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Redescription of *Cearadactylus atrox* (Pterosauria, Pterodactyloidea) from the Early Cretaceous Romualdo Formation (Santana Group) of the Araripe Basin, Brazil

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REDESCRIPTION OF *CEARADACTYLUS ATROX* (PTEROSAURIA, PTERODACTYLOIDEA) FROM THE EARLY CRETACEOUS ROMUALDO FORMATION (SANTANA GROUP) OF THE ARARIPE BASIN, BRAZIL

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ABSTRACT—Based on one of the first cranial pterosaur specimens unearthed from the Romualdo Formation (Araripe Basin), *Cearadactylus atrox* has caused disagreement among paleontologists regarding its relationships. Ranging from an ornithocheirid, an indetermined pterodactyloid, to a ctenochasmatid, some authors even regarded this species as representing a distinct suprageneric clade. Further preparation of the holotype that was transferred to the collections of the Museu Nacional/UFRJ (MN 7019-V) revealed several new features allowing a redescription and reevaluation of the phylogenetic position of this species. Among the new observations, it is clear that the rostral end of this specimen had been glued to the skull, rendering previous anatomical interpretations incorrect. There is no rostral gap, and the expanded rostral end of the premaxillae is larger than the dentary, rather than smaller. *Cearadactylus atrox* is here considered a valid taxon that can be diagnosed by a dentary groove that bifurcates at the rostral end, orbit and naris in a high position relative to the nasoantorbital fenestra, and a comparatively small number of teeth (32–36 maxillary, 22–26 mandibular), decreasing in size towards the posterior end. Phylogenetically, it is placed as the sister group of the Anhangueridae, forming a large clade of Brazilian forms (*Tropeognathus* and *Anhanguera*), which has a European taxon (*Ornithocheirus compressirostris*) as its sister group.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

During the past 40 years the Araripe Basin has yielded some of the best-preserved pterosaur material found so far (e.g., Kellner, 2006). These specimens were unearthed from the Romualdo Formation, which is regarded as Aptian/Albian in age (Pons et al., 1990). Many of the formally described taxa from this deposit have been included in phylogenetic analyses (e.g., Kellner, 2003), aerodynamic and biomechanical studies (Costa et al., 2010; Palmer and Dyke, 2012), ecological studies (Martill, 2007; Vila Nova et al., 2011; Sayão et al., 2012), and morphometric analyses (Vila Nova and Sayão, 2012). Some even revealed the presence of exceptionally well-preserved soft tissue (Martill and Unwin, 1989; Kellner, 1996).

One of the first species described from this basin was *Cearadactylus atrox*, which is based on an almost complete skull (lacking the occipital region and the braincase) and an occluded lower jaw. First mentioned in an abstract by Leonardi and Borgomanero (1983), the species was formally described 2 years later (Leonardi and Borgomanero, 1985).

Since its description, the systematic position of *C. atrox* has been disputed. First, Leonardi and Borgomanero (1983)

referred this taxon to the Ornithocheiridae, but later regarded it as a pterodactyloid of unknown affinities (Leonardi and Borgomanero, 1985). In a popular review of the Pterosauria, Wellnhofer (1991) erected the family Cearadactylidae, comprising only *Cearadactylus atrox*. Reviewing part of the pterosaur fauna of the Araripe Basin, Kellner and Tomida (2000) considered this species a member of the Pteranodontoidea, closely related to the anhanguerid clade. More recently Unwin (2002) referred *Cearadactylus atrox* to the Ctenochasmatidae and questioned the allocation of *Cearadactylus? ligabuei*, described by Dalla Vecchia (1993), to that genus, stating that *Cearadactylus* should be limited to the type species (i.e., *Cearadactylus atrox*).

Initially part of the Borgomanero collection (F-PV-93; Leonardi and Borgomanero, 1985), this material was kindly donated by Ragnhild Borgomanero to the Museu Nacional/UFRJ (Rio de Janeiro, Brazil; MN 7019-V), after her husband, Dr. Guido Borgomanero, passed away.

In 2009, this specimen was fully prepared by one of the authors (B.C.V.-N.), and it became clear that the rostral end had been broken and glued back in an inverted position. Furthermore, this detailed preparation showed that several anatomical features were incorrectly described. Here we provide a detailed redescription of the holotype and only known material of *C. atrox*, and discuss its phylogenetic position within the Pterodactyloidea, testing previous hypotheses.

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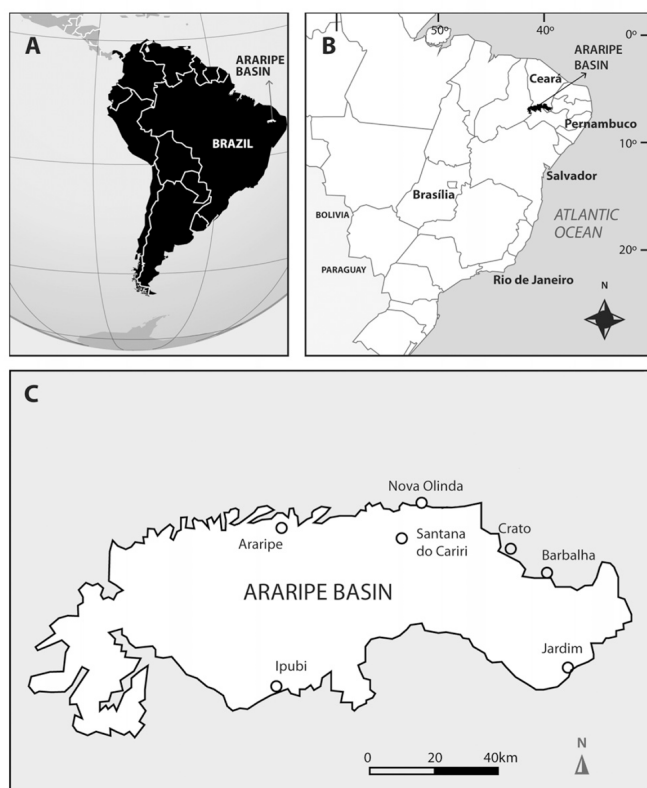


FIGURE 1. Location map of the Araripe Basin and main cities. There is no further information regarding the provenance of the specimen (after Sayão et al., 2011).

GEOLOGIC SETTING

The origin of the Araripe Basin is related to the separation of the South American and African continents, and the opening of the South Atlantic Ocean (Neumann and Cabrera, 1999). The stratigraphic arrangement of the deposits in the basin has been a subject of controversy, with many different (and sometimes conflicting) proposals (Martill, 2007). Here we follow Valença et al. (2003), who elevated the former Santana Formation to a group and its three members, from the older to the younger, the Crato, Ipuebi, and Romualdo members, to formation status.

The Romualdo Formation (Fig. 1) is composed of overlapping layers of shales, marls, and limestones (Assine, 2007), and has an extensive history of fossil discoveries (e.g., Maisey, 1991). Among the most interesting vertebrates are pterosaurs and fishes, whereas other tetrapods are less common (e.g., Bittencourt and Langer, 2011, 2012). The majority of fossils are found in carbonate concretions (Fara et al., 2005), which are responsible for the exquisite preservation (e.g., Saraiva et al., 2007), contrary to most other occurrences, where specimens are either very fragmentary or flattened (e.g., Wellnhofer, 1991; O'Connor et al., 2011).

SYSTEMATIC PALEONTOLOGY

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

PTERANODONTOIDEA sensu Kellner, 2003

CEARADACTYLUS ATROX Leonardi and Borgomanero, 1985
(Figs. 3–6)

Emended Diagnosis—Large pteranodontoid pterosaur with the following autapomorphies: dentary groove reaching the rostral tip of the bone, with a bifurcated end; posterior and ventral limits of the nasoantorbital fenestra forming a right angle. It can be further distinguished from other pteranodontoids by the following combination of characters: orbit and naris above the middle of the nasoantorbital fenestra; comparatively small number of teeth (16–18 maxillary, 11–13 mandibular on each side); teeth decreasing in size towards the posterior end.

Description—The holotype of *C. atrox* (MN 7019-V) is an almost complete skull, lacking the occipital region and braincase. It is anteroposteriorly elongated, with a preserved length of 515 mm (Fig. 2). Although preserved three-dimensionally, the specimen shows some lateral distortion, with a few cranial elements displaced from their original anatomical position, including the right quadrate, which is below the dorsal margin of the nasoantorbital fenestra. The bone surface of the right side is not well preserved and shows signs of erosion due to weathering prior to collection. The lower jaw was isolated from the skull, allowing observation of the palate (Fig. 3). There are two fractures, one in the rostrum and another in the occipital region. These were restored using a resin paste (prior to being deposited in the museum's collection), which was also used in the reconstruction of the rostral teeth, increasing their sizes and creating an artificial appearance that did not match the original anatomy of the skull. A small fragment of the rostral portion contact with the rest of the skull is missing. During preparation, it became clear that the rostral portion was glued back to the remaining part of the skull inverted, with the



FIGURE 2. *Cearadactylus atrox* holotype (MN 7019-V) before final preparation, as described by Leonardi and Borgomanero (1985). Scale bar equals 100 mm.

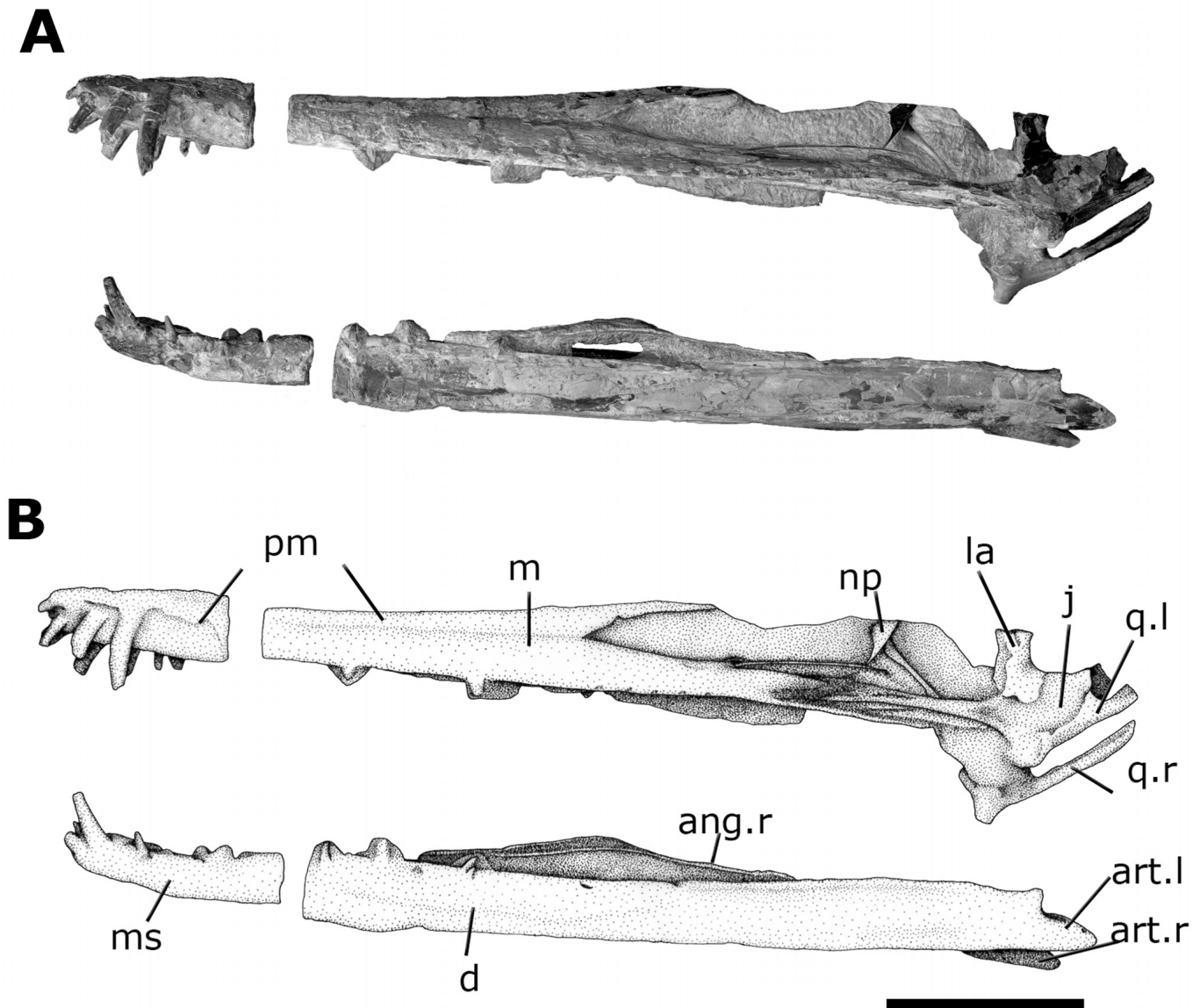


FIGURE 3. **A**, holotype of *Cearadactylus atrox* (MN 7019-V) after preparation in left lateral view. The rostral portion was broken, and is shown in the correct position; **B**, sketch of *Cearadactylus atrox*, showing the preserved bones. **Abbreviations:** **ang.r**, angular (right); **art.l**, articular (left); **art.r**, articular (right); **d**, dentary; **j**, jugal; **la**, lacrima; **m**, maxilla; **ms**, mandibular symphysis; **np**, nasal process; **pm**, premaxilla; **q.l**, quadrate (left); **q.r**, quadrate (right). Scale bar equals 100 mm.

lower jaw attached to the maxilla and the premaxillae-maxillae connected with the dentary. The dentary groove, which starts anterior to the rostral fracture, reaches the tip of the lower jaw. The palatal ridge also starts anterior to the fracture ending at the rostral tip of what was thought to be the dentary, confirming this inversion. This artificial appearance misled authors regarding the anatomy of this species.

As typical for the Pterodactyloidea, the nasoantorbital opening occupies a considerable portion of the skull, reaching around 38% of the preserved length, being estimated to occupy about one-third of the length between the squamosal and the rostral tip of the premaxilla. It reaches the 13th alveolus, and forms an almost straight angle with the posterioventral corner of the jugal, differing from the obtuse angle seen in *Anhanguera* and '*Or-*

nithocheirus' *compressirostris* (Kellner and Tomida, 2000; Andres and Ji, 2008).

The premaxilla is the main bone in the upper rostral portion, and reaches the dorsorostral margin of the nasoantorbital fenestra. However, its caudal end is not preserved, being at least 330 mm long. In left lateral view, the contact between the premaxilla and maxilla is delimited by a shallow groove. The remnant of a small sagittal crest is seen in the dorsal surface of the premaxilla, extending from the rostral tip to at least the 5th premaxillary alveolus (Fig. 4), indicating that *Cearadactylus* had such a cranial structure, contrary to previous descriptions (Leonardi and Borgomanero, 1985; Wellnhofer, 1991; Dalla Vecchia, 1993; Kellner and Tomida, 2000; Fastnacht, 2001; Unwin, 2002; Veldmeijer, 2003).

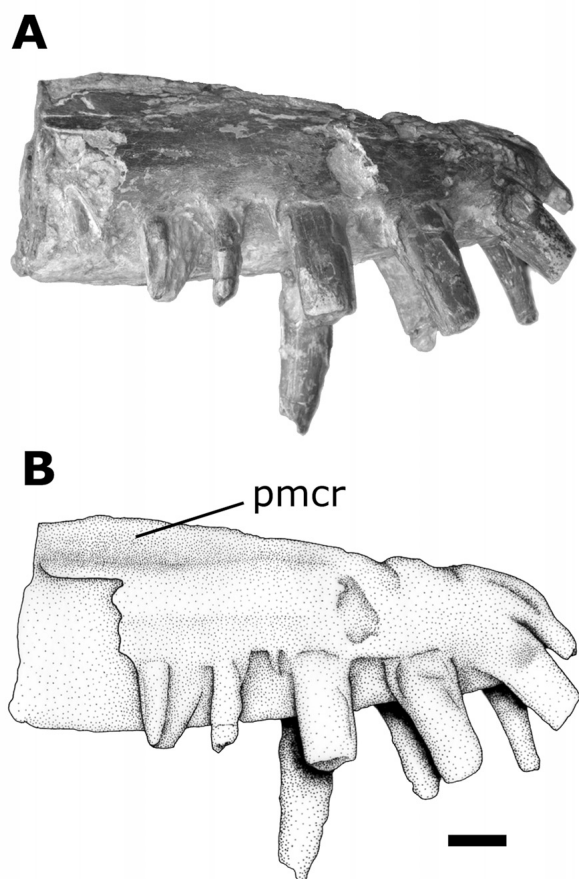


FIGURE 4. **A**, rostral portion of the *Cearadactylus atrox* premaxilla in right lateral view; **B**, sketch of the rostral portion, where the basis of the premaxillary sagittal crest is indicated. **Abbreviation:** pmcr, premaxillary crest. Scale bar equals 10 mm.

In ventral view, the premaxilla shows an elevation (palatal ridge) starting at the rostral fracture, which continues caudally until the middle portion of the palate (Fig. 5), similar to other anhanguerids (Wellnhofer, 1987; Kellner and Tomida, 2000). It is smoother than the one present in *Tropeognathus mesembrinus*, and disappears near the nasoantorbital fenestra.

The maxilla represents most of the ventral surface of the skull, a common feature within pterodactyloids. The right one is incomplete, with only a fragment preserved close to the nasoantorbital fenestra. The alveoli are not well preserved, and it is difficult to confirm their exact number, but around 16 alveoli are identified on the left side (only two with teeth). They extend until the midlength of the nasoantorbital fenestra.

All bones related to the braincase and upper part of the nasoantorbital fenestra are lacking, except for the process of the nasal, which is displaced inside this fenestra. This process is essentially a thin, well-developed bone blade that almost reaches the ventral surface of the skull, different from the reduced structure seen in the Tapejaridae and Azhdarchidae, but similar to that in the Anhangueridae (Kellner and Langston, 1996; Kellner and Tomida, 2000; Kellner, 2004). At least in the preserved portion, it lacks foramina, contrary to the condition observed in *Anhanguera piscator* and *A. santanae* (Kellner and Tomida, 2000).

Although incomplete, the jugal forms the lower margins of the orbit and the lower temporal fenestra. Its suture with the quadrate

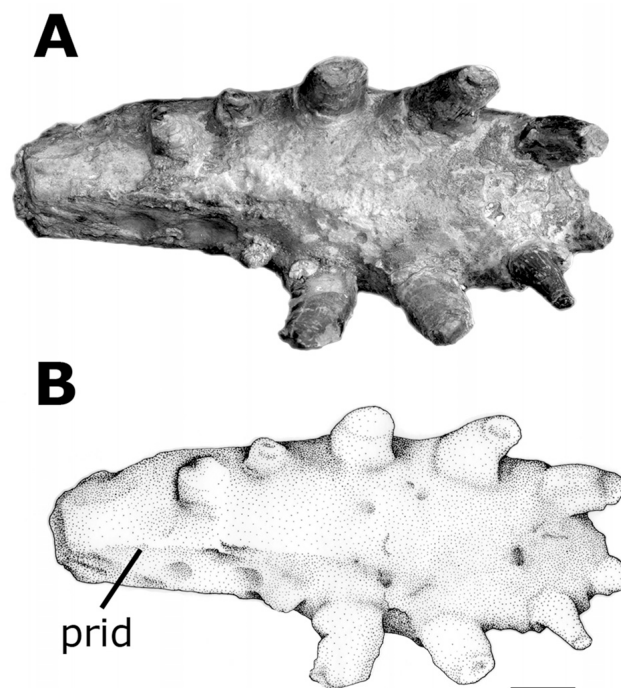


FIGURE 5. **A**, rostral portion of the *Cearadactylus atrox* premaxilla in ventral view; **B**, sketch of the same, with palatal ridge indicated. **Abbreviation:** prid, palatal ridge. Scale bar equals 10 mm.

tojugal is not discernible, and together with the quadrate, these bones form a single fused structure. The rostral ramus of the jugal narrows rostrally and ends as a thin bone plate.

As pointed out before, the right quadrate was displaced underneath the left. Its posterior region connects with a long and thin prolongation of the bone, forming the helicoidal structure seen in many pterodactyloids (e.g., Campos and Kellner, 1985; Bennett, 2001).

The lower jaw is almost complete. The right side has most of the external surface badly preserved. Some jaw elements are displaced, and the surangulars cannot be observed. Most ornithocheiroids with a premaxillary sagittal crest also show a dentary crest, as seen in *Anhanguera* and *Tropeognathus*; on the contrary, *C. atrox* does not possess any trace of a dentary sagittal crest, being in this respect similar to *Brasileodactylus* (Kellner, 1984; Sayão and Kellner, 2000). The dentaries are nearly complete and slightly compressed, forming most of the jaw. They are fused into a large symphysis, which is 110 mm long, occupying about 20% of the total jaw length. This condition is similar to *Tropeognathus*, but smaller than in *Anhanguera* (Wellnhofer, 1987; Kellner and Tomida, 2000). A medial groove is present and reaches the distal extremity of the dentaries, as observed in *Brasileodactylus* (Kellner, 1984; Sayão and Kellner, 2000; Veldmeijer et al., 2005). In *C. atrox*, however, this groove does bifurcate at the rostral tip, differing from that in *Brasileodactylus araripensis* (Fig. 6).

The symphysis bears six alveoli on each side, with teeth in the 1st, 3rd, and 5th alveoli of the left side. Five more alveoli are present anterior to the anterior margin of the left nasoantorbital fenestra, totaling 11 teeth on each side of the lower jaw. The angulars are thin bones, not fused to the dentaries, and are displaced from their original positions. Due to the taphonomy, they are positioned between the lower jaw and the maxilla, and the right

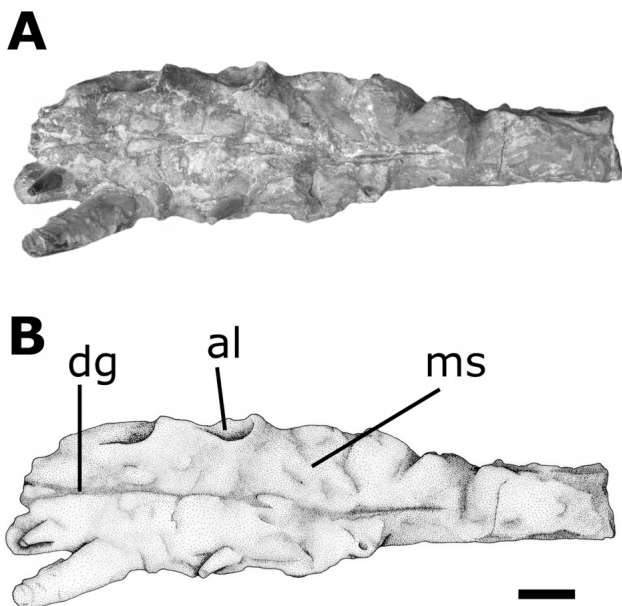


FIGURE 6. **A**, *Cearadactylus atrox* rostral portion of the dentary in dorsal view; **B**, sketch showing the bifurcated end of the groove. **Abbreviations:** al, alveolus; dg, dental groove; ms, mandibular symphysis. Scale bar equals 30 mm.

angular is partially displaced to lie inside the nasoantorbital fenestra.

The left articular is firmly connected to the dentary, but the suture between them is still evident. The right articular is displaced medially, with the rostral tip absent. Due to the position and thickness of this bone, it is possible to assume that it reached beyond the regions corresponding to the nasoantorbital fenestra. Rostrally, the articular extends as a long and thin element until at least the 10th dentary alveolus.

The rostral teeth are elongated, thin, and slightly curved posteriorly, and directed somewhat forward and outward. Starting from the 6th tooth, the teeth become smaller, more vertical, and straighter, so that they are less curved toward the posterior region. Many alveoli are damaged, and only three dentary and seven premaxillary alveoli bear teeth. We identified 16 maxillary alveoli in the left side and 11 in the dentary. The portion lost from

the rostral fracture could bear one or at most two pairs of alveoli, so we state the dental formula of *C. atrox* as 16–18 maxillary teeth per side and 11–13 in each dentary.

In both the maxilla and dentary, the first four pairs of teeth are larger than the others, but they are smaller than previously thought (Leonardi and Borgomanero, 1985; Unwin, 2002). The 3rd tooth measures 35 mm in height, whereas from the 6th alveolus to the posterior end the teeth reach around 10 mm. The left upper 8th and 16th alveoli, as well as the left lower 5th and 11th show replacement teeth. The dentition gradually decreases in size posteriorly. This differs from the condition in *Anhanguera*, in which the 5th and 6th teeth are smaller than the 4th and 7th (Wellnhofer, 1977, 1985, 1991; Wellnhofer et al., 1983; Kellner, 1984, 2003; Kellner and Tomida, 2000).

PHYLOGENETIC ANALYSIS

In order to establish the phylogenetic position of *C. atrox* (MN 7019-V), we used three different published matrices (Andres and Ji, 2008; Wang et al., 2009; Lü et al., 2010; see Supplementary Data for characters scores). All matrices were analyzed using the same parameters as used by the original authors, with heuristic searches implemented in the programs PAUP* 4.0b10 (Swofford, 2003) and TNT version 1.0 (Goloboff et al., 2008). Resampling was conducted with bootstraps and jackknifing, with 1000 replicates for each data set, and Bremer index support was calculated for each consensus tree.

The analysis using the data set of Andres and Ji (2008) resulted in 334 most parsimonious trees (MPTs). The heuristic search placed *C. atrox* in a polytomy with the Anhangueridae (sensu Andres and Ji, 2008), a clade consisting of *Tropeognathus mesembrinus*, *Liaoningopterus gui*, *Anhanguera blittersdorffi*, *A. santanae*, and *A. piscator* (Fig. 7), with ‘*Lonchodectes*’ (or ‘*Ornithocheirus*,’ according to which author is followed) *compressirostris* as its sister group. This result was previously recovered by Sayão et al. (2012) and the addition of *C. atrox* did not result in any change to their tree topology. The main characteristics that separate *C. atrox* from the Anhangueridae are as follows: lack of a dentary sagittal crest (character 45) and the posteroventral limit of the nasoantorbital fenestra forming a right angle (character 8; differing from the more rounded and concave condition in Anhangueridae).

The majority consensus tree published by Lü et al. (2010) recovered *Cearadactylus* as a member of the Ctenochasmatidae, probably as a result of incorporating the previous anatomical interpretations (and scoring) of Unwin (2002). By rescoring *C. atrox* in this data set, we recovered a different result. The search conducted with TNT found 392 MPTs (Fig. 8). The majority consensus tree of this analysis placed *C. atrox* within Ornithocheiri-

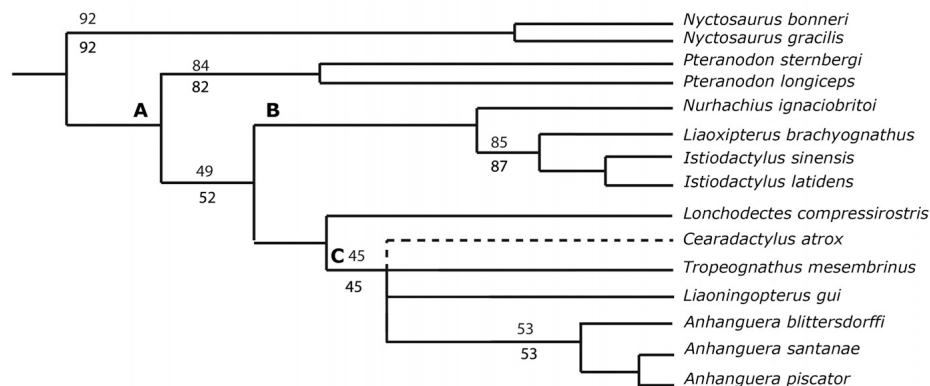


FIGURE 7. Detail of the strict consensus tree of 334 MPTs showing the position of *C. atrox* using the Andres and Ji (2008) data set and clade names. **A**, Pteranodontoidea; **B**, Istiodactylidae; **C**, Anhangueridae. Upper values are bootstraps and lower figures are jackknife values. Consistency index = 0.486 and retention index = 0.808 for the consensus tree.

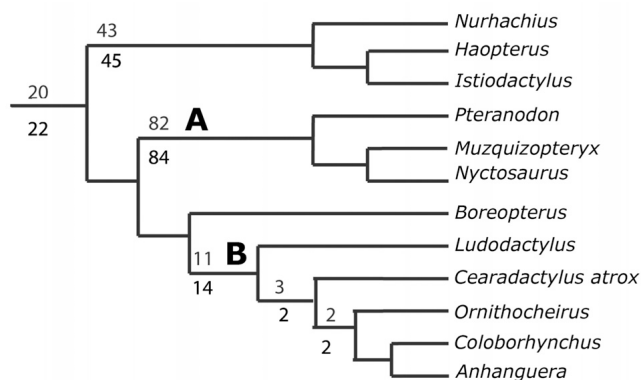


FIGURE 8. Detail of the majority consensus tree of 392 MPTs showing the position of *C. atrox* using the modified Lü et al. (2010) data set. **A**, Istiodactylidae; **B**, Ornithocheiridae. Upper values are bootstraps and lower are figures are jackknife values. Consistency index = 0.434 and retention index = 0.798 for the consensus tree.

dae as the sister group of *Ornithocheirus* (considered by Lü et al. [2010] as including *Tropeognathus*, but see Rodrigues and Kellner [2008]) + *Coloborhynchus* + *Anhanguera*. This result is mainly based on characters related to the nasoantorbital fenestra and dentition. In *Cearadactylus atrox*, the dorsal margin of the nasoantorbital opening is delimited by a thin bone bar, whereas in *Ornithocheirus*, *Coloborhynchus*, and *Anhanguera* this structure is absent (character 8). *Cearadactylus atrox* differs from *Ludodactylus*, *Coloborhynchus*, and *Anhanguera* in having a straight ventral margin of the skull (character 11). Furthermore, the posterior margin of the nasoantorbital fenestra in *C. atrox* forms a right angle, whereas in *Coloborhynchus* and *Anhanguera* it is concave (character 22). *C. atrox* also lacks a dentary sagittal crest (character 46).

The dentition also shows a distinct pattern in these closely related species. *C. atrox* has a dimorphodont pattern (character 48), with the preserved rostral teeth about three times the size of the maxillary ones. This rostral dentition is formed by less than 11 pairs of alveoli (character 51) and the maxillary teeth are small, spaced (character 49), and laterally compressed, with a slight triangular shape (character 62). Such a combination of character states is unique to *C. atrox*.

The position of *C. atrox* within the Ornithocheiridae as the sister taxon to (*Ornithocheirus* + (*Coloborhynchus* + *Anhanguera*)) has very low support, with bootstrap values of only 3%. The inclusion of an intermediate taxon should not highly influence this index, as has also been noted in other studies (e.g., Penny et al., 1992; Kearney and Clark, 2003; Strauss and Atanassov, 2006), indicating that this result should be viewed with caution. The clade Ornithocheiridae is weakly supported (11% bootstrap and 14% jackknife values) with *Ludodactylus* as the basal taxon. *Cearadactylus*, however, changes position with other species in many trees. Despite that, it always falls close to Anhangueridae. This result contradicts the study of Unwin (2002), in which *C. atrox* was regarded as the sister taxon of the clade composed by *Gnathosaurus* + *Pterodactylus longicollum* (Fig. 9).

Wang et al. (2009) provided the smallest data set of the three phylogenetic proposals addressed here, being an expanded and updated version of Kellner's (2003) matrix. Despite the comparatively small number of characters, the topology of the consensus tree shows high support values, with some branches having bootstrap and jackknife values above 80%. This consensus tree is very

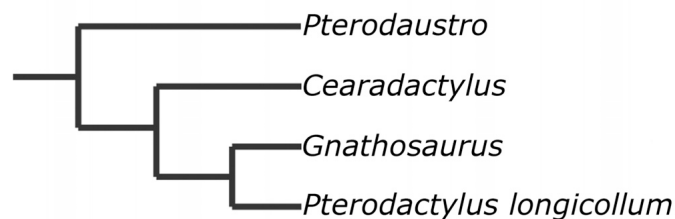


FIGURE 9. The putative phylogenetic position of *Cearadactylus atrox* based on the Lü et al. (2010) data set, according to Unwin (2002). These relationships are changed here, due to new character data available from the more fully prepared holotype.

similar to the one obtained from the data set of Andres and Ji (2008). *Cearadactylus* falls out as the sister group of Anhangueridae (sensu Kellner, 2003), with '*Ornithocheirus compressirostris*' as the sister taxon to them (*C. atrox* + Anhangueridae; Fig. 10). The support values of these branches are similar, being generally low (15% bootstrap and 17% jackknife values).

'Ornithocheirus compressirostris' differs from *C. atrox* by lacking a premaxillary sagittal crest (character 15) and finely serrated teeth (character 48). *Anhanguera piscator* and *A. santanae* show a foramen in the nasal process (character 21), which is absent in *C. atrox*. The lacrimal process of the jugal (character 23) in *C. atrox* is subvertical, differing from that in closely related taxa. The palatal ridge (character 34) of *C. atrox* is not as strong as in *Tropeognathus mesembrinus*, being similar to that of *Anhanguera*. The absence of a dentary sagittal crest (character 41) separates *C. atrox* from all known anhanguerids.

DISCUSSION

The high pterosaur diversity recorded from the Araripe Basin is well known (e.g., Kellner and Tomida, 2000; Barrett et al., 2008) and the possibility that it is overestimated has been noted several times (e.g., Campos and Kellner, 1985; Martill and Naish, 2006; Unwin and Martill, 2007). Some have made a potential parallel with the initial stages of pterosaur studies based on material from the Cambridge Greensand and the Solnhofen Basin, where the great number of specimens fueled the establishment of many taxa (Bennett, 1995, 1996; Unwin, 2001). Taxonomic reviews of the specimens from these European deposits led several authors to propose a reduction in the number of species present (Bennett, 1996; Unwin, 2001). Indeed, Araripe pterosaurs were first named based on very fragmentary or incomplete specimens, potentially creating a similar scenario (Price, 1971; Wellhofer, 1977; Kellner, 1984; Witton, 2009). Taking this into account, the holotype and only known specimen of *C. atrox* was compared with other toothed pteranodontoids.

Regarding ontogeny, some sutures are not visible but the presence of unfused elements such as the right articular and both angulars suggest that the holotype of *C. atrox* represents a subadult individual (Bennett, 1993; Kellner and Tomida, 2000; Ösi and Prondvai, 2009).

The posterior limit of the nasoantorbital fenestra, forming a straight angle with the ventral border (as already observed in the original description; Leonardi and Borgomanero, 1985) distinguishes *C. atrox* from all other species. The premaxillary teeth, however, are very different from how they were previously interpreted, due to removal of the epoxy resin that was used to enhance the fossil. Although we cannot establish the actual length of the largest tooth, it is unlikely to have been 48 mm long as proposed by Leonardi and Borgomanero (1985) and as subsequently followed by later studies (e.g., Unwin, 2002; Steel et al., 2005).

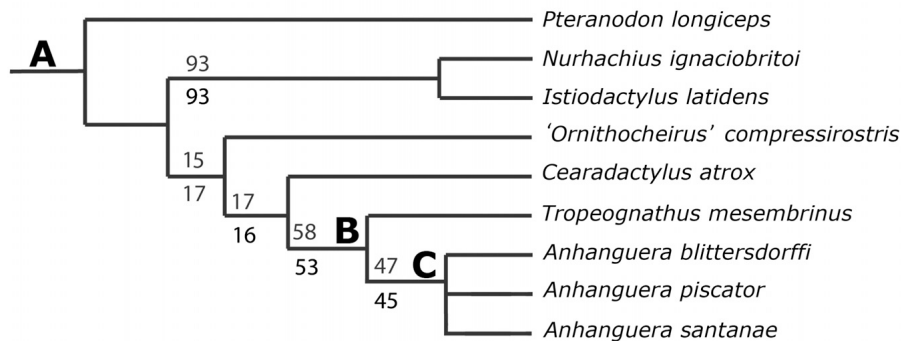


FIGURE 10. Detail of the strict consensus tree of 240 MPTs showing the position of *C. atrox* based on the modified Wang et al. (2009) data set and clade names. **A**, Pteranodontoidea; **B**, Anhangueridae; **C**, *Anhanguera*. Upper values are bootstraps and the lower figures are jackknife values. Consistency index = 0.678 and retention index = 0.880 for the consensus tree.

Recently, Unwin (2002) reinterpreted several features of *C. atrox*, placing this species in the Ctenochasmatidae, a conclusion followed by other authors (e.g., Steel et al., 2005; Lü et al., 2010; Vidarte and Calvo, 2010). However, as noted above, the mandibular symphysis of *C. atrox* was glued to the rest of the skull inverted with respect to the premaxilla and, therefore, all characters related to these areas require revision. *C. atrox* does not possess a rostral portion of the mandible that is more expanded than the premaxilla (Kellner and Tomida, 2000; Unwin, 2002), and based on the preserved parts of the jugal, quadratojugal, and quadrate this species lacks a 'high cheek,' as has been proposed for Ctenochasmatidae (Unwin, 2002; Martill et al., 2006; Bennett, 2007; Andres et al., 2010).

The tooth dimorphism is not as conspicuous as proposed by Unwin (2002), with the largest premaxillary tooth (the 3rd) reaching at most three times the size of the smaller maxillary tooth (11th). Unwin (2002) also stated that *C. atrox* has a nonlinear pattern to the dentition, with the 5th tooth smaller than the 6th, 7th, and 8th. This relationship has not been observed by us and, despite the premaxillary teeth being larger than the others, the maxillary teeth diminish in size uniformly towards the posterior end. Although the dentition is similar in size to that of anhanguerids and *Brasileodactylus* (Kellner and Tomida, 2000) the typical *Anhanguera* feature of the 5th and 6th teeth being smaller than the 4th and 7th (Kellner and Tomida, 2000; Kellner, 2003) is not observed in *C. atrox*. This species also has fewer teeth than in all anhanguerids, with the exception of *Tropeognathus mesembrinus* (Wellnhofer, 1987; Kellner and Tomida, 2000).

One of the first jaws found in the Araripe Basin, *Brasileodactylus araripensis* (Kellner, 1984) bears many anatomical characteristics similar to *C. atrox*, indicating a possible systematic affinity. Both possess a groove on the dentary that is visible in ventral view and an expanded mandibular symphysis (Kellner, 1984; Veldmeijer et al., 2005, 2009). Some differences, however, confirm that they are two distinct taxa. Among these is the spacing between the rostral alveoli that in *B. araripensis* exceeds the actual diameter of the alveoli, whereas in *C. atrox* the reverse is true (i.e., interalveolar spacing smaller than the alveoli diameter; Kellner, 1984; Veldmeijer et al., 2009). Furthermore, the dentary in *B. araripensis* is rather flat in its rostral portion, but this is less evident in *C. atrox*. Lastly, the dentary groove reaches the rostral tip of the bone in both taxa, but in *C. atrox* it terminates with a bifurcated end.

Tropeognathus mesembrinus differs from *C. atrox* in having a well-developed dentary sagittal crest, a better-developed and deeper palatal ridge, and a less expanded distal end to the rostrum (Wellnhofer, 1987; Kellner and Tomida, 2000). '*Cearadactylus ligabuei*' is based on an incomplete skull (Dalla Vecchia, 1993) that might comprise a mixture of different specimens. Therefore, *Cearadactylus atrox* is considered to be the only taxon of the

genus, a decision that has been proposed by other authors and that is followed herein (Steel et al., 2005; Veldmeijer et al., 2005; Wang et al., 2009). The main difference between *Anhanguera piscator* and *C. atrox* is the lack of a dentary sagittal crest in the latter. Unfortunately, in *Anhanguera piscator* the jaws are occluded (Kellner and Tomida, 2000) and there is no information regarding the palatal ridge and dentary groove.

A pterosaur described recently from the Romualdo Formation was first published as *Coloborhynchus spielbergi* and later referred to *Anhanguera* (Veldmeijer, 2003; Kellner, 2006; Rodrigues and Kellner, 2008). One of its most notable characteristics is the large premaxillary sagittal crest, which reaches the base of the nasoantorbital fenestra (Veldmeijer, 2003). *Anhanguera spielbergi* possesses a tooth pattern similar to *C. atrox*, both in terms of tooth numbers (at least 36 versus 32–36 in *C. atrox*) and distribution, with the tooth rows reaching a point level with the middle of the nasoantorbital fenestra (Veldmeijer, 2003). Despite these similarities, *Anhanguera spielbergi* differs from *C. atrox* in having a well-developed sagittal crest that reaches the base of the nasoantorbital fenestra, the presence of a dentary sagittal crest, and in the dentary groove not reaching the rostral tip of the jaw.

Regarding the phylogenetic placement of *C. atrox*, reanalysis of all three phylogenetic data sets considered above suggests that this taxon is phylogenetically close to the anhanguerids and other toothed pteranodontoids, although the internal organization of these branches changes depending upon the characters and character scores constituting the original data sets. None of these analyses recovers *C. atrox* as a member of the archaeoptero-dactyloid clade Ctenochasmatidae, contrary to the proposal of Unwin (2002).

CONCLUSIONS

Additional preparation of the unique specimen of *Cearadactylus atrox* demonstrates that the rostrum was glued back to the jaw in an inverted position, leading to several anatomical misinterpretations. Among these is that *C. atrox* possesses a premaxillary sagittal crest and lacks a 'high cheek' (contra Unwin, 2002). Comparison with other toothed pterosaur taxa from the Araripe Basin shows that *Cearadactylus atrox* is a valid taxon. Furthermore, incorporation of these new data into the data sets published by Andres and Ji (2008), Wang et al. (2009), and Lü et al. (2010) indicates that *Cearadactylus atrox* is the sister group of Anhangueridae (sensu Kellner, 2003), and is not a member of the archaeoptero-dactyloid clade Ctenochasmatidae (contra Unwin, 2002).

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LITERATURE CITED

- Andres, B., and Q. Ji. 2008. A new pterosaur from the Liaoning Province of China, the phylogeny of the Pterodactyloidea, and convergence in their cervical vertebrae. *Palaeontology* 51:453–469.
- Andres, B., J. M. Clark, and X. Xing. 2010. A new rhamphorhynchid pterosaur from the Upper Jurassic of Xinjiang, China, and the phylogenetic relationships of basal pterosaurs. *Journal of Vertebrate Paleontology* 30:163–187.
- Assine, M. L. 2007. Bacia do Araripe. *Boletim de Geociências. Petrobras* 15:371–389.
- Barrett, P. M., R. J. Butler, N. P. Edwards, and A. R. Milner. 2008. Pterosaur distribution in time and space: an atlas. *Zitteliana B* 28:61–107.
- Bennett, S. C. 1993. The ontogeny of *Pteranodon* and other pterosaurs. *Paleobiology* 19:92–106.
- Bennett, S. C. 1995. A statistical study of *Rhamphorhynchus* from the Solnhofen Limestone of Germany: year-classes of a single large species. *Journal of Paleontology* 69:569–580.
- Bennett, S. C. 1996. Year-classes of pterosaurs from the Solnhofen Limestone of Germany: taxonomic and systematic implications. *Journal of Vertebrate Paleontology* 16:432–444.
- Bennett, S. C. 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. *Palaeontographica, Abteilung A* 260:1–112.
- Bennett, S. C. 2007. A review of the pterosaur *Ctenochasma*: taxonomy and ontogeny. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 245:23–31.
- Bittencourt, J. S., and M. C. Langer. 2011. Mesozoic dinosaurs from Brazil and their biogeographic implications. *Anais da Academia Brasileira de Ciências* 83:23–60.
- Bittencourt, J. S., and M. C. Langer. 2012. Os dinossauros do Mesozoico brasileiro e as relações biogeográficas entre África e América do Sul; pp. 299–321 in V. Gallo, H. M. A. Silva, P. M. Brito, and F. J. Figueiredo (eds.), *Paleontologia de Vertebrados: Relações entre América do Sul e África*. Interciência, Rio de Janeiro.
- Campos, D. A., and A. W. A. Kellner. 1985. Panorama of the flying reptiles study in Brazil and South America. *Anais da Academia Brasileira de Ciências* 57:453–466.
- Costa, F. R., O. Rocha-Barbosa, and A. W. A. Kellner. 2010. Stance biomechanics of *Anhanguera piscator* Kellner and Tomida, 2000 (Pterosauria, Pterodactyloidea) using tridimensional virtual animation. *Acta Geoscientica Sinica* 31:15–16.
- Dalla Vecchia, F. M. 1993. *Cearadactylus? ligabuei*, nov. sp., a new Early Cretaceous (Aptian) pterosaur from Chapada do Araripe (Northeastern Brazil). *Bolletino della Societa Paleontologica Italiana* 32:401–409.
- Fara, E., A. A. F. Saraiva, D. A. Campos, J. K. R. Moreira, D. C. Siebra, and A. W. A. Kellner. 2005. Controlled excavations in the Romualdo Member of the Santana Formation (Early Cretaceous, Araripe Basin, northeastern Brazil): stratigraphic, palaeoenvironmental and palaeoecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 218:145–161.
- Fastnacht, M. 2001. First record of *Coloborhynchus* (Pterosauria) from the Santana Formation (Lower Cretaceous) of the Chapada do Araripe, Brazil. *Paläontologische Zeitschrift* 75:23–36.
- Goloboff, P., A. J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786.
- Kaup, J. 1834. Versuch einer Eintheilung der Säugethiere in 6 Stämme und der Amphibien in 6 Ordnungen. *Isis* 3:311–315.
- Kearney, M., and J. M. Clark. 2003. Problems due to missing data in phylogenetic analyses including fossils: a critical review. *Journal of Vertebrate Paleontology* 23:263–275.
- Kellner, A. W. A. 1984. Ocorrência de uma mandíbula de Pterosauria (*Brasileodactylus araripeensis*, nov. gen.; nov. sp.) na formação Santana, Cretáceo da Chapada do Araripe, Ceará, Brasil; pp. 578–590 in Sociedade Brasileira de Paleontologia (ed.), *Anais do 33 Congresso Brasileiro de Geologia*, Rio de Janeiro, 28 October–4 November 1984. Publicações Avulsas da Sociedade Brasileira de Geologia.
- Kellner, A. W. A. 1996. Fossilized theropod soft tissue. *Nature* 379:32.
- Kellner, A. W. A. 2003. Pterosaur phylogeny and comments on the evolutionary history of the group; pp. 105–137 in E. Buffetaut and J. M. Mazin (eds.), *Evolution and Palaeobiology of Pterosaurs*. Geological Society Special Publications 217.
- Kellner, A. W. A. 2004. New information on the Tapejaridae (Pterosauria, Pterodactyloidea) and discussion of the relationships of this clade. *Ameghiniana* 41:521–534.
- Kellner, A. W. A. 2006. Pterossauros—Os Senhores do Céu do Brasil. Vieira and Lent Press, Rio de Janeiro, 176 pp.
- Kellner, A. W. A., and W. Langston. 1996. Cranial remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from Late Cretaceous sediments of Big Bend National Park, Texas. *Journal of Vertebrate Paleontology* 16:222–231.
- Kellner, A. W. A., and Y. Tomida. 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian–Albian), northeastern Brazil. *National Science Museum Monographs* 17:1–135.
- Leonardi, G., and G. Borgomanero. 1983. *Cearadactylus atrox* nov. gen., nov. sp.; novo Pterosauria (Pterodactyloidea) da Chapada do Araripe, Ceará, Brasil; p. 17 in Ministério de Minas e Energia–DNPM (ed.), *Resumos do 8 Congresso Brasileiro de Paleontologia*, Rio de Janeiro, 1–7 September 1983. Ministério de Minas e Energia–DNPM, Rio de Janeiro, Brazil.
- Leonardi, G., and G. Borgomanero. 1985. *Cearadactylus atrox* nov. gen., nov. sp.: novo Pterosauria (Pterodactyloidea) da Chapada do Araripe, Ceará, Brasil. *Coletânea de Trabalhos Paleontológicos, Série Geologia* 1:78–80.
- Lü, J., D. M. Unwin, X. Jin, Y. Liu, and Q. Ji. 2010. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. *Proceedings of the Royal Society B* 277:383–389.
- Maisey, J. G. (ed.). 1991. *Santana Fossils: An Illustrated Atlas*. T. F. C. Publications, Neptune City, New Jersey, 459 pp.
- Martill, D. M. 2007. The age of the Cretaceous Santana Formation fossil Konservat Lagerstätte of northeast Brazil: a historical review and an appraisal of the biostratigraphic utility of its palaeobiota. *Cretaceous Research* 28:895–920.
- Martill, D. M., and D. Naish. 2006. Cranial crest development in the azhdarchoid pterosaur *Tupuxuara*, with a review of the genus and tapejarid monophyly. *Palaeontology* 49:925–941.
- Martill, D. M., and D. M. Unwin. 1989. Exceptionally well preserved pterosaur wing membrane from the Cretaceous of Brazil. *Nature* 340:138–140.
- Martill, D. M., E. Frey, C. M. Bell, and G. C. Diaz. 2006. Ctenochasmatid pterosaurs from Early Cretaceous deposits in Chile. *Cretaceous Research* 27:603–610.
- Neumann, V. H., and L. Cabrera. 1999. Una Nueva Propuesta Estratigráfica para la tectonosecuencia post-rifte de la Cuenca de araripe, Noreste de Brasil. *Atas do 5 Simpósio sobre o Cretáceo do Brasil e 1 Simpósio sobre el Cretácico de América del Sur*, 28 August–2 September 1999. Universidade Estadual Paulista, Rio Claro, Brazil.
- O'Connor, P. M., J. J. W. Sertich, and F. K. Manthi. 2011. A pterodactyloid pterosaur from the Upper Cretaceous Lapurr sandstone, West Turkana, Kenya. *Anais da Academia Brasileira de Ciências* 83:309–315.
- Ösi, A., and K. E. Prondvai. 2009. Forgotten pterosaurs in Hungarian collections: first description of *Rhamphorhynchus* and *Pterodactylus* specimens. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 252:167–180.
- Palmer, C., and G. Dyke. 2012. Constraints on the wing morphology of pterosaurs. *Proceedings of the Royal Society B* 279:1218–1224.
- Penny, D., M. D. Hendy, and M. A. Steel. 1992. Progress with methods for constructing evolutionary trees. *Trends in Ecology and Evolution* 7:73–79.

- Plieninger, F. 1901. Beitrage zur Kenntniss der Flugsaurier. *Palaeontographica* 48:65–90.
- Pons, D., P. Y. Berthou, and D. A. Campos. 1990. Quelques observations sur la palynologie de l'Aptien supérieur et de l'Albien do bassin d'Araripe (N-E Du Brasil); pp. 142–252 in *Atas do 1º Simposio sobre a Bacia do Araripe e das Bacias interiores do Nordeste, Crato, 14–16 June 1990*. Sociedade Brasileira de Paleontologia, Crato, Brazil.
- Price, L. I. 1971. A presença de Pterosauria no Cretáceo Inferior da Chapada do Araripe, Brasil. *Anais da Academia Brasileira de Ciências* 43:451–461.
- Rodrigues, T., and A. W. A. Kellner. 2008. Review of the pterodactyloid pterosaur *Coloborhynchus*. *Zitteliana B* 28:219–228.
- Saraiva, A. A. F., M. H. Hessel, N. C. Guerra, and E. Fara. 2007. Condições Calcárias da Formação Santana, Bacia do Araripe: uma proposta de classificação. *Estudos Geológicos* 17:40–58.
- Sayão, J. M., and A. W. A. Kellner. 2000. Description of a pterosaur rostrum from the Crato Member, Santana Formation (Aptian–Albian) northeastern, Brazil. *Boletim do Museu Nacional* 54:1–8.
- Sayão, J. M., A. A. F. Saraiva, and A. M. K. Uejima. 2011. New evidence of feathers in the Crato Formation supporting a reappraisal on the presence of Aves. *Anais da Academia Brasileira de Ciências* 83:197–210.
- Sayão, J. M., B. C. Vila Nova, and P. S. Romano. 2012. Considerações sobre os padrões de distribuição geográfica dos Pterodactyloidea (Archosauria, Pterosauria); pp. 281–300 in V. Gallo, H. M. A. Silva, P. M. Brito, and F. J. Figueiredo (eds.), *Paleontologia de Vertebrados: Relações entre América do Sul e África*. Interciência, Rio de Janeiro.
- Steel, L., D. M. Martill, D. M. Unwin, and J. D. Winch. 2005. A new pterodactyloid pterosaur from the Wessex Formation (Lower Cretaceous) of the Isle of Wight, England. *Cretaceous Research* 26:686–699.
- Strauss, R. E., and M. N. Atanassov. 2006. Determining best subsets of specimens and characters in the presence of large amounts of missing data. *Biological Journal of the Linnean Society* 88:309–328.
- Swofford, D. L. 2003. PAUP* 4.0. Sinauer Associates, Sunderland, Massachusetts.
- Unwin, D. M. 2001. An overview of the pterosaur assemblage from the Cambridge Greensand (Cretaceous) of Eastern England. *Mitteilungen Museum für Naturkunde Berlin, Geowissenschaftlichen Reihe* 4:189–222.
- Unwin, D. M. 2002. On the systematic relationships of *Cearadactylus atrox*, an enigmatic Early Cretaceous pterosaur from the Santana Formation of Brazil. *Mitteilungen Museum für Naturkunde Berlin, Geowissenschaftlichen Reihe* 5:239–263.
- Unwin, D. M., and D. M. Martill. 2007. Pterosaurs of the Crato Formation; pp. 475–524 in D. M. Martill, G. Bechly, and R. F. Loveridge (eds.), *The Crato Fossil Beds of Brazil—Window into an Ancient World*. Cambridge University Press, New York.
- Valença, L. M. M., V. H. Neumann, and J. M. Mabeoone. 2003. An overview on Callovian–Cenomanian intracratonic basins of Northeast Brazil: onshore stratigraphic record of the opening of the southern Atlantic. *Geologica Acta* 1:261–276.
- Veldmeijer, A. J. 2003. Description of *Coloborhynchus spielbergi* sp. nov. (Pterodactyloidea) from the Albian (Lower Cretaceous) of Brazil. *Scripta Geologica* 125:35–139.
- Veldmeijer, A. J., H. J. M. Meijer, and M. Signore. 2009. Description of pterosaurian (Pterodactyloidea: Anhangueridae, *Brasileodactylus*) remains from the Lower Cretaceous of Brazil. *Deinsea* 13:9–40.
- Veldmeijer, A. J., M. Signore, and H. J. M. Meijer. 2005. *Brasileodactylus* (Pterosauria, Pterodactyloidea, Anhangueridae); an update. *Cranium* 22:45–56.
- Vidarte, C. F., and M. M. Calvo. 2010. Un nuevo pterosaurio (Pterodactyloidea) en el Cretácico Inferior de La Rioja (España). *Boletín Geológico y Minero* 121:311–328.
- Vila Nova, B. C., and J. M. Sayão. 2012. On wing disparity and morphological variation of the Santana Group pterosaurs. *Historical Biology* 24:567–574.
- Vila Nova, B. C., A. A. F. Saraiva, J. K. R. Moreira, and J. M. Sayão. 2011. Controlled excavations of the Romualdo Formation Lagerstätte (Araripe Basin, Brazil) and pterosaur diversity: remarks due to new findings. *Palaios* 26:173–179.
- Wang, X.-L., A. W. A. Kellner, S. Jiang, and X. Meng. 2009. An unusual long-tailed pterosaur with elongated neck from western Liaoning of China. *Anais da Academia Brasileira de Ciências* 81:793–812.
- Wellnhofer, P. 1977. *Araripedactylus dehmi* Nov. gen., Nov. sp., ein neuer Flugsaurier aus der Unterkreide Von Brasilian]. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 17:157–167.
- Wellnhofer, P. 1985. Neue Pterosaurier aus der Santana Formation (Apt.) der Chapada do Araripe, Brasilien. *Palaeontographica, Abteilung A* 187:105–182.
- Wellnhofer, P. 1987. New crested pterosaurs from the Lower Cretaceous of Brasil. *Mitteilungen der Bayerischen Staatssammlung für Paleontologie und Historische Geologie* 27:175–186.
- Wellnhofer, P. 1991. *The Illustrated Encyclopedia of Prehistoric Flying Reptiles*. Barnes and Noble Books, New York, 124 pp.
- Wellnhofer, P., E. Buffetaut, and P. Gigase. 1983. A pterosaurian notarium from the Lower Cretaceous of Brazil. *Paläontologische Zeitschrift* 57:147–157.
- Witton, M. P. 2009. A new species of *Tupuxuara* (Thalassodromidae, Azhdarchoidea) from the Lower Cretaceous Santana Formation of Brazil, with a note on the nomenclature of Thalassodromidae. *Cretaceous Research* 30:1293–1300.

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