NEW DYROSAURID REMAINS (CROCODYLIFORMES, MESOEUCROCODYLIA) FROM THE PALEOCENE OF THE PARAÍBA BASIN, NE BRAZIL

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ABSTRACT – The fossil crocodyliforms from the Paraíba Basin in Northeastern Brazil are represented by two species, *Hyposaurus derbianus*, (uncertain age) and *Guarinisuchus munizi*, from the Paleocene Maria Farinha Formation. Herein we present new material of a dyrosaurid also collected in deposits of the Maria Farinha Formation, representing cranial, axial and appendicular remains. The specimens are housed at Centro Acadêmico de Vitória, Universidade Federal de Pernambuco (CAV–UFPE) and at Universidade Federal Rural de Pernambuco (UFRPE). The most important contribution of this find is a well-preserved mandibular specimen (CAV 0056-V) with 16 alveoli on the left side and 13 on the right side. Nine complete or partial tooth crowns are preserved, in positions 1–5. The teeth are conical and homodont with vertical striations. The largest teeth are located at positions d1 and d4. The biggest occlusion pits are located between positions d2 and d3. The seventh alveoli are reduced and close to the eighth alveoli. The mandible, CAV 0056-V, possesses three foramina in the anterior portion of the dentaries and the mandibular symphysis extends to the posterior margins of the d11–d12 dentary alveoli. Based on the features presented in the mandible and the other fossils recovered, we attribute these materials to Dyrosauridae, particularly, to *Guarinisuchus* cf. *G. munizi*.

Key words: Crocodyliformes, Dyrosauridae, NE Brazil, Paleocene, Paraíba Basin.

RESUMO – Os Crocodyliformes fósseis da Bacia da Paraíba, Nordeste brasileiro, são representados por duas espécies, *Hyposaurus derbianus* de idade incerta e *Guarinisuchus munizi*, dos estratos paleocênicos da Formação Maria Farinha. Aqui são apresentados novos materiais de dyrosaurídeo da Formação Maria Farinha, representados por fragmentos craniais, axiais e apendiculares. Os espécimes estão armazenados no Centro Acadêmico de Vitória da Universidade Federal de Pernambuco (CAV–UFPE) e na Universidade Federal Rural de Pernambuco (UFRPE). O novo material contém uma mandíbula bem preservada (CAV 0056-V), com 16 alvéolos do lado esquerdo e 13 do lado direito. Nove coroas dentárias estão preservadas total ou parcialmente completas, nas posições 1–5. Os dentes são homodontes com forma cônica e estrias verticais. Os dentes de maior comprimento estão localizados nas posições d1 e d4. As maiores marcas de oclusão ocorrem entre as posições d2 e d3. Os alvéolos d7 apresentam dimensões reduzidas e ocorrem próximos aos alvéolos d8. A mandíbula, CAV 0056-V apresenta três forames na porção anterior dos dentários e a sínfise mandibular estende-se até a borda posterior dos alvéolos dentários d11–d12. Portanto, fundamentado nas características apresentadas na mandíbula e pelos outros espécimes, nós associamos estes materiais à Dyrosauridae, particularmente, *Guarinisuchus* cf. *G. munizi*.

Palavras-chave: Crocodyliformes, Dyrosauridae, NE Brasil, Paleoceno, Bacia da Paraíba.

INTRODUCTION

Dyrosauridae de Stefano, 1903, is an extinct neosuchian family found possibly as early as the Early–Late Cretaceous boundary (see Young *et al.*, 2016) to early Eocene (Benton & Clark, 1988; Brochu *et al.*, 2002; Jouve *et al.*, 2005a). These

crocodyliforms are found from marine, nearshore (Troxell, 1925; Brochu *et al.*, 2002; Jouve & Schwartz, 2004; Hill *et al.*, 2015), and freshwater environmental deposits (Buffetaut, 1978; Khosla *et al.*, 2009; Hastings *et al.*, 2010, 2011, 2015).

This family is commonly formed by meso- to longirostrine forms with a mostly tubular rostrum (Scharwarz-Wings,

2014), except for *Cerrejonisuchus improcerus* Hastings, Bloch, Cadena & Jaramillo, 2010 and *Anthracosuchus balrogus* Hastings, Bloch & Jaramillo, 2014, from the Paleocene Cerrejón Formation of northeastern Colombia. Phylogenetic analyses of Dyrosauridae have often supported its close relationship with Pholidosauridae (Jouve *et al.*, 2006; Holliday & Gardner, 2012; Pritchard *et al.*, 2013).

The occurrences of dyrosaurid remains indicate a wide geographic distribution, including Asia (Buffetaut, 1978; Storrs, 1986; Langston, 1995; Khosla *et al.*, 2009), North America (Denton *et al.*, 1997; Shiller *et al.*, 2016), South America (Argollo *et al.*, 1987; Barbosa *et al.*, 2008; Hastings *et al.*, 2010, 2011, 2015; Andrade & Sayão, 2014), and possibly Europe (Buffetaut & Lauverjat, 1978). However, most dyrosaurid fossils have been found in Africa (Halstead, 1975; Buffetaut, 1980, 1983; Jouve & Schwarz, 2004; Jouve, 2005; Jouve *et al.*, 2005a, 2006; Hill *et al.*, 2008; Young *et al.*, 2016).

The development of different feeding strategies and diverse ways of locomotion possibly gave dyrosaurids an advantage over marine reptiles and freshwater crocodyliforms allowing the success of this group as survivors across the K–Pg transition (Barbosa *et al.*, 2008; Andrade & Sayão, 2014; Hastings *et al.*, 2015; Puértolas-Pascual *et al.*, 2015).

Two species of dyrosaurids have been described from NE Brazil, *Hyposaurus derbianus* Cope, 1886, with no precise location provided, and *Guarinisuchus munizi* Barbosa, Kellner & Viana, 2008, that was found in outcrops of the Maria Farinha Formation, Danian of Poty Quarry, in the coastal zone of the Paraíba Basin (Barbosa *et al.*, 2008; Riff *et al.*, 2012).

Here we describe new material that belongs to Dyrosauridae. All fossils were collected from the same site in the Poty Quarry that the holotype of *Guarinisuchus munizi* was found (Figure 1). The material is housed in the paleontological collections of Centro Acadêmico de Vitória, Universidade Federal de Pernambuco (CAV–UFPE) and Universidade Federal Rural de Pernambuco (UFRPE), Brazil. The material examined comprises two isolated teeth, an incomplete mandible with articulated dentaries, a dorsal vertebra, an osteoderm, a proximal end of a femur, a proximal end of the right tibia and distal ends of the right and left tibiae. Except for UFRPE 2814, which was collected previously, all fossils were found together forming an association. Therefore, the present analysis focuses on this new dyrosaurid record for the Maria Farinha Formation.

Institutional abbreviations. CAV, Centro Acadêmico de Vitória, Vitória de Santo Antão, Brazil; CNRST-SUNY, Centre National de la Recherche Scientifique et Technologique du Mali, Mali – Stony Brook University, New York, USA; DG-CTG-UFPE, Departamento de Geologia, Centro de Tecnologia e Geociências, Universidade Federal de Pernambuco, Recife, Brazil; IGM, Museo Geológico, at the Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Bogotá, Colombia; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MRAC, Musée d'Afrique Centrale, Tervuren, Belgique; NJSM, New Jersey State Museum, Trenton, USA; OCP DEK-GE, Office

Chérifien des Phosphates, Direction de l'Exploitation de Khouribga – Geologie Exploitation, Khouribga, Morocco; UF, Florida Museum of Natural History, University of Florida, Gainesville, USA; UFRPE, Universidade Federal Rural de Pernambuco, Recife, Brazil; UPMC, Université Pierre et Marie Curie, Paris, France; Vb, Laboratoire de Paléontologia des Vertébrés et de Paléontologia Humaine, Université Pierre et Marie Curie, Paris, France; VPL/JU/IR, Vertebrate Paleontology Laboratory/Jammu University/ intertrappean reptiles, Jammu, India.

GEOLOGICAL SETTING

The coastal zone of the Paraíba Basin is bounded by the Pernambuco Shear Zone to the south and the Mamanguape High to the north (Barbosa *et al.*, 2003; Barbosa, 2007; Silva *et al.*, 2011). The stratigraphic column of the Paraíba Basin is composed of Cretaceous, Paleocene and Miocene deposits and a variety of Quaternary sediments related to the development of coastal systems (Rossetti *et al.*, 2011, 2012; Lima *et al.*, 2017).

The sedimentary cover of the Paraíba Basin in its coastal zone is not extensive, reaching a maximum thickness of only 400 m in the region of Itamaracá Island. The coastal region is divided into three main depocenters, Olinda, Alhandra and Miriri, from south to north respectively. The sedimentary filling of this basin is mainly composed of six formations: (1) the Coniacian?/Santonian Beberibe Formation, consisting of continental sandstones, siltstones and claystones (Beurlen, 1967a,b; Muniz, 1993; Barbosa, 2007); (2) the middle Campanian/upper Maastrichtian Itamaracá Formation, consisting of transitional and sandy limestones, marls and dolostones (Beurlen, 1967a,b; Tinoco, 1971; Souza & Lima Filho, 2005; Moura, 2007); (3) the Maastrichtian Gramame Formation, consisting of marls, limestones and marly limestones from a shallow marine platform (Beurlen, 1967a; Albertão *et al.*, 1994; Gertsch *et al.*, 2013); (4) the Danian Maria Farinha Formation, consisting of limestones, dolostones, marly limestones and sandy limestones formed on a shallow marine platform (Albertão *et al.*, 1994; Stinnesbeck & Keller, 1995; Keller & Stinnesbeck, 1996; Koutsoukos, 1998; Barbosa *et al.*, 2003; Barbosa & Lima Filho, 2006; Barbosa, 2007; Gertsch *et al.*, 2013); (5) the Eocene Tambaba Formation, consisting of dolostones, and limestones deposits formed in reefal-lagoon systems (Correia Filho *et al.*, 2015); and (6) the Miocene Barreiras Formation, consisting of continental sandstones, siltstones and claystones (Rossetti *et al.*, 2011). We adopted the stratigraphic hypothesis of Correia Filho *et al.* (2015) that proposed the Tambaba Formation as Eocene reefal carbonate deposits that was previously treated as the upper part of the Paleocene Maria Farinha Formation (Beurlen, 1967a).

The specimens treated in this study were collected in deposits of the Maria Farinha Formation. This formation is composed of limestones, marly limestones and thick levels of marls in its lower portion (Barbosa & Lima Filho, 2006; Nascimento-Silva *et al.*, 2011) (Figure 1). The Maria Farinha

Figure 1. A, location of the Paraíba Basin in the continental platform of northeastern Brazil (black star), and image of the outcrop, including a limestone bed, at the Poty Quarry, Pernambuco State, where the fossil studied in this paper was collected (black arrow). B, stratigraphic section of the Maastrichtian–Paleocene succession exposed in the Poty Quarry. The section shows the position of the fossil discussed in this paper, and the location of the *Guarinisuchus munizi* holotype that was found at the same site.

Formation was formed during a period of sea level oscillations that affected the Paraíba Basin, and its upper portion exhibits evidence of a regression that affected the record of this unit in the coastal zone (Mabesoone & Alheiros, 1991; Keller & Stinnesbeck, 1996; Barbosa & Lima Filho, 2006; Nascimento-Silva *et al.*, 2011).

Fossil vertebrates from the Paraíba Basin have been mentioned in the literature since the end of 19th Century (Cope, 1886; Woodward, 1907; Maury, 1930). The record of fossil reptiles from the Paraíba Basin was first mentioned by Cope (1886), then later by Price (1953a,b; 1957). This group is represented in the basin mostly by marine organisms such as mosasaurs, of which remains were collected in the Itamaracá and Gramame formations, and plesiosaurs (two taxa identified at the family level – Elasmosauridae and Pliosauridae). Elasmosauridae remains were collected in the Itamaracá and Gramame formations while Pliosauridae occurs only in the Itamaracá Formation. Scarce material of one pterosaur was also described from the Gramame Formation, *Nyctosaurus lamegoi* Price, 1953b. Remains of crocodiles and turtles have been recovered from the Maria Farinha Formation (Price, 1953b; Gallo *et al.*, 2001; Oliveira & Romano, 2007; Silva *et al.*, 2007; Barbosa *et al.*, 2008; Oliveira & Deantoni, 2013; Carvalho *et al.*, 2016; Romano, 2016).

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970
DYROSAURIDAE de Stefano, 1903

Guarinisuchus Barbosa, Kellner & Viana, 2008

Guarinisuchus cf. *G. munizi* Barbosa,
Kellner & Viana, 2008
(Figures 2–4)

Holotype. (DG-CTG-UFPE 5723), Skull and mandible, ulna, cervical and caudal vertebrae, ribs, dermal scutes and isolated teeth.

New referred specimens. *Guarinisuchus* cf. *munizi*, partial right postorbital (CAV 0072-V), partial right jugal (CAV 0073-V), incomplete mandible (CAV 0056-V), two isolated teeth (CAV 0057-V and CAV 0074-V), osteoderm (CAV 0013-V), partial dorsal vertebra (UFRPE 5142), right proximal femur (CAV 0010-V), right proximal tibia (UFRPE 2814), right distal tibia (CAV 0012-V), left distal tibia (CAV 0011-V).

Geological and geographical precedence. Maria Farinha Formation, Paraíba Basin, Poty Quarry site, region of Paulista (7°54' 47"S, 34°51' 00"W), Municipality of Recife, Pernambuco State, Brazil.

Age. Early Paleocene (Late Danian).

DESCRIPTION AND COMPARISON

Postorbital. The postorbital fragment (CAV 0072-V) measures 60 mm; it is broken and incomplete (Figure 2). It is possible to identify this bone as a part of an anterior portion of the right postorbital, since this bone in Dyrosauridae is very elongated (Barbosa *et al.*, 2008). It has a dorsal surface ornamented by pits and a broad anterior branch with a well-developed anterolateral process that constitutes the postorbital spur as observed in an unnumbered specimen described by Buffetaut (1976) and the specimen Vb 602 (currently UPMC)

in Buffetaut *et al.* (1990). This feature has not been described by Barbosa *et al.* (2008) for the holotype of *Guarinisuchus munizi*. Its anteromedial branch has a rugose depression, probably to meet the frontal (Figure 3A). This depression exhibits in its posterior corner an edge of 90° that forms the anterolateral margin of the supratemporal fenestra, from there the postorbital becomes slender posteriorly.

Jugal. CAV 0073-V is a right jugal that bears a canal along its medial surface (Figure 3C). Dorsolaterally, it is ornamented with irregularly spaced pits and furrows (Figures 2, 3B). The siphonial foramen is lacking in the medial view in this specimen, as in *Guarinisuchus munizi*. In contrast to this feature, *Rhabdognathus aslerensis* Jouve, 2008 (CNRST-SUNY-190) (Brochu *et al.*, 2002) and *Cerrejonisuchus improcerus* (UF/IGM 29) (Hastings *et al.*, 2010) share the condition of presence of the siphonial foramen in medial view.

Mandible. The specimen CAV 0056-V includes dentaries and the splenials, but the articular, angular and surangular bones are not preserved. The mandible is elongated and narrow and it is partially complete; the d1 to d6 alveoli are preserved on the left side and the d1 to d13 alveoli on the right side (Figures 4A–B). Based on the holotype of *Guarinisuchus munizi* (DG-CTG-UFPE 5723), it is possible to estimate that a total number of alveoli on each side of the mandible is between 17 and 18. On the right side of the jaw the d10 alveolus is lacking. Nine complete or partial tooth crowns are preserved in CAV 0056-V, and they are in the positions d1 to d5. The first tooth is oriented anterodorsally and the largest teeth are located at positions d1 and d4. Likewise, the d4 tooth is the largest in *Dyrosaurus phosphaticus* Thomas, 1893 (MNHN ALG 3 and MNHN APH 27) (Jouve, 2005) and in *Dyrosaurus maghribensis* Jouve, Iarochène, Bouya & Amaghazaz, 2006 (OCP DEK-GE 253), (Jouve *et al.*, 2006). The alveolar edges of d4 are higher than the edges of the other alveoli. The d7 alveoli are reduced and close to the eighth alveoli border as described for *D. maghribensis* (OCP DEK-GE 253) (Jouve *et al.*, 2006) and *C. improcerus* (UF/IGM 29) (Hastings *et al.*, 2010); this pattern was also found in an unidentified dyrosaurid, VPL/JU/IR/400, from Maastrichtian strata in India (Khosla *et al.*, 2009). The tenth alveolus is not preserved on the right side of the dentary. Inter-alveolar occlusal pits are distributed among the alveoli on the lateral margin of both sides of the mandible, and they are smaller and shallower than the alveoli. The largest diastema is located between d2 and d3, probably to fit enlarged 3rd premaxillary teeth (Jouve *et al.*, 2006; Hastings *et al.*, 2010). There are three neurovascular foramina near the medial margin of the third alveoli, two on the left side and one on the right side. One foramen is present on the right side of the holotype of *G. munizi* as well. Nevertheless, it was not possible to confirm the foramina on the left side, since this part was not preserved in the holotype of *G. munizi*. The symphyseal teeth have broad bases and become narrow towards their apices, as was observed in *Acherontisuchus guajiraensis* Hastings, Bloch & Jaramillo, 2011 (UF/IGM 34 and UF/IGM 35). The length of the symphysis in the new mandibular material is 26.51 cm and posteriorly it reaches the level of the d12–d13 dentary alveoli

Figure 2. Schematic drawing of the *Guarinisuchus munizi* skull showing the anatomical positions of the postorbital and jugal fragments described here. Skull in dorsal (A) and in right lateral (B) views. Scale bar = 10 cm.

in the left side. We are unable to assess the total length of the symphysis in the holotype of *G. munizi*, because the anterior portion in DG-CTG-UFPE 5723 is missing. The symphysis in the holotype of *G. munizi* ends approximately at the position of the d14 alveolus (Barbosa *et al.*, 2008). In *Acherontisuchus guajiraensis* the symphysis extends posteriorly to the position of the d17 alveolus in UF/IGM 34, and between the d18 and d19 alveoli in UF/IGM 35 (Hastings *et al.*, 2011). In *Arambourgisuchus khouribgaensis* Jouve *et al.*, 2005, OCP DEK-GE 18, the symphysis ends posteriorly at the position of the d16 tooth. In *D. maghribensis*, OCP DEK-GE 253, the symphysis reaches, posteriorly, the position of the d17–d21 alveoli (Jouve *et al.*, 2006). In *C. improcerus*, UF/IGM 30, the mandibular symphysis ends posteriorly at approximately the level of the d9 alveolus, due to its short snout (Hastings *et al.*, 2010). The symphysis CAV 0056-V is much higher than wider (Figure 5). The width/ratio is similar in CAV 0056-V and other *Guarinisuchus* specimens. On the posterior surface of the symphyseal border, two depressions are separated by a thin longitudinal bar on the medial surface of the splenials (Figures 4E–F). These depressions constitute the intermandibular foramina, which accommodate the intramandibularis muscle, filling the Meckel's canal (Schwarz-Wings, 2014). The suture between the dentary and splenial forms a depression in dorsal view. In ventral view, the splenial seems to end anteriorly at the position of the d9 alveolus (Figures 4C–D); in dorsal view it reaches the position of the d8. In ventral view, it shows a long and narrow anterior process that intercepts the medial borders of the dentaries and constitutes around 35 per cent of the length of the symphysis. The splenial forms

Figure 3. Bone elements of *Guarinisuchus munizi*. **A**, right postorbital, CAV 0072-V, in dorsal view; **B–C**, right jugal, CAV 0073-V, in lateral (**B**) and medial (**C**) views; **D–E**, isolated teeth, CAV 0057-V and CAV 0074-V in lingual view, respectively; **F**, isolated osteoderm, CAV 0013-V, in dorsal view; **G–J**, dorsal vertebra, UFRPE 5142, in cranial (**G**), left lateral (**H**), caudal (**I**) and ventral (**J**) views; **K**, proximal portion of the right femur, CAV 0010-V, in frontal view; **L–M**, proximal portion of the right tibia, UFRPE 2814, in anterior and lateral views; **N**, distal portion of the left tibia, CAV 0011-V, in posterior view; **O**, distal portion of the right tibia, CAV 0012-V, in posterior view. **Abbreviations:** **cnc**, cnemial crest; **ld**, longitudinal depression. Scale bars: A–C, F–K, N, O = 10 mm; D, E = 5 mm; L, M = 50 mm.

the medial edges of the alveoli from the d10 position to the posterior-most alveolus. In *D. maghribensis*, OCP DEK-GE 253, these bones reach anteriorly to the position of the d11 to d14 teeth (Jouve *et al.*, 2006). Reduction of tooth size, from the anterior to the posterior portion of the mandible, has been described for some dyrosaurids species (Jouve & Schwartz, 2004; Jouve, 2005; Hastings *et al.*, 2011). Postsymphyseal alveoli are smaller than symphyseal alveoli in the specimen described here as well.

Dentition. CAV 0057-V and CAV 0074-V are two isolated teeth that were found together with the mandible, but they do not fit in any alveolus of the mandible, but their characteristics are identical to the teeth preserved in the mandible. The apicobasal heights of the teeth are 27.31 mm for CAV 0057-V and 14.13 mm for CAV 0074-V; both teeth are conical, elongated and homodont (Figures 3D–E). The teeth have a circular cross section and their labial and lingual surfaces are

marked by well-developed, straight carinae. The ‘twisted’ carina characteristic of *Hyposaurus* (NJSJ 12293) (Denton *et al.*, 1997) is not present. The tooth crowns are posteriorly curved, which is a feature present in other dyrosaurids (Cope, 1886; Barbosa *et al.*, 2008), and they also present a broad base and acute apex. Longitudinal striae are present on both lingual and labial surfaces of isolated teeth as described for *Acherontisuchus guajiraensis*, UF/IGM 34, (Hastings *et al.*, 2011). In *Arambourgisuchus khouribgaensis* (OCP DEK-GE 18 and OCP DEK-GE 269) striae are present in some teeth (Jouve *et al.*, 2005a). In *Cerrejonisuchus improcerus*, UF/IGM 29, striations were not detected (Hastings *et al.*, 2010). **Osteoderm.** CAV 0013-V represents an osteoderm not imbricated with a subquadrangular shape. Its dorsal surface is ornamented (Figure 3F) by irregular pits and a smooth ventral surface.

Dorsal vertebra. A single dorsal vertebra was recovered

Figure 4. Mandible and its schematic drawing of *Guarinisuchus* cf. *G. munizi* CAV 0056-V, in dorsal (A–B), ventral (C–D) and posterior (E–F) views, from the Poty Quarry of the Maria Farinha Formation, Early Paleocene. **Abbreviations:** d, dentary; d1–16, alveoli of the dentary; fo, foramina; ifo, intermandibular foramina; sp, splenial. Dashed thick lines represent missing bone, dashed thin line represents a probable suture and dotted lines indicate occlusal pits. Scale bars: A–D = 50 mm; E, F = 10 mm.

(UFRPE 5142), which has an amphicoelous centrum (Figures 3G–J). Considering the absence of a hypapophysis in UFRPE 5142, it is not possible to define the position of the vertebra, although we here tentatively suggest that this piece constitutes a posterior dorsal vertebra probably located between the sixth and fifteenth positions (Jouve *et al.*, 2006), or between the eighth and thirteenth positions (Hastings *et al.*, 2011). In ventral view the width of the central constriction is 31.12 mm (Figure 3J), similar to the value described for a vertebra UF/IGM 37 of *Acherontisuchus guajiraensis*, 32 mm (Hastings *et al.*, 2011). The centrum height is 48.1 mm, which is 88 per cent of the centrum length (54.7 mm). In *Acherontisuchus guajiraensis*, the centrum height corresponds to 71 per cent of the centrum length.

Femur. CAV 0010-V is the proximal end of a right femur (Figure 3K), which expands medially and has a preserved proximodistal length of 58.8 mm. It is laterally compressed with a cranial rounded articular surface forming a joint for the acetabulum. The fourth trochanter is located on the craniomedial surface.

Tibiae. UFRPE 2814 is a proximal epiphysis of a right tibia (Figures 3L–M) with a diameter that is approximately 58.5 mm. It is bulky and its extremities present a lateral expansion and arched shape, similar to the hyposaurine tibia of CNRST-SUNY 286 (Hill *et al.*, 2015). At the caudolateral edge, there is a protuberance above the articular surface with the fibula, which has been observed in *Congosaurus bequaerti* (MRAC 1815 and MRAC 1816) (Jouve & Schwarz, 2004; Schwarz *et al.*, 2006). In lateral view, UFRPE 2814 shows the cnemial crest and a longitudinal depression, probably for insertion of the extensor tendon (Figure 3M). There are slightly longitudinal striations and grooves in the proximal portion. In anterior view, there is a longitudinal depression formed mainly by the articular surface of the epiphysis. There are two tibial distal epiphyses, one corresponding to the left (CAV 0011-V) and the other to the right side (CAV 0012-V) (Figures 3N–O). In the anterior view, they are convex, with the lateral and medial portions projected posteriorly to form the medial and lateral condyles. The condyles are separated by a longitudinal anterior depression, which forms the articular surface for the astragalus.

DISCUSSION

The record of South American dyrosaurids consists of five species found in Brazil and Colombia. The new material can be attributed to a derived dyrosaurid according to the longirostrine jaw; homodont dentition with tooth crowns posteriorly curved and reduced seventh alveolus on the mandible. The specimen CAV 0056-V has seven pre-splenial dentary alveoli and according to Young *et al.* (2016) in hyposaurine dyrosaurids this feature varies from nine to fourteen pre-splenial alveoli.

Dyrosaurid taxonomy is extremely dependent on cranial and mandibular features (Halstead, 1975; Jouve, 2005; Jouve *et al.*, 2005b; Jouve, 2007; Hastings *et al.*, 2010, 2011, 2015; Young *et al.*, 2016). Although the comparative material is limited, the present study assigned these fossils to *Guarinisuchus* cf. *G. munizi* based on characters of the most well-preserved specimen: the mandible and its dentition. Moreover, the remaining cranial material is very fragmentary and does not preserve most of the diagnostic features. Although there are not enough characters to accomplish a stronger comparison between the holotype and the new specimens, it seems reasonable that the new Maria Farinha Formation findings be ascribed to *G. munizi* until more fossils become available for the species.

As observed by Jouve & Schwarz (2004) and Jouve *et al.* (2006), mandibular features vary according to the size and age of the individual. Furthermore, mandibles are often susceptible to intraspecific variability (Jouve, 2007), and it is difficult to use them as diagnostic characters. The symphysis in CAV 0056-V ends at approximately the d11–d12 alveoli and the dentary of the holotype of *G. munizi* ends approximately at the level of the d14 alveolus. We suggest that this difference could be due to individual or ontogenetic variation.

After the description of the *Guarinisuchus munizi* holotype, no additional material has been formally assigned to this species. The specimens described here were found associated, coming from the same stratigraphic level of the quarry where the *G. munizi* holotype was found.

The preservation of the anterior portion of the mandible, CAV 0056-V, which is not preserved in the *G. munizi* holotype, allows for the identification of three foramina on the medial dentary margins. The present record may widen the morphological variation of *G. munizi* or contribute to a potential new taxon based on more complete specimens.

Data on the width/height ratio of the mandible were plotted for CAV 0056-V and different specimens of *Hyposaurus*, *Congosaurus*, *Rhabdognathus*, *Atlantosuchus* and *Guarinisuchus* (Figure 5). CAV 0056-V, *G. munizi* holotype and other specimens related to *G. munizi* have the highest mandibles. On the other hand, the mandibles of *Hyposaurus* specimens are the widest among Dyrosauridae (Salih *et al.*, 2015). The similar width/height ratio values of CAV 0056-V and *Guarinisuchus* fossils distinguished these specimens from other dyrosaurids, which corroborate to include the new material as *Guarinisuchus*.

The reduction of the seventh mandibular alveolus and its close placement to the eighth alveolus represents a dyrosaurid

apomorphy described for dyrosaurid remains found in Maastrichtian deposits of India (Khosla *et al.*, 2009). Salih *et al.* (2015) described this feature in a specimen attributed to *Hyposaurus* from ?Campanian–Maastrichtian deposits of Sudan. In North America, Denton *et al.* (1997) mentioned this feature for *Hyposaurus rogersii* found in Danian deposits (Wiest *et al.*, 2016). In the Paleocene of Colombia, Hastings *et al.* (2010) recorded it for *Cerrejonisuchus improcerus*, and in the Eocene of Morocco Jouve *et al.* (2006) recognized it in *Dyrosaurus maghribensis*.

The long-snouted condition observed in CAV 0056-V is a characteristic of most derived dyrosaurids like *Guarinisuchus munizi*, which was probably an active hunter of small prey. This is likely due to adaptations of *G. munizi* and similar dyrosaurids to a semi-aquatic life and fast swimming (Andrade & Sayão, 2014), and the development of the specialized feeding apparatus of longirostrine dyrosaurids. The tubular rostrum would have created less resistance in water when catching prey. However, this type of rostrum shape is fragile, which restricts potential prey size (Schwarz-Wings, 2014). Long snouts are an advantage to many crocodiles due to the reduction in hydrodynamic drag for swimming and prey capture (Walmsley *et al.*, 2013). The homodont dentition with acute apices also represents an advantage for catching small prey (Schwarz-Wings, 2014). Some authors proposed that a longirostrine rostrum indicates a piscivorous behavior (Jouve *et al.*, 2006; Hastings *et al.*, 2011), although there is no direct evidence of this relation for dyrosaurids (Schwarz-Wings, 2014). Considering that there is no precise stratigraphic location for *Hyposaurus derbianus*, the new findings constitute a significant contribution to the Brazilian dyrosaurids, representing the third occurrence in the country. They seem to have been restricted to the Paleocene of Northeast Brazil, and to shallow marine environments. Based on the rostrum morphotypes of Dyrosauridae in South America (Barbosa *et al.*, 2008; Hastings *et al.*, 2010, 2011, 2015), it is possible to conjecture that these animals may have had different feeding behavior and diet, which implies that the group adapted to occupy different niches in Paleocene freshwater and marine environments.

CONCLUSION

The new material of crocodyliforms from the Danian Maria Farinha Formation in Northeast Brazil is described for the right postorbital and jugal, mandible, isolated teeth, an isolated osteoderm, dorsal vertebra, femur and tibiae.

In the mandible, the seventh alveoli are reduced and close to the eighth alveoli, an important apomorphy of dyrosaurids (Buffetaut, 1976; Jouve *et al.*, 2006). Also, the amount of pre-splenial alveoli is in accordance with that of other described mandibles of hyposaurine dyrosaurids. Based on morphological analysis of the new specimens, we assign these to *Guarinisuchus* cf. *G. munizi*, whose holotype was found in the same locality and strata where the new material was collected.

Figure 5. Scatter plot showing width/height ratios along the mandible of *Hyposaurus*, *Congosaurus*, *Rhabdognathus*, *Atlantosuchus* and *Guarinisuchus* specimens. Measures taken between the alveoli, according to its position on the mandible. Data for all taxa except CAV 0056-V and other *Guarinisuchus munizi* specimens are from the study by Jouve (2007).

The new mandibular material, CAV0056-V, preserves the anterior portion which is absent in the *Guarinisuchus munizi* holotype, and it allowed the identification of the presence of three neurovascular foramina near the medial margin of the third dentary alveoli. Preservation of the mandible, CAV 0056-V, verified that the symphyseal length ends at approximately the d11 to d12 alveoli. The dentary of the *G. munizi* holotype ends approximately at the d14 alveolus. We suggest that this variation may be due to individual or ontogenetic variation. However, more contributions based on new materials will be essential to support this assessment. In conclusion, according to the characters described to date, the dyrosaurids from the Danian Maria Farinha Formation were longirostrine forms and probably active hunters of small preys that inhabited the marine environment.

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