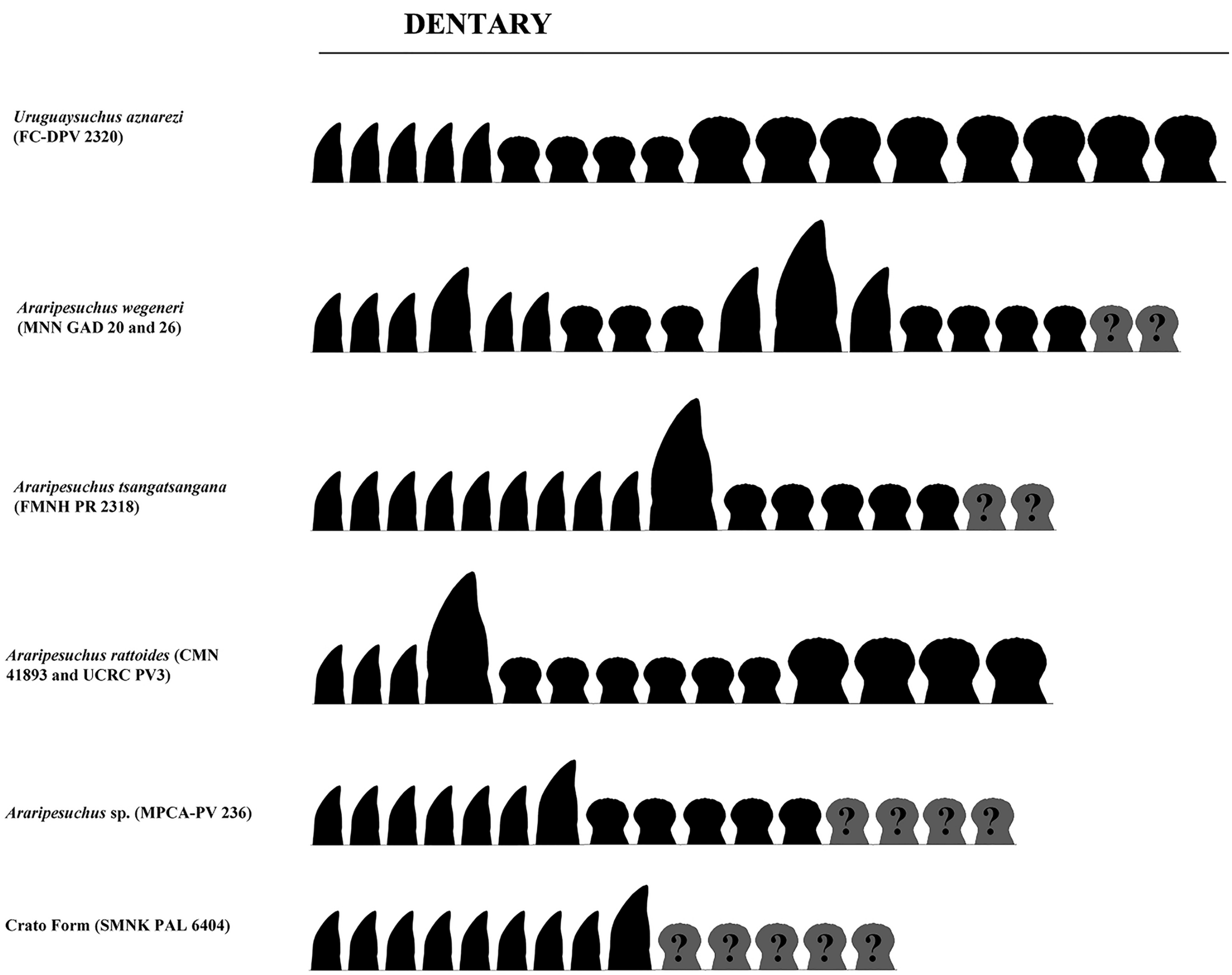

Figure 3. Schematic chart showing the variation of dentary dentition in *Araripesuchus* and *Uruguaysuchus* species.

The premaxillary teeth of *Araripesuchus* species are all subconical in shape with a slightly distolingually curvature. In *A. wegeneri* and Crato Form SMNK PAL 6404 the base of each teeth is bulbous, what gives them a blunter shape. The crowns are subcircular in cross-section, as in most mesoeucrocodylians, and separated from the roots by a mild to moderate constriction. Crown surfaces are smooth in all species but *A. wegeneri*, which shows marked apicobasal striations and a series of five to six fine denticles per millimeter, at the apical carinae (Sereno & Larsson 2009). In most *Araripesuchus* species the mesial margins of the teeth are curved and usually slightly longer in comparison to the straight distal ones, except in *A. tsangatsangana* that have symmetrical straight mesial and distal edges. The premaxillary incisiform of *Uruguaysuchus* are similar in shape to those of *A. gomesii* and *A. tsangatsangana*, however in the former taxon the enamel surface bears some light wrinkles. A similar morphology is observed in the five teeth of *Montealtosuchus*, which have finely serrated keels (Carvalho et al. 2007).

Araripesuchus lacks the premaxillary hypertrophied caniniform teeth present in other notosuchians (Lecuona & Pol 2008), either as single (e.g., *Notosuchus*, *Mariliasuchus*) or paired (e.g., *Chimaerasuchus*, *Sphagesaurus*) elements.

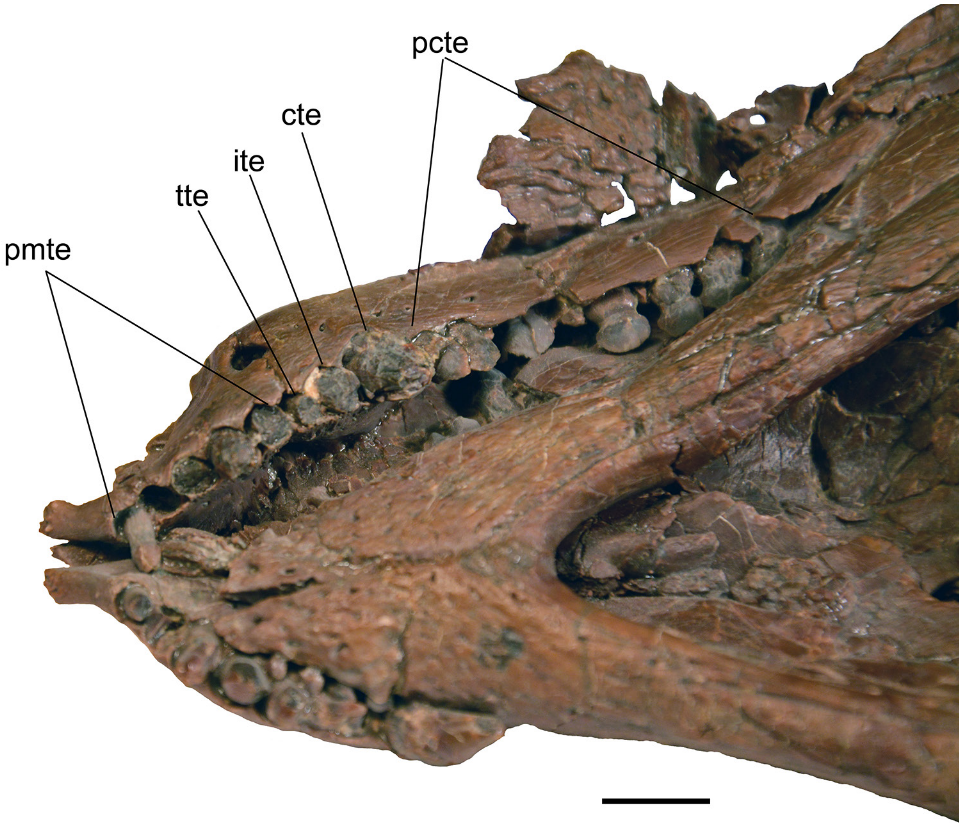

Figure 4. Detail of the skull of the specimen SMNK PAL 6404 (Crato Form) in ventral view showing the dentition. Scale bar = 10 mm. cte, caniniform tooth/ teeth; ite, incisiform tooth/teeth; pcte, postcaniniform tooth/teeth; pmte, premaxillary tooth/ teeth; transitional tooth/teeth.

Despite that, there is still some size variation between species. The third premaxillary teeth are slightly enlarged in *A. wegeneri* and in *Uruguaysuchus*, whereas in *A. gomesii*, *A. patagonicus* and *A. tsangatsangana* the fourth teeth are the large ones (Figure 2). In Crato Form SMNK PAL 6404 the last three teeth are slightly larger than the two anterior-most elements, being the fourth one the larger (Figure 4). The premaxillary alveoli are arranged in straight rows that are oblique oriented, diverging posteriorly toward the maxilla. This pattern of orientation follows the external contour of the bone and is observed in all *Araripesuchus* species with preserved alveoli. A similar orientation is present in *Libycosuchus*, however the angle formed between each tooth row is larger in this species (Sereno & Larsson 2009).

Maxillary teeth

Araripesuchus species have a minimum of seven maxillary teeth, as observed in *A. buitreraensis* (Fernández Dumont et al. 2020), and a maximum of fourteen teeth in *A. wegeneri* according to the number of preserved alveoli (Figure 2). However, the precise number of teeth is still unknown in Crato Form SMNK PAL 6404 and *A. patagonicus*, so it could be larger than the current estimations. The tooth count in *Uruguaysuchus* is estimated in thirteen based on the preserved alveoli. The number of teeth is usually linked to the length of the maxilla and most crocodylomorphs have a tooth count of eight, or more, maxillary teeth, even in some brevirostrine forms (Romer 1956). However, a trend for the extreme reduction of the dental formula is observed in some “protosuchians” (e.g., *Orthosuchus*, *Zosuchus*, *Endentosuchus*), baurusuchids, and “advanced notosuchians” like Sphagesauridae, *Notosuchus*

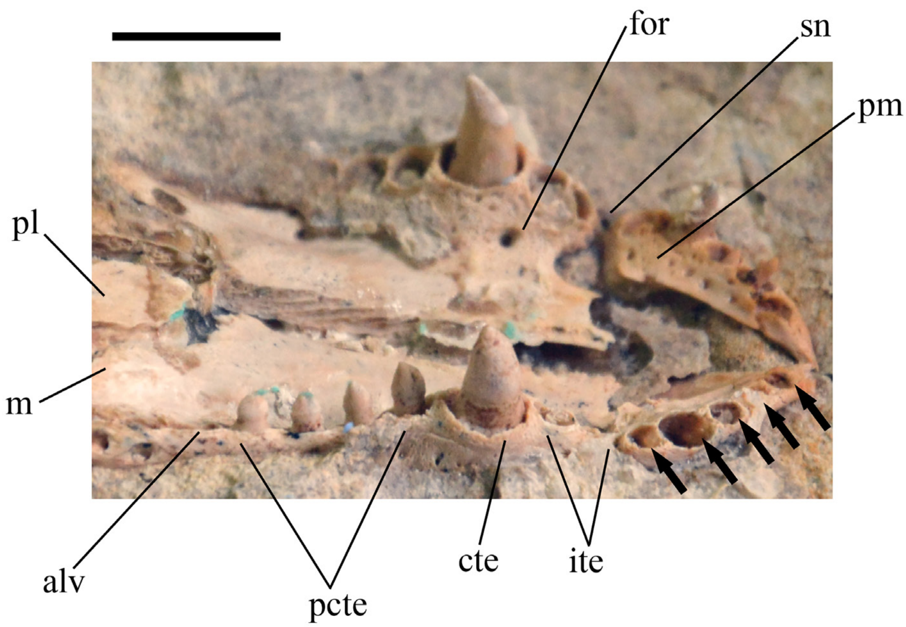

Figure 5. ***Araripesuchus* gomesii (MN 7061-V) showing the lateral view of the palate. The maxillary dentition is shown in detail. Black arrows indicate the presence of five premaxillary alveoli. Scale bar = 10 mm. alv, alveolus/alveoli; cte, caniniform tooth/teeth; for, foramen/foramina; ite, incisiform tooth/teeth; m, maxilla; pcte, postcaniniform tooth/teeth; pl, palatine; pm, premaxilla; sn, slit-like notch.**

and *Mariliasuchus* (Nash 1975, Riff & Kellner 2001, Pol & Norell 2004, Pol et al. 2004, Andrade & Bertini 2008, Lecuona & Pol 2008, Iori et al. 2011).

All *Araripesuchus* species show a relatively well-developed regionalization of the maxillary dentition, showing incisiform, caniniform and postcaniniform teeth (Figure 2). The presence of all types of crown morphology in the maxillary dental series is observed in most notosuchians, except for *Notosuchus*, *Mariliasuchus* and sphagesaurids, which lack the first two morphotypes (Lecuona & Pol 2008, Iori et al. 2011). The incisiform of *Araripesuchus* are small and show both asymmetrical (*A. gomesii*) and symmetrical carinae (*A. wegeneri*, *A. tsangatsangana*, *A. buitreraensis*). The two anterior-most teeth of the maxilla can be considered incisiforms and are observed in *Uruguaysuchus* and all *Araripesuchus* species (Figure 2). The second incisiform is always larger than the first one, but not exceeding half the length of the hypertrophied caniniform tooth, as observed in *A. gomesii*, *A. wegeneri* and *A. buitreraensis*. However, in *Uruguaysuchus* and some peirosaurids (e.g., *Uberabasuchus*, *Montealtosuchus*) the second maxillary teeth are clearly longer than half the caniniform length (Carvalho et al. 2004, 2007, Soto et al. 2011).

The hypertrophied caniniform teeth of the Notosuchia have a general conical shape, and most differences between groups are observed in the patterns of surface ornamentation, number, and position of carinae, and presence of serration or denticles. *A. buitreraensis* has huge caniniforms (e.g., MPCA-PV 242) that are comparatively longer than those observed in any other uruguaysuchid (Fernández Dumont et al. 2020). In *A. gomesii* and *A. buitreraensis* the caniniform morphology is rather simple; the enamel surface is smooth, and the curved mesial carina is longer than the straight distal one, without denticles. On the other hand, the enamel surface in *A. wegeneri* has a more complex structure, with delicate fluting and finely denticulated carinae, showing about five to six denticles per millimeter (Sereno & Larsson 2009). The density of denticles in the maxillary teeth of *A. wegeneri* (5-6/mm) is higher to that observed in *Baurusuchus* (2-3/mm), *Pissarrachampsa* (3-4/mm) and *Sahitisuchus* (3-3.5/mm) (Riff & Kellner 2001, Montefeltro et al. 2011, Pol et al. 2012, Kellner et al. 2014). Unfortunately, the density of denticles in the dentition of the peirosaurid crocodylomorphs is still poorly known, but the associated teeth of *Barcinosuchus* show 11-12 denticles per millimeter (Leardi & Pol 2009). *Uruguaysuchus* has a unique set of four apicobasal carinae, however without serrations or denticles (Soto et al. 2011).

The dentition of the posterior maxillary region shows most of the variation in shape and number of teeth in different crocodyliforms, such as "protosuchians", hylaeochampsids, and Notosuchia. The postcaniniforms of *Araripesuchus*, especially regarding the species *A. wegeneri*, are like those of *Uruguaysuchus*. *A. gomesii*, *A. patagonicus*, and Crato Form SMNK PAL 6404 have lanceolate first postcaniniforms, whereas *A. wegeneri* and *A. tsangatsangana* only the first and second teeth exhibit this shape. Posteriorly, the crowns are highly buccolingually flattened in both *Araripesuchus* and *Uruguaysuchus*, giving them a rounded apical profile in labial/lingual view (i.e. "spatulate" morphology). The constriction between the roots and the crowns are extremely developed, creating a marked basal "neck" (Figure 4 and 6). Some peirosaurids show a similar, yet much more gentle constriction (Carvalho et al. 2004, 2007). The crowns have smooth carinae in *A. tsangatsangana*, however in *Uruguaysuchus* and *A. wegeneri* they are denticulate. The presence of denticles in the posterior dentition of *A. gomesii* (AMNH 24450) was suggested by Soto et al. (2011), but this is not yet confirmed. A central cusp is present in *A. wegeneri*, Crato Form SMNK PAL 6404 and *Uruguaysuchus*, which can be considered at first as homologous due their similarities in size, shape, and location.

Araripesuchus and *Uruguaysuchus* have a relatively high number of postcaniniform teeth despite having short rostra (Figure 1 and 2). A more blunter crown morphology is present in the posterior-most postcaniniforms of a few South American peirosaurids, such as *Pepesuchus* and *Uberabasuchus* (Carvalho et al. 2004, Campos et al. 2011). On the other hand, the african peirosaurid *Hamadasuchus* shows a postcaniniform morphology that resembles the dentition of sebecid crocodylomorphs, with more conical and slightly curved teeth (Larsson & Sues 2007). Baurusuchidae shows an extreme reduction in number of postcaniniform dentition, bearing only two small conical teeth (Riff & Kellner 2001, Montefeltro et al. 2011).

The most specialized postcaniniform dentition is observed in Sphagesauridae and some other notosuchians, such as *Adamantinasuchus*, *Candidodon*, *Malawisuchus*, *Pakasuchus*, *Yacarerani*, and *Chimaerasuchus* (Ösi 2013, Pol et al. 2014). Sphagesaurids are often described as having molariform teeth with crown ornamentation composed by multicusped keels (Iori et al. 2011, Pol et al. 2014). However, multicuspidate teeth are not directed related to the molarization of the dentition (e.g., *Simosuchus*). Thus, the presence of molariform crowns is currently restricted to the edentosuchids from the Lower Cretaceous of China (Pol et al. 2004), *Iharkutosuchus* (Ösi & Weishampel 2009), and several notosuchians, which is the case of *Adamantinasuchus*, *Candidodon*, *Malawisuchus*, *Pakasuchus*, *Yacarerani* and *Chimaerasuchus* (Carvalho 1994, Wu et al. 1995, Gomani 1997, Nobre & Carvalho 2006, Novas et al. 2009, O'Connor et al. 2010).

Dentary teeth

The dentary series is extremely variable among *Araripesuchus* species (Figure 3). The first teeth are small and have incisiform crowns that are slightly mesially deflected. SMNK PAL 6404 has diminutive symphyseal teeth that are smaller even in comparison to other

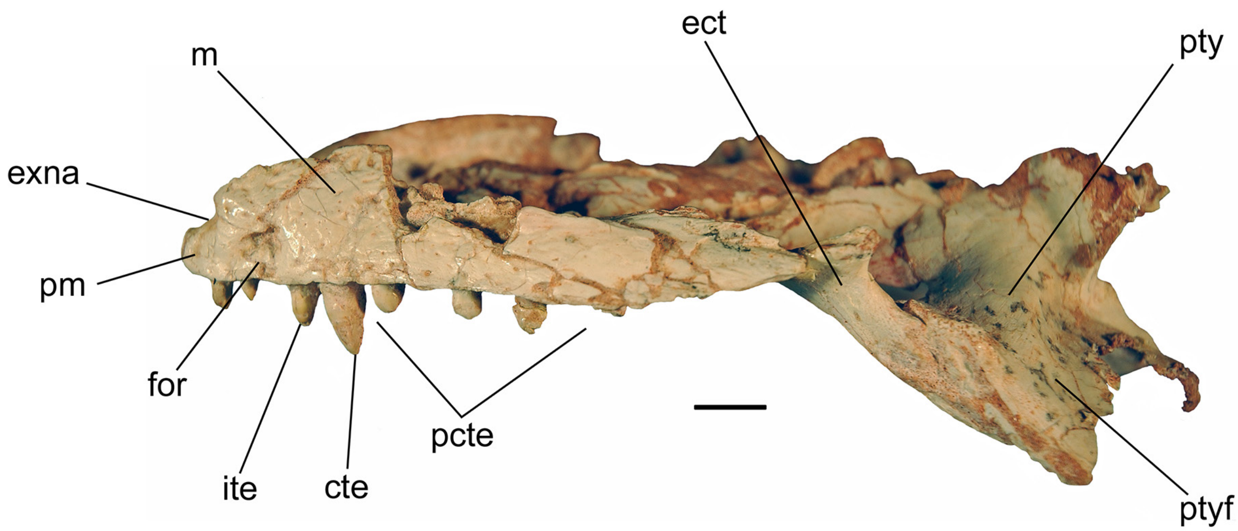

Figure 6. **Cranial remains of *Uruguaysuchus aznarezi* (FC-DPV 2320) in left lateral view. Scale bar = 10 mm. cte, caniniform tooth/teeth; ect, ectopterygoid; exna, external nares; for, foramen/foramina; ite, incisiform tooth/teeth; m, maxilla; pcte, postcaniniform tooth/teeth; pm, premaxilla; pty, pterygoid; ptyf, pterygoig flange.**

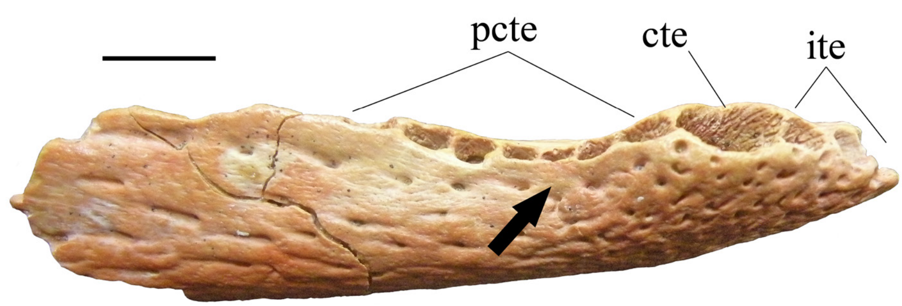

Figure 7. **Dentary of the holotype of *Araripesuchus rattoides* (CMN 41893) in right lateral view. Black arrow indicates the lateral mandibular concavity. Scale bar = 10 mm. cte, caniniform tooth/teeth; ite, incisiform tooth/teeth; pcte, postcaniniform tooth/teeth.**

uruguaysuchids. However, important exceptions are observed in *Araripesuchus rattoides* (Figure 7) and *Araripesuchus* sp. MPCA-PV 236 (Figure 8), which show procumbent alveoli like those of *Mariliasuchus* and *Yacarerani* (Zaher et al. 2006, Novas et al. 2009). Also, *A. rattoides* shows larger first and fourth alveoli, which are not observed in other *Araripesuchus*. In *A. gomesii*, *A. tsangatsangana*, Crato Form SMNK PAL 6404, and *Uruguaysuchus* the incisiform are symmetrical and conical, with straight to slightly curved mesial and distal edges. However, *A. wegeneri* has asymmetrical leaf-shaped anterior dentary incisiform, which mesial carinae are longer and much curved in comparison to the distal ones (Figure 3). Another important difference of *A. wegeneri* is the presence of denticles also in the dentary teeth.

The incisiform dentition is not restricted to the anterior-most portion of the dentary, even in species that have an enlarged anterior tooth. Therefore, the transition from the incisiform to the postcaniniform tooth crown pattern usually occurs in the mid-posterior region of the mandibular symphysis. Also, the total number of incisiform helps establishing where in the mandible the change between morphotypes occurs. A reduction in the incisiform series is observed in *Uruguaysuchus* (five teeth) and *Araripesuchus* sp. MPCA-PV 236 (six teeth), in comparison to *A. wegeneri* (eight teeth) and *A. tsangatsangana* (nine teeth). Thus, in the South American taxa, the postcaniniforms are present in the symphyseal region, whereas in the African species they are observed only posterior to the mandibular symphysis. The reduction of the incisiform series is also observed in more complex-toothed crocodyliforms, such as *Edentosuchus* and some "advanced notosuchians" (Pol et al. 2004, Zaher et al. 2006, Lecuona & Pol 2008).

A remarkable feature shared between *A. wegeneri*, *A. tsangatsangana*, and Crato Form SMNK PAL 6404 is the presence of one posterior enlarged incisiform teeth. However, the homology of these teeth is unclear. They seem to be similar in morphology in *A. tsangatsangana* and the Crato Form, but they are quite different in *A. wegeneri*. Also, such teeth occupy different positions on the dentary; respectively the tenth and eleventh alveoli in *A. tsangatsangana* and *A. wegeneri*, and the ninth position in the Crato Form. The Nigerian species shows a leaf-shaped tooth, which is stout and bears well-developed curved mesial and distal carinae (Figure 9). The carinae are finely denticulate and slightly lingually deflected, creating two marked grooves between each of them and the lingual surface of the crown. The hypertrophied lanceolate tooth of *A. tsangatsangana* is remarkably high and relatively slender (Figure 10). Their mesial and distal carinae are straight and sharp, without denticles. Labially, the crown surface shows three distinct facets that are separated by two well-marked apicobasal ridges. The hypertrophied tooth of Crato Form is conical and shows a strongly curved posterior carina.

Highly hypertrophied caniniforms, such as those observed in baurusuchids, sebecids and peirosaurids, are essentially missing in uruguaysuchids (Riff & Kellner 2001, Martinelli et al. 2012, Kellner et al. 2014). The absence of such teeth in this region is not a surprise, giving that the mandibular symphysis is always very shallow in *Araripesuchus* (Figure 10) and *Uruguaysuchus* (Figure 11). However, *A. gomesii*, *A. wegeneri*, and at least one specimen of *A. tsangatsangana* (FMNH PR 2297) show enlarged fourth dentary teeth. Although clearly not hypertrophied, these enlarged teeth deviate from the pattern of small symphyseal elements observed in *A. tsangatsangana* (FMNH PR 2318 and UA 8720), Crato Form SMNK PAL 6404, *Araripesuchus* sp. MPCA-PV 236, and *Uruguaysuchus*. The Moroccan taxon *Araripesuchus rattoides* shows a rather different morphology in comparison to all *Araripesuchus* and *Uruguaysuchus* species. The fourth alveolus is much larger than any other in the symphyseal series, with a minimum diameter twice as large as the adjacent tooth sockets (Figure 12). Also, the large alveolus is placed at an elevated portion of the dentary. All those traits indicate that the fourth dentary tooth of *Araripesuchus rattoides* was in fact hypertrophied.

The postcaniniform series shows a few common features in *A. wegeneri*, *A. tsangatsangana* and *Uruguaysuchus*. These animals have labiolingually compressed teeth with "spatulate" shape, i.e. apically rounded with a constriction at the base of the crown. The basal compression is not very developed in the malagasy *Araripesuchus*. Apical cusps are present in *A. wegeneri* and *Uruguaysuchus*, and fine denticles ornament their edges. The labial surface of the enamel bears shallow ridges in the postcaniniform teeth of *A. tsangatsangana*. However, a completely different morphology is present in the specimen *Araripesuchus* sp.

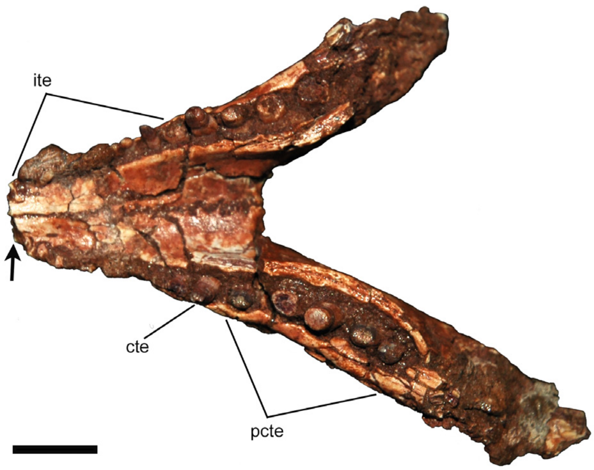

Figure 8. Dentary of *Araripesuchus* sp. (MPCA-PV 236) in dorsal view. Black arrow shows region where the procumbent alveoli and teeth are located. Scale bar = 10 mm. cte, caniniform tooth/teeth; ite, incisiform tooth/teeth; pcte, postcaniniform tooth/teeth.

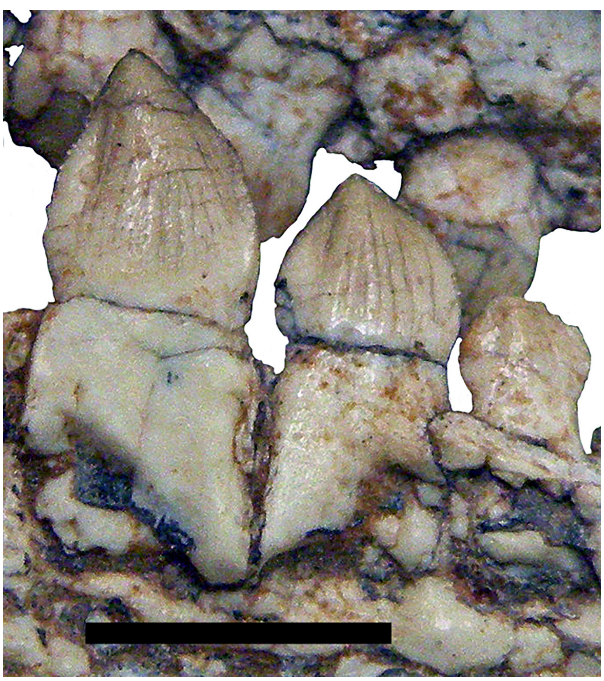

Figure 9. Detail of the enlarged dentary tooth of *Araripesuchus wegeneri* (MNN GAD 20) in lingual view. Scale bar = 10 mm.

MPCA-PV 236. The posterior teeth are much more robust and poorly labiolingually compressed in comparison to those observed in other *Araripesuchus* and *Uruguaysuchus* species. Although most of tooth crowns are missing, it is possible to infer a more bulbous shape for them, resembling the posterior crushing teeth of some living and fossil eusuchians (Ösi & Barrett 2011).

CONCLUSIONS

The dental patterns are clearly distinct between Uruguaysuchidae species, with highly variable tooth count, variation in size and position of the morphotypes and alveoli. Some of those variation have systematic and taxonomic importance. The new specimen MN 7061-V shows that *A. gomesii* has five premaxillary teeth instead of four, and the previous interpretation by Price (1959) was probably due a preservation artifact. Information regarding the dentition of the specimen SMNK PAL 6404 reveals a combination of characters unique among uruguaysuchids (i.e. the last three maxillary teeth are slightly larger than others, presence of a transitional tooth located at the suture between premaxilla and maxilla) that together with other osteological differences and similarities (vide Frey & Salisbury 2007, Figueiredo 2015) suggests this is a new *Araripesuchus* species. There are no preserved teeth in *A. rattoides*, however its alveoli pattern indicates a dentition that was rather different in comparison to all other uruguaysuchids, with exceptionally large first and fourth alveoli. The remarkably dorsoventrally high symphysis of the mandible also differs the Moroccan taxon from other *Araripesuchus*, and all those features combined points to a genus-level differentiation.

The dentition patterns observed in Uruguaysuchidae can represent foraging specializations in this clade, suggesting different life habits and feeding strategies (Sereno &

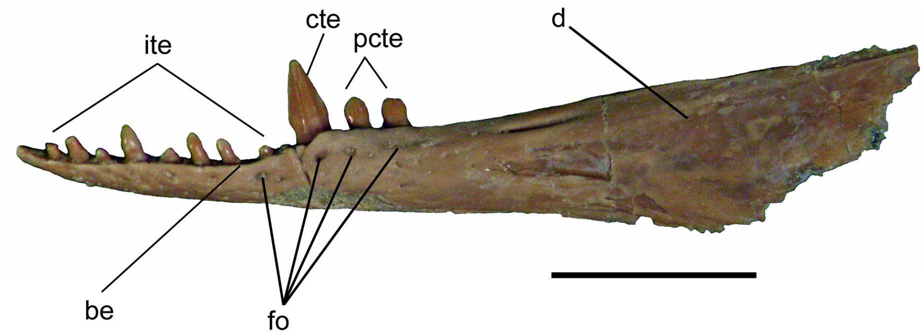

Figure 10. Left dentary bone of *Araripesuchus tsangatsangana* (FMNH PR 2318) in left lateral view. Scale bar = 10 mm. be, buccal emargination; cte, caniniform tooth/teeth; d, dentary; for, foramen/foramina; ite, incisiform tooth/teeth; pcte, postcaniniform tooth/teeth.

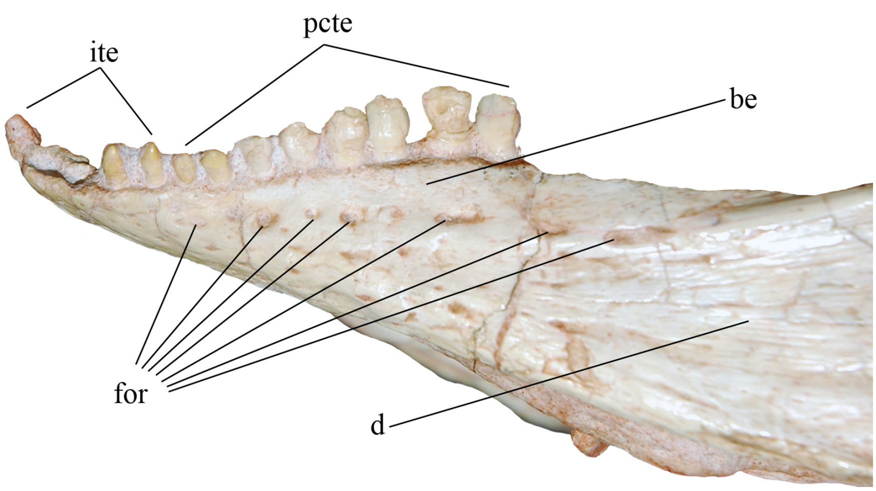

Figure 11. Detail of the anterior region of the mandible of *Uruguaysuchus aznarezi* (FC-DPV 2320) in left lateral view. Out of scale. be, buccal emargination; d, dentary; for, foramen/foramina; ite, incisiform tooth/teeth; pcte, postcaniniform tooth/teeth.

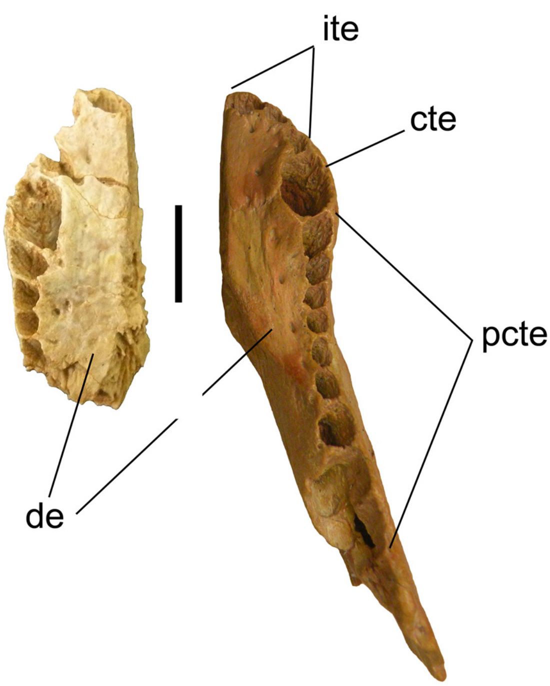

Figure 12. Dentary of *Araripesuchus rattoides* UCRC PV3 (left) and the holotype CMN 41893 (right) in dorsal view. Scale bar = 10 mm. de, dentary; cte, caniniform tooth/teeth; ite, incisiform tooth/teeth; pcte, postcaniniform tooth/teeth.

Larsson 2009). None of the *Araripesuchus* or *Uruguaysuchus* species have typical discrete characters that suggest a strict herbivore diet, such as the presence of chisel-like incisiforms, broad and flat crowns in the postcaniniform teeth, or molarization of the posterior-most teeth. This is the case even for the species in which tooth-tooth occlusion and apical wear facets in the crowns (e.g., *A wegeneri*), which is an indicative of oral processing of food, but not herbivory (Ösi 2013). Recent data on the dental complexity of *Araripesuchus gomesii* showed their teeth are compatible with insectivorous or omnivorous diets (Melstrom & Irmis 2019). However, it is important to note that the specimen AMNH 24450 is a juvenile animal, and ontogenetic dietary partitioning is well-known in living crocodilians (e.g., Tucker et al. 1996, Platt et al. 2006). Therefore, adult *A. gomesii* could have different feeding habits.

Scavenging behavior is widespread among living crocodilians (Selva et al. 2019) and was suggested for some notosuchians, like the Sphagesauridae (Kellner et al. 2011a). De Valais et al. (2012) analyzed trace marks in bones from La Buitrera locality, Argentina, and found no evidence of scavenging habits for *Araripesuchus*. However, the authors point out that many marks made by mammals were compatible with the presence of large caniniforms and procumbent incisiforms, features observed in *Araripesuchus rattoides*.

Uruguaysuchidae could be found throughout Gondwana and all species of *Araripesuchus* shared their habitats with other crocodyliforms, like peirosaurids and mahajangasuchids. Niche partitioning and ecological specialization could help avoiding competition with other crocodyliforms, and it is probably an important process in explaining the high taxonomic diversity of the group during the Cretaceous. Studies on the paleoecology of Crocodyliformes are still necessary (e.g., Dantas et al. 2018) to stablish the resources potentially consumed by these animals.

Acknowledgments

The authors would like to express their sincere gratitude to Dr. Diogenes de Almeida Campos (Departamento Nacional de Produção Mineral, Museu de Ciências da Terra, Rio de Janeiro, Brazil), one of the greatest Brazilian paleontologists of our generation. Dr. Campos was responsible for the academic training and supporting of several students and professionals, including both authors (AWAK and RGF). He collected, described, and cared for hundreds of fossil specimens and championed the Brazilian paleontology for the past decades. Dr. James M. Clark (George Washington University, USA) is thanked for the supervision during the 1-year sandwich doctorate for one of the authors (RGF) in the Robert Weintraub Program in Systematics and Evolution at The George Washington University (USA). We are in debt to Msc. Helder de Paula Silva (Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil) who chemically prepared the specimen MN 7961-V. We thank the following people who granted access to collections and specimens under their care: Msc. Rodrigo da Rocha Machado (Departamento Nacional de Produção Mineral, Museu de Ciências da Terra, Rio de Janeiro, Brazil); Dr. Daniel Perea (Facultad de Ciencias, Universidad de la Republica, Montevideo, Uruguay); Dr. Jorge O. Calvo and Dr. Juan Porfiri (Universidad Nacional del Comahue, Centro Palentologico Lago Barreales, Neuquen, Argentina); Dr. Carlos Munhoz and Dr. Ignácio Cerda (Museo Paleontologico Carlos Ameghino, Cipolletti, Argentina); Dr. Diego Pol (Museo Paleontológico Egídio Feruglio, Trelew, Argentina); Dr. Paul Sereno and Mr. Robert Masek (University of Chicago, Chicago, USA); Dr. Mark A. Norell and Carl M. Mehling (American Museum of Natural History, New York City, USA). We thank two anonymous reviewers for their comments that greatly improved this manuscript. This research was partially funded by the Fundação de Desenvolvimento Carlos Chagas Filho de Amparo à Pesquisa do Estado do rio de Janeiro (FAPERJ # E-26/202.905/2018 to AWAK) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq #313461/2018-0 to AWAK; CNPq #140501/2011-8 and #201641/2012-7 to RGF).

REFERENCES

ANDRADE MB & BERTINI RJ. 2008. Morphology of the dental carinae in *Mariliasuchus amarali* (Crocodylomorpha, Notosuchia) and the pattern of tooth serration among basal Mesoeucrocodylia. Arq Mus Nac 66(1): 63-82.

ANDRADE MB, YOUNG MT, DESOJO JB & BRUSATTE SL. 2010. The evolution of extreme hypercarnivory in Metriorhynchidae

(Mesoeucrocodylia: Thalattosuchia) based on evidence from microscopic denticle morphology. J Vertebr Paleontol 30(5): 1451-1465.

BUFFETAUT E. 1981. Die biogeographische Geschichte der Krokodilier, mit Beschreibung einer neuen Art, *Araripesuchus wegeneri*. Geol Rundsch 70: 611-624.

CAMPOS DA, OLIVEIRA GR, FIGUEIREDO RG, RIFF D, AZEVEDO SAK, CARVALHO LB & KELLNER AWA. 2011. On a new peirosaurid crocodyliform from the Upper Cretaceous, Bauru Group, southeastern Brazil. An Acad Bras Cienc 83(1): 317-327.

CARDIA DFF, BERTINI RJ, CAMOSSI LG & LETIZIO LA. 2019. First record of Acanthocephala parasites eggs in coprolites preliminary assigned to Crocodyliformes from the Adamantina Formation (Bauru Group, Upper Cretaceous), São Paulo, Brazil. An Acad Bras Cienc 91: e20170848. DOI 10.1590/0001-3765201920170848.

CARVALHO IS. 1994. *Candidodon*: um crocodilo com heterodontia (Notosuchia, Cretáceo Inferior - Brasil). An Acad Bras Cienc 66 (3): 331-346.

CARVALHO IS, RIBEIRO LCB & AVILLA LS. 2004. *Uberabasuchus terrificus* sp. nov. a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. Gondwana Res 7(4): 975-1002.

CARVALHO IS, VASCONCELLOS FM & TAVARES SAS. 2007. *Montealtosuchus arrudacamposi*, a new peirosaurid crocodile (Mesoeucrocodylia) from the Late Cretaceous Adamantina Formation of Brazil. Zootaxa 1607: 35-46.

CLARK JM, JACOBS L & DOWNS WR. 1989. Mammal-like dentition in a Mesozoic crocodylian. Science 244: 1064-1066.

DANTAS MAT, MELOTTI M, RODRIGUES T & FIGUEIREDO RG. 2018. Isotopic paleoecology (δ C, δ O) of early Cenomanian (Upper Cretaceous) vertebrates from North Africa and Brazil: ecological niche and overlap. In: Simpósio Brasileiro de Paleontologia de Vertebrados, 9, Teresina. Boletim de Resumos ... , Teresina p. 39.

DE VALAIS S, APESTEGUÍA S & GARRIDO AC. 2012. Cretaceous small scavengers: feeding traces in tetrapod bones from Patagonia, Argentina. PLoS One 7(1): e29841.

DRUMHELLER SK & WILBERG EW. 2020. A synthetic approach for assessing the interplay of form and function in the crocodyliform snout. Zool J Linn Soc-Lond 188(2): 507-521.

FERNÁNDEZ DUMONT ML, BONA P, POL D & APESTEGUÍA S. 2020. New anatomical information on *Araripesuchus buitreraensis* with implications for the systematics of Uruguaysuchidae (Crocodyliforms, Notosuchia). Cretaceous Res 113: 104494.

FIGUEIREDO RG. 2015. Review of the genus *Araripesuchus* Price, 1959 (Crocodylomorpha) with the description of a new specimen from the Lower Cretaceous Araripe Basin of Brazil and comments on paleobiogeography. Rio de Janeiro: Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Museu Nacional, Universidade Federal do Rio de Janeiro, 984 p.

FREY E & SALISBURY SW. 2007. Crocodilians from the Crato Formation: evidence for enigmatic species. In: Martill DM, Bechly G & Loveridge RF (Eds), The Crato Fossil beds of Brazil: Window to an ancient world. Cambridge University Press, p. 463-474.

GASPARINI Z. 1971. Los Notosuchia del Cretácico de América del Sur como un nuevo infraorden de Mesosuchia (Crocodilia). Ameghiniana 8(2): 83-103.

GOMANI EM. 1997. A crocodyliform from the Early Cretaceous Dinosaur Beds, Northern Malawi. J Vertebr Paleontol 17(2): 280-294.

IORI FV, MARINHO TS, CARVALHO IS & CAMPOS ACA. 2011. Padrão dentário dos esfagessaurídeos (Crocodyliformes, Sphagesauridae). In: Carvalho IS, Srivastava NK, Strohnchoen O & Lana CC (Eds), Paleontologia: Cenários de Vida Volume 4. Editora Interciência, p. 585-594.

JACOBS LL, WINKLER DA, KAUFULU ZM & DOWNS WR. 1990. The Dinosaur Beds of northern Malawi, Africa. Natl Geogr Res 6(2):196-204.

KELLNER AWA. 1987. Ocorrência de um novo crocodiliano no Cretáceo Inferior da Bacia do Araripe, Nordeste do Brasil. An Acad Bras Cienc 59(3): 219-232.

KELLNER AWA, CAMPOS DA, RIFF D & ANDRADE MB. 2011a. A new crocodylomorph (Sphagesauridae, Notosuchia) with horn-like tubercles from Brazil. Zool J Linn Soc-Lond 163 (s1): s57-s65.

KELLNER AWA, FIGUEIREDO RG, AZEVEDO SAK & CAMPOS DA. 2011b. A new cretaceous notosuchian (Mesoeucrocodylia) with bizarre dentition from Brazil. Zool J Linn Soc-Lond 163 (s1): s109-s115.

KELLNER AWA, PINHEIRO AEP & CAMPOS DA. 2014. A new sebecid from the Paleogene of Brazil and the crocodyliform radiation after the K-Pg boundary. PLoS ONE 9(1): e81386.

KELLNER AWA, RODRIGUES T, COSTA FR, WEINSCHÜTZ LC, FIGUEIREDO RG, SOUZA GAD, BRUM AS, ELEUTÉRIO LHS, MUELLER CW & SAYÃO JM. 2019. Pterodactyloid pterosaur bones from Cretaceous deposits of the Antarctic Peninsula. An Acad Bras Cienc 91: e20191300. DOI 10.1590/0001-3765201920191300.

LARSSON HCE & SUES H-D. 2007. Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Marocco. Zool J Linn Soc-Lond 149: 533-567.

LEARDI JM & POL D. 2009. The first crocodyliform from the Chubut Group (Chubut Province, Argentina) and its phylogenetic position within basal Mesoeucrocodylia. Cretaceous Res 30(6): 1376-1386.

LECUONA A & POL D. 2008. Tooth morphology of *Notosuchus terrestris* (Notosuchia: Mesoeucrocodylia): New evidence and implications. C R Palevol 7: 407-417.

MARINHO TS & CARVALHO IS. 2009. An armadillo-like sphagesaurid crocodyliform from the Late Cretaceous of Brazil. J South Amer Earth Sci 27(1): 36-41.

MARTIN JE & DE LAPPARENT DE BROIN F. 2016. A miniature notosuchian with multicuspid teeth from the Cretaceous of Morocco. J Vertebr Paleontol 36(6): e1211534. DOI 10.1080/02724634.2016.1211534.

MARTINELLI AG, SERTICH JJW, GARRIDO AC & PRADERIO A. 2012. A new peirosaurid from the Upper Cretaceous of Argentina: Implications for specimens referred to *Peirosaurus torminni* Price (Crocodyliformes: Peirosauridae). Cretaceous Res 37: 191-200.

MELSTROM KM & IRMIS RB. 2019. Repeated evolution of herbivorous crocodyliforms during the age of dinosaurs. Current Biol 29(14): 2389-2395.

MONTEFELTRO FC, LARSSON HCE & LANGER MC. 2011. A new baurusuchid (Crocodyliformes, Mesoeucrocodylia) from the Late Cretaceous of Brazil and the phylogeny of Baurusuchidae. PLoS ONE 6(7): e21916.

NASH DS. 1975. The morphology and relationships of a crocodilian, *Orthosuchus stormbergi*, from the Upper Triassic of Lesotho. Ann S Afr Mus 67: 227-329.

NOBRE PH & CARVALHO IS. 2006. *Adamantinasuchus navae*: A new Gondwanan Crocodylomorpha (Mesoeucrocodylia) from the Late Cretaceous of Brazil. Cretaceous Res 10: 370-378.

NOBRE PH, CARVALHO IS, VASCONCELLOS FM & SOUTO PR. 2008. Feeding behavior of the Gondwanic Crocodylomorpha *Mariliasuchus amarali* from the Upper Cretaceous Bauru Basin, Brazil. Gondwana Res 13(1): 139-145.

NOVAS FE, PAIS DF, POL D, CARVALHO IS, SCANFERLA A, MONES A & RIGLOS MS. 2009. Bizarre notosuchian crocodyliform with associated eggs from the Upper Cretaceous of Bolivia. J Vertebr Paleontol 29(4): 1316-1320.

O'CONNOR PM, SERTICH JJW, STEVENS NJ, ROBERTS EM, GOTTFRIED MD, HIERONYMUS TL, JINNAH ZA, RIDGELY R, NGASALA SE & TEMBA J. 2010. The evolution of mammal-like crocodyliforms in the Cretaceous Period of Gondwana. Nature 466: 748-751.

ORTEGA F, GASPARINI Z, BUSCALIONI AD & CALVO JO. 2000. A new species of *Araripesuchus* (Crocodylomorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). J Vertebr Paleontol 20: 57-76.

ÖSI A. 2013. The evolution of jaw mechanism and dental function in heterodont crocodyliforms. Historical Biol 26 (3): 279-414.

ÖSI A & BARRETT PM. 2011. Dental wear and oral food processing in *Caiman latirostris*: analogue for fossil crocodylians with crushing teeth. Neues Jahrb Geol Palaontol Abh 261(2): 201-207.

ÖSI A & WEISHAMPEL DB. 2009. Jaw mechanism and dental function in the Late Cretaceous basal eusuchian *Iharkutosuchus*. J Morphol 270(8): 903-920.

POL D. 2003. New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Cretaceous of Brazil. J Vertebr Paleontol 23(4): 817-831.

POL D & NORELL MA. 2004. A new crocodyliform from Zos Canyon, Mongolia. Am Mus Novit 3445: 1-36.

POL D, JI SA, CLARK JM & CHIAPPE LM. 2004. Basal crocodyliforms from the Lower Cretaceous Tugulu Group (Xinjiang, China), and the phylogenetic position of *Edentosuchus*. Cretaceous Res 25: 603-622.

POL D, LEARDI JM, LECUONA A & KRAUSE M. 2012. Postcranial anatomy of *Sebecus icaeorhinus* from the Cretaceous of Patagonia. J Vertebr Paleontol 32(2): 328-354.

POL D, NASCIMENTO PM, CARVALHO AB, RICCOMINI C, PIRES-DOMINGUES RC & ZAHER H. 2014. A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. PLoS ONE 9(4): e93105.

PLATT SG, RAINWATER TR, FINGER AG, THORBJARNARSON JB, ANDERSON TA & MCMURRY ST. 2006. Food habits, ontogenetic dietary partitioning and observations of foraging behaviour of Morelet's crocodile (*Crocodylus moreletii*) in northern Belize. Herpetol J 16(3): 281-290.

PRASAD GVR & LAPPARENT DE BROIN F. 2002. Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. Ann Paleontol 88(1): 19-71.

PRICE LI. 1959. Sobre um crocodilídeo notossúquio do Cretácico Brasileiro. Boletim (DGM-RJ) 118: 1-55.

RIFF D & KELLNER AWA. 2001. On the dentition of *Baurusuchus pachecoi* Price (Crocodyliformes, Metasuchia) from the Upper Cretaceous of Brazil. Bol Mus Nac Geologia 59: 1-15.

RIFF D & KELLNER AWA. 2011. Baurusuchid crocodyliforms as theropod mimics: clues from the skull and appendicular morphology of *Stratiotosuchus maxhechti* (Upper Cretaceous of Brazil). Zool J Linn Soc-Lond 163(s1): S37-S56.

ROMER AS. 1956. Osteology of the Reptiles. The University of Chicago Press, 772 p.

SELVA N, MOLEÓN M, SEBASTIÁN-GONZÁLEZ E, DEVAULT TL, QUAGGIOTO MM, BAILEY DM, LAMBERTUCCI AS & MARGALIDA A. 2019. Vertebrate Scavenging Communities. In: Olea PP et al. (Eds), Cham: Carrion Ecology and Management, Wildlife Research Monographs 2, Springer, Cham, Switzerland, p. 71-99.

SERENO PC & LARSSON HCE. 2009. Cretaceous crocodyliforms from the Sahara. Zookeys 28: 1-143.

SOTO M, POL D & PEREA D. 2011. A new specimen of *Uruguaysuchus aznarezi* (Crocodyliformes: Notosuchia) from the middle Cretaceous of Uruguay and its phylogenetic relationships. Zool J Linn Soc-Lond 163(s1): s173-s198.

SOUZA RG & CAMPOS DA. 2019. New Crocodyliform specimens from Recôncavo-Tucano Basin (Early Cretaceous) of Bahia, Brazil. An Acad Bras Cienc 91: e20170382. DOI 10.1590/0001-3765201720170382.

STUBBS TL, PIERCE SP, RAYFIELD EJ & ANDERSON PS. 2013. Morphological and biomechanical disparity of crocodile-line archosaurs following the end-Triassic extinction. Proc R Soc B 280(1770): 20131940.

TOLJAGIC O & BUTLER RJ. 2013. Triassic-Jurassic mass extinction as trigger for the Mesozoic radiation of crocodylomorphs. Biol Lett 9(3): 20130095.

TUCKER AD, LIMPUS CJ, MCCALLUM HI & MCDONALD KR. 1996. Ontogenetic dietary partitioning by *Crocodylus johnstoni* during the dry season. Copeia 4: 978-988.

TURNER AH. 2006. Osteology and phylogeny of a new species of *Araripesuchus* (Crocodyliformes: Mesoeucrocodylia) from the Late Cretaceous of Madagascar. Historical Biol 18(3): 255-369.

WILBERG EW. 2017. Investigating patterns of crocodyliform cranial disparity through the Mesozoic and Cenozoic. Zool J Linn Soc-Lond 181(1): 189-208.

WU X-C, SUES H-D & SUN A. 1995. A plant-eating crocodyliform reptile from the Cretaceous of China. Nature 376: 678-680.

ZAHER H, POL D, CARVALHO AB, RICCOMINI C, CAMPOS D & NAVA W. 2006. Redescription of the cranial morphology of *Mariliasuchus amarali*, and its phylogenetic affinities (Crocodyliformes, Notosuchia). Am Mus Novit 3512: 1-40.

How to cite

FIGUEIREDO RG & KELLNER AWA. 2021. Morphological variation in the dentition of Uruguaysuchidae (Crocodyliformes: Notosuchia). An Acad Bras Cienc 93: e20201594. DOI 10.1590/0001-3765202120201594.

Manuscript received on October 4, 2020;
accepted for publication on February 4, 2021

RODRIGO G. FIGUEIREDO[1]
https://orcid.org/0000-0002-4304-6434

ALEXANDER W.A. KELLNER[2]
http://orcid.org/0000-0001-7174-9447

[1]Universidade Federal do Espírito Santo, Departamento de Biologia, Alto Universitário, s/n, Guararema, 29500-000 Alegre, ES, Brazil

[2]Universidade Federal do Rio de Janeiro, Laboratório de Sistemática e Tafonomia de Vertebrados Fósseis, Setor de Paleovertebrados, Departamento de Geologia e Paleontologia, Museu Nacional, Quinta da Boa Vista s/n, São Cristóvão, 20940-040 Rio de Janeiro, RJ, Brazil

Correspondence to: **Rodrigo Giesta Figueiredo**
E-mail: rodrigo.figueiredo@ufes.br

Author Contributions

RGF and AWAK contributed to the design and development of the study, to the analysis of the results, and to the writing of the manuscript.