Anhanguera taxonomy revisited: is our understanding of Santana Group pterosaur diversity biased by poor biological and stratigraphic control?

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Abstract

Background. Anhanguerids comprise an important clade of pterosaurs, mostly known from dozens of three-dimensionally preserved specimens recovered from the Lower Cretaceous Romualdo Formation (northeastern Brazil). They are remarkably diverse in this sedimentary unit, with eight named species, six of them belonging to the genus *Anhanguera*. However, such diversity is likely overestimated, as these species have been historically diagnosed based on subtle differences, mainly based on the shape and position of the cranial crest. In spite of that, recently discovered pterosaur taxa represented by large numbers of individuals, including juveniles and adults, as well as presumed males and females, have crests of sizes and shapes that are either ontogenetically variable or sexually dimorphic.

Methods. We describe in detail the skull of one of the most complete specimen referred to *Anhanguera*, AMNH 22555, and use it as a case study to review the diversity of anhanguerids from the Romualdo Formation. In order to accomplish that, a geometric morphometric analysis was performed to assess size-dependent characters with respect to the premaxillary crest in the 12 most complete skulls bearing crests that are referred in, or related to, this clade, almost all of them analyzed first hand.

Results. Geometric morphometric regression of shape on centroid size was highly statistically significant ($p = 0.0091$) and showed that allometry accounts for 25.7% of total shape variation between skulls of different centroid sizes. Premaxillary crests are both taller and anteroposteriorly longer in larger skulls, a feature consistent with ontogenetic growth. A new diagnosis is proposed for *Anhanguera*, including traits that are nowadays known to be widespread within the genus, as well as ontogenetic changes.

AMNH 22555 cannot be referred to "*Anhanguera santanae*" and, in fact, "*Anhanguera santanae*", "*Anhanguera araripensis*", and "*Anhanguera robustus*" are here considered *nomina dubia*.

Discussion. Historically, minor differences in crest morphology have been used in the definition of new anhanguerid species. Nowadays, this practice resulted in a considerable difficulty in referring well-preserved skulls into known taxa. When several specimens are analyzed, morphologies previously believed to be disparate are, in fact, separated by a continuum, and are thus better explained as individual or temporal variations. Stratigraphically controlled excavations ~~o~~in the Romualdo Formation have showed evidence for faunal turnover regarding fish communities. It is thus possible that some of the pterosaurs from this unit were not coeval, and might even represent anagenetic morphotypes. Unfortunately, amateur collecting of fossils in the Romualdo Formation~~ fossils~~, aimed especially at commerce, resulted in the lack of stratigraphic data for~~of~~ virtually all its pterosaurs and precludes testing of these further hypotheses.

Introduction

The Anhangueridae is a clade known at the present time from several localities worldwide, including named species from Brazil, the United States, Morocco, China and England (Rodrigues & Kellner, 2013). From these, the majority of the known material comes from the Romualdo Formation (Araripe Basin, northeastern Brazil), a well-known fossil *Lagerstätte* where they figure as the most abundant and ~~speciose~~specious clade of tetrapods, with eight named species (*Tropeognathus mesembrinus*, *Maaradactylus kellneri* and six species of *Anhanguera*), as well as several related ones and dozens of referred specimens. Even though this taxonomy has already been disputed by several authors (Kellner & Tomida, 2000; Fastnacht, 2001; Unwin, 2001; Veldmeijer, 2003), the species abundance seems nonetheless remarkable.

Although the first descriptions of pterosaurs from the Romualdo Formation date from as early as the 1970s (Price, 1971), well-preserved skull material only began to be described in the 1980s and 1990s. In February 1985, Wellnhofer described a number of specimens from the Romualdo Formation, naming two new species based on fossils comprising skull material: "*Santanadactylus*" *araripensis* and "*Araripesaurus*" *santanae*; both genera were previously described based on postcranial material. Later that same year, Campos and Kellner described the new genus and species *Anhanguera blittersdorffi*, based on a complete skull. In 1987, Wellnhofer described two further species, *Tropeognathus mesembrinus* and "*Tropeognathus robustus*". With broader knowledge of these Romualdo Formation anhanguerids, some taxonomic proposals arose, placing all these species in the genus *Anhanguera* (Kellner, 1990). Additional specimens but no new named species were described by Wellnhofer (1991); among them, ~~was~~ AMNH 22555~~:~~ is an incomplete skeleton~~,~~ including a skull and a fragmentary mandible. It was the most complete skeleton then known from the Romualdo Formation and served as the basis for the first anhanguerid skeleton reconstruction ever made (Wellnhofer, 1991). This specimen was regarded by Wellnhofer (1991) as conspecific with the holotype of "*Anhanguera santanae*" (previously in the genus "*Araripesaurus*"). Remarkably, two other almost complete skeletons including skulls were later described and referred to the species *Anhanguera piscator* (Kellner & Tomida, 2000) and "*Coloborhynchus*" *spielbergi* (Veldmeijer, 2003).

Today, several skulls (both described and undescribed) are hosted in a myriad of publically accessible collections and thus enabling~~e~~ the examination of a larger sample. Recent proposals (Kellner & Tomida, 2000; Rodrigues & Kellner, 2008) referred to the genus *Anhanguera* the species *A. blittersdorffi*, "*A. araripensis*", "*A. santanae*", "*A. robustus*", *A. piscator* and *A. spielbergi*. Those taxa are mostly diagnosed by subtle differences on cranial anatomy, mainly focused on the morphology and position of the cranial crest, a character presumably sexually dimorphic and/or ontogeny-dependent (Bennett, 1992, Manzig et al., 2014, Wang et al., 2014). The supposedly diagnostic features of *Anhanguera* species are so discrete and ambiguous that it is virtually impossible to attribute new material to any of the proposed taxa with certainty, indicating a probable artificial inflation on the diversity of species within the genus. This issue is diagnostic of a poor understanding of *Anhanguera* intraspecific variation, what may include characters related to sex and ontogeny.

Here we reanalyze the skull of the specimen AMNH 22555, originally referred as "*Anhanguera santanae*" by Wellnhofer (1991), an assumption that was thereafter echoed by other authors (e.g. Kellner & Tomida, 2000; Veldmeijer, 2003). A new description is justified by the fact that Wellnhofer (1991), assuming that AMNH 22555 was not significantly different from "*A. santanae*" holotype, only devoted one paragraph for the skull in its original description. The new description of AMNH 22555 is here used as a case study to assess possible reasons behind the problematical taxonomy of *Anhanguera*. Following a geometric morphometric approach to establish size-dependent characters within *Anhanguera*-like pterosaurs, we make a reassessment of the putative diagnostic features of each of the proposed *Anhanguera* species, resulting in new taxonomic propositions. We also discuss the possibility that a poorly understood stratigraphy is undermining our knowledge of Santana Group pterosaur diversity, by hiding a putative connection between different *Anhanguera* morphotypes and temporally distinct fossil-bearing strata.

Institutional abbreviations

AMNH – American Museum of Natural History, New York, USA

MHNS – Museu de História Natural de Sintra, Sintra, Portugal

MN – Museu Nacional / Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

MPSC – Museu de Paleontologia, Santana do Cariri, Brazil

NHMUK – Natural History Museum, London, UK

NSM – National Science Museum, Tokyo, Japan

DBAV-UERJ – Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil

RGM – National Natuurhistorisch Museum / Naturalis, Leiden, The Netherlands

SAO – Sammlung Oberli, a private collection belonging to Mr. Urs Oberli, Sankt Gallen, Switzerland

SMNK – Staatliches Museum für Naturkunde, Karlsruhe, Germany

SNSB-BSPG – Staatliche Naturwissenschaftliche Sammlungen Bayerns / Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany

Materials and Methods

Geological setting

All the specimens up to now assigned to the genus *Anhanguera* come from the Romualdo Formation (Albian) of the Araripe Basin, northeastern Brazil (Figure 1). The Romualdo Formation is characterized by conglomeratic sandstones followed by a transgressive sequence of green and black shales (Assine, 2007). Within the black shales, the presence of several layers rich in carbonate concretions is noticeable, with lateral continuity throughout the basin (Fara et al., 2005; Saraiva et al., 2007; Vila Nova et al., 2011). The genesis of these layers is associated with mass mortality events, followed by the formation of early diagenetic concretions that entrapped a large number of elements of the biota.

Studied material

In order to assess the biological and stratigraphic biases that may have impacted on the taxonomy of *Anhanguera*, we reevaluate the specimen AMNH 22555 (commonly referred as *"Anhanguera santanae"*, Figure 2) through a comprehensive cranial description. Although this particular specimen was often mentioned and illustrated in specialized literature (e.g. Wellnhofer, 1991; Kellner & Tomida, 2000), a detailed description is still pending ~~lacking~~ and, as will be demonstrated, its attribution to "*Anhanguera santanae"* is mainly based on superficial resemblance. AMNH 22555 is a partial pterosaur skeleton, composed of an almost complete skull, proximal end of the right mandibular ramus (Figure 2, F, G), nearly all vertebral elements (Figure 2, A-E), some ribs, scapulae and coracoids (Figure 2, H, I), an almost complete pelvis and some limb elements, including~~—~~ carpals and metacarpals (Figure 2, J, K), femoral and humeral fragments, incomplete radius and ulna, pteroid, ~~metacarpals~~ and foot phalanges (Figure 2). With the sole exception of *Anhanguera piscator* (which was accessed through the cast MN 5023-V) and *Maaradactylus kellneri* (holotype MPSC R 2357), all other specimens here used for comparison and allometric regressions, were examined first hand by the authors.

Allometric regressions

In order to assess size-dependent characters within *Anhanguera*-like pterodactyloids, we used geometric morphometrics in a series of 12 skulls attributed to *Anhanguera* and closely-related taxa (*Anhangueria sensu* Rodrigues and Kellner, 2013), namely:

Con formato: Fuente: Cursiva

Anhanguera blittersdorffi (holotype, MN 4805-V), *Anhanguera piscator* (holotype, NSM-PV 19892), *Anhanguera spielbergi* (holotype, RGM 401 880), *Anhanguera* sp. (NHMUK R 11978), *Anhanguera* sp. (SAO 16494), *Anhanguera* sp. (SMNK PAL 1136), *Anhanguera* sp. (MN 4735-V, referred to "*Anhanguera araripensis"* by Kellner and Tomida, 2000), SMNK PAL 3895 (referred to *Cearadactylus atrox* by Campos, Headden & Frey, 2013), *Barbosania gracilirostris* (holotype, MHNS/00/85), *Maaradactylus kellneri* (holotype, MPSC R 2357, based on the reconstruction provided by Bantim et al., 2014), *Tropeognathus mesembrinus* (holotype, SNSB-BSPG 1987 I 46) and *Tropeognathus* cf. *T. mesembrinus* (MN 6594-V, based on the reconstruction provided by Kellner et al., 2013).

Comentario [GP1]: And why was not included Anhanguera santanae?

Two-dimensional coordinates were captured for 17 landmarks using digital photographs of specimens in lateral aspect and the software TPSDig (Rohlf, 2010). Landmarks were chosen as follow: 1, posteriormost edge of squamosal; 2, dorsalmost edge of the frontoparietal crest; 3, contact between prefrontal and supraorbital, at the dorsal margin of the orbit; 4, contact between jugal and lacrimal; 5, posterior limit of the lateral shelf of the jugal, at the base of the ascending process of this bone; 6, contact between frontoparietal and postorbital, at the posterior margin of the orbit; 7, ventral edge of the quadrate; 8, anterior limit of the lateral shelf of the jugal, at the base of the ascending process of this bone; 9, contact between lacrimal and nasal, at the dorsal margin of the nasoantorbital fenestra; 10, contact between premaxilla and maxilla, at the anterior margin of the nasoantorbital fenestra; 11, posterior extension of the premaxillary crest; 12, dorsalmost extension of the premaxillary crest; 13, mid-length between landmarks 11 and 12, as projected on the dorsal margin of the premaxillary crest; 14, anterior extension of the premaxillary crest; 15, mid-length between landmarks 12 and 14, as projected on the dorsal margin of the premaxillary crest; 16, anterior tip of the rostrum; 17, mid-length between landmarks 7 and 16, as projected on the ventral margin of the maxilla (Figure 3).

The main goal of our analyses was to detect and describe morphologic variation attributable to the increase of skull size, especially with respect to the premaxillary crest. Although our study is mainly focused on the genus *Anhanguera*, the inclusion of closely-related taxa bearing premaxillary ornaments was justified by the assumption that homologous structures in phylogenetically related animals probably shared functions and growth patterns. The analyses were carried out with the MorphoJ software package, version 1.06a (Klingenberg, 2011). The allometric regression included centroid size as a proxy for cranial size (independent variable) and the shape score *s* proposed by Drake and Klingenberg (2008) (dependent variable), which includes shape changes predicted by allometry, as well as residual variations that are not dependent to size. MorphoJ algorithm allowed us, then, to identify ~~isolate~~ morphological ~~shape~~ changes entirely related to allometry from the residual variations. A permutation test against the null hypothesis of independence was made in order to test the statistical significance of the regressions (10,000 rounds).

As the landmark plotting for *Maaradactylus kellneri* (MPSC R 2357) and *Tropeognathus* cf. *T. mesembrinus* (MN 6594-V) was based on tentative reconstructions provided in the literature, respectively by Bantim et al. (2014) and Kellner et al. (2013), a second regression analysis ~~was made~~ with the exclusion of those specimens was also performed.

Bantim et al. (2015) also carried out allometric regressions in order to investigate cranial crest development within Anhangueridae. These authors, however, used a limited sample of six specimens and restricted their analyses to linear values of crest length and height in order to assess morphology.

Results

Allometric regressions

Our first analysis, including the whole sample of 12 skulls attributed to *Anhanguera* and closely related taxa, detected a highly statistically significant ($p = 0.0091$) regression of shape on centroid size. Allometry alone accounts for 25.7% of total shape variation between skulls of different centroid sizes (Figure 3). The pattern of allometric growth shows a pronounced upward shift of landmarks associated to the premaxillary crest (12, 13 and 15), demonstrating a clear trend of dorsal growth of this structure following the increase in size. It is also evident that landmarks related to the posterior and anterior limits of the premaxillary crest are, respectively, posteriorly and anteriorly displaced in larger specimens (Figure 3). This pattern of anteroposterior growth of the crest means that larger specimens of *Anhanguera*-like pterosaurs tend to have premaxillary crests beginning closer to the nasoantorbital fenestra than smaller ones. The distance between the anterior extension of the nasoantorbital fenestra and the posterior end of the crest is also affected by the occurrence of a proportionally longer nasoantorbital fenestra in larger specimens. Also, the anterior end of the crest presents a positive trend of displacement towards the anterior tip of the rostrum in larger skulls. Notably, the orbits show negative allometric growth, with larger specimens bearing proportionally smaller orbits.

The second analysis, in which *Maaradactylus kellneri* (MPSC R 2357) and *Tropeognathus* cf. *mesembrinus* (MN 6594-V) were excluded, also demonstrates strong effects of centroid size on shape, with allometry accounting for 22.73% of total shape variation. This second regression was less statistically significant ($p = 0.058$). All the morphological trends detected in the first analysis were recovered.

We also analyzed the residual (uncorrelated with size) component of variation for each specimen, in an attempt to identify individual morphological disparity, potentially attributable to interspecific dissimilarity. Some specimens indeed show a considerable amount of residual variation of shape, unpredicted by our regression model. Specimen MN 4735-V, attributed by Kellner and Tomida (2000) to "*Anhanguera araripensis*", for instance, has a much bigger premaxillary crest than what would be expected for an animal of its size class, while *Anhanguera piscator* holotype (NSM-PV 19892) has a proportionally small crest. Notably, some of the residual variation observed in other specimens ~~are~~ is attributable to diagenetic modification of fossils, such as an upward shift of the rostrum in NHMUK R 11978 and in the *Maaradactylus kellneri* holotype (MPSC R 2357). Most of the observed residual components of variation, however, are difficult to describe as discrete traits and seem to vary continuously on our sample, with disparate morphologies linked together by a set of intermediaries.

Comentario [GP2]: How many? Could you please, provide a percent or an estimative proportion of specimens that resulted morphologically variable?

Comentario [GP3]: Thus, you will need more than one specimen of each species to a better interpretation of the significance of this character.

The skull of AMNH 22555

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Anhangueria Rodrigues and Kellner, 2013

Anhangueridae Campos and Kellner, 1985

Anhanguera Campos and Kellner, 1985

Anhanguera sp.

Locality and horizon. Romualdo Formation, Araripe Basin, Albian, northeastern Brazil. According to Wellnhofer (1991), the specimen comes from Jardim municipality in the state of Ceará (previously Barra do Jardim), but most likely its exact locality is undetermined.

Anatomical description. The skull of AMNH 22555 is nearly complete and best preserved in right lateral aspect (Figure 4, 5). Even so, rostral elements anterior to the nasoantorbital fenestrae are crushed and laterally compressed in this view. Posterior skull bones are broken and disarticulated in left lateral view, in which the absence of bones such as the left jugal and lacrimal obliterates the edges of skull openings. The palate anterior to the choanae is well preserved, whereas posterior palatal bones are, mostly, absent. Parts of the right pterygoid lie inside the nasoantorbital opening, in lateral view. Despite the fact that the alveolar margin of the maxillae is intact anteriorly, with the presence of some teeth (mostly broken) and empty alveoli, the ventral margins of both the left and right maxillae are eroded and incomplete posteriorly, preventing an accurate estimation of the number of tooth positions. The posterior skull roof is almost intact, with a slight lateral displacement of the frontoparietals. Above the nasoantorbital openings, the outer bone layer of the dorsal margin of the fused premaxillae is eroded. The dorsal limits of the premaxillae are badly crushed throughout the anterior half of the skull, preventing the reconstruction of the sagittal crest anatomy. In occipital view, only the broad supraoccipital plate and right opisthotic are fairly well preserved.

In general, the skull bones are disarticulated and, sometimes, displaced from their original positions. The premaxillae and maxillae, as well as the frontals and parietals, are tightly fused with each other, displaying the ordinary condition for pterodactyloids. Some postcranial bones, known to fuse in mature individuals, show the unfused condition in AMNH 22555, indicating that this specimen is osteologically immature (Wellnhofer, 1991; Bennett, 1993). Those elements include separate scapulae and coracoids, as well as proximal and distal carpals (Figure 2, H-K). The first five dorsal vertebrae show very thick neural spines and prezygapophyses fused with the postzygapophyses of the adjacent vertebra, indicating that a notarium was present in mature individuals of this species (Figure 2, B).

Comentario [GP4]: Incomplete?

Premaxilla. The fused premaxillae comprise~~ose~~ most of the skull roof, with their posterior ends above the orbits, where they contact the frontoparietals. Although the left premaxilla is considerably well preserved throughout its whole extension, the right element is badly crushed anteriorly to the nasoantorbital fenestra. Sutures between the premaxillae and maxillae can only be observed close to the nasoantorbital fenestrae, especially on the left side of the skull (where this region is best preserved). Anteriorly, the ventral limits of the premaxillae are not clear, and the number of tooth positions associated with these bones cannot be inferred. The dorsal surface of the premaxillae is broken in the region anterior to the nasoantorbital fenestrae, making it difficult to determine the presence of a sagittal crest. However, this broken dorsal border extends above the projection of the surface dorsal to the nasoantorbital openings, which may indicate that the crest was present. It is probable that the premaxillae also composed the anterior part of the palate, where the bone is strongly pierced by small foramina. However, due to bone fusion, it is impossible to determine the exact contribution of the premaxillae to the palatal surface. There is a discrete anterior expansion of the skull, with the rostrum being about 1.5–2 mm wider at the level of the 4th tooth sockets than at the 3rd and 5th alveoli. This is more reminiscent of the slight expansion seen in *Tropeognathus mesembrinus*, but at this point it cannot be ruled out that the expansion could grow larger with maturity.

Maxilla. Bordered dorsally by the premaxillae, the maxillae form the anterior and part of the ventral margins of the nasoantorbital fenestrae. Because the suture lines between the maxillae and premaxillae are located at the anterodorsal border of the nasoantorbital fenestrae, the maxillae also make a small contribution to the dorsal margin of these openings. Ventrally, the palatal plates of the maxillae (see Ősi et al., 2010; Pinheiro & Schultz, 2012) fuse together, forming a well-developed palatal ridge that ends about 50 mm before the anterior limits of the choanae. The dental margins of the maxillae form strong rims, and some of the rostral teeth (especially the 7th to 10th tooth pairs) are surrounded at their bases by robust bony collars, generally punctured by foramina on their medial side. Because the jugal processes of both maxillae are broken, the posterior limits of these bones cannot be determined. Anterior to the 9th tooth pair, the ventral margins of the maxillae gently curve upwards, and the anteriormost teeth are inserted at level with the ventral margins of the orbits.

Nasal. Together with the lacrimals, the nasals form the posterodorsal margins of the nasoantorbital fenestrae. The right nasal is better preserved than the left one, and shows an irregular shape, with acute anterior and posterior extensions. The dorsal margin is straight and contacts the premaxillae. The nasals have lateral longitudinal ridges, probably indicating the contact area with the lacrimals (in AMNH 22555, these bones are slightly displaced). The nasals have concave posterior margins, fitting the convex prefrontals and supraorbitals. The ventral surfaces of the acute anterior processes of the nasals are perforated by well-developed foramina. The nasoantorbital openings are completely filled with carbonaceous matrix and, thus, the medial contact between the left and right nasals, as well as the ventral nasal process, are obscured.

Prefrontal. Only the right prefrontal is preserved. Dorsally, this bone makes contact with the nasal and the supraorbital, whereas ventrally it shows a rectilinear suture with the lacrimal. The prefrontal contributes to part of the anterodorsal margin of the orbit.

Supraorbital. Both supraorbitals are preserved. These bones are roughly triangular in dorsal aspect and compose part of the skull roof above the orbits. The contact between the supraorbitals and frontoparietals is marked by grooves, which are deeper at their posterior limits. The supraorbitals are also partially covered by the posterior extension of the premaxillae.

Frontoparietal. There is no visible distinction between the frontals and parietals, but a clear suture line divides the left and right elements of these bones. The frontoparietals form almost the entire skull roof above the orbits and the upper temporal fenestrae, being overlaid anteriorly by the slender posterior extension of the premaxillae that projects between the left and right frontoparietals. Above the upper temporal fenestrae, the dorsal margin of the frontoparietals forms a short crest that probably provided a greater area of origin for the *musculus adductor mandibulae externus*.

Jugal. Only the right jugal is preserved. This is a robust element, mostly composed of three strong processes that contribute to the boundaries of several skull openings. The maxillary process of the jugal extends anteriorly, forming part of the posteroventral margin of the nasoantorbital fenestra as well as it contributes to the lateral margin of the palatal subtemporal fenestra. This process is broken in the preserved jugal of AMNH 22555, preventing an estimation of how far anteriorly the contact with the maxillae was located. The lacrimal process of the jugal is directed dorsally, with a slight anterior inclination, and forms part of the anterior margin of the orbit, as well as part of the posterior margin of the nasoantorbital fenestra. The spot where this process connects with the main corpus of the jugal is depressed, forming a distinct lateral shelf, so that the whole process is medially displaced with respect to the remainder of the bone. The contact with the lacrimal occurs at about one fourth of the total height of the orbit. The most developed jugal process is the posterior, postorbital~~,~~ one. This bony extension is very thick anteriorly, but becomes narrower throughout its posterodorsal end, where it contacts the postorbital via an overlapping joint. The postorbital process of the jugal composes most of the posterior edge of the orbit, and the whole anterior border of the lower temporal fenestra.

Postorbital. Both postorbitals are preserved; the left one is completely displaced from its original position and the right one shows a slight medial displacement. These bones have a roughly triangular outline and occupy a central position on the temporal region of the skull. The postorbitals make contact dorsally with the frontoparietals, anteriorly with the posterior processes of the jugals and posteriorly with the squamosals. The edges of these bones contribute to the margins of both the upper and lower temporal fenestrae, and also have a small participation in the posterior borders of the orbits.

Lacrimal. In AMNH 22555, only the right lacrimal is preserved. This bone is triangular in shape, making contact with the prefrontal and the nasal dorsally and overlying the lacrimal process of the jugal ventrally. The posterior edge of the lacrimal bears a well-developed, lateromedially broad process directed inside the orbit. The lacrimal is pierced by a vast foramen for the exit of the naso-lacrimal duct, which occupies most of the main corpus of this bone.

Squamosal. The squamosal is a curved bone, with its concavity directed anteriorly, where this element composes most of the posterior border of the lower temporal fenestra. Dorsally, the squamosal contacts the postorbital and frontoparietals. Between these bones there is a smaller concavity that bounds the ventral margin of the upper temporal fenestra. The squamosal ends ventrally with two acute processes. The anterior one sutures with the slim quadratojugal, whereas the posterior runs parallel to the quadrate and is probably the origin site of the *musculus depressor mandibulae*. The posterior, convex edge of squamosal makes contact with the opisthotic.

Quadratojugal. This slender bone makes contact with the main corpus of the jugal anteriorly and with one of the ventral processes of the squamosal posteriorly, delimiting ventrally the lower temporal fenestra.

Quadrate. Only the right quadrate is completely preserved. This bone contacts laterally the squamosal, quadratojugal and part of the jugal. The anteroventral end of the quadrate expands to form the helical articular surface with the lower jaw. The quadrate shaft runs medially, parallel to the ventral extension of the squamosal. The inclination of the quadrate with respect to the ventral margin of the maxilla is about 145 degrees.

Supraoccipital. The supraoccipital is a broad plate that forms a large portion of the occiput. Above the dorsal margin of the *foramen magnum*, this bone develops a low sagittal crest, probably linked to the origin of the *musculus rectus capitis*. Lateral to the crest, the supraoccipital is pierced by two large pneumatic foramina. The dorsal border of the right posttemporal fenestra is preserved, showing that this opening was inclined downwards (Figure 5).

Opisthotic. In AMNH 22555, both the right and left opisthotics are broken and displaced from their original positions. Although the right element is better preserved, little anatomical information can be drawn from this bone. It can be observed that the opisthotics were configured as wide plates that occupied a considerable portion of the occiput.

Palatine. The structures traditionally regarded, in most pterosaurs, as the palatines were recently reinterpreted as a secondary surface formed by ventral plates of the maxillae (see Ősi et al., 2010; Pinheiro & Schultz, 2012). The high degree of synostosis, common in Pterodactyloidea, makes the individualization of palatal elements difficult. In anhanguerids, the palatines probably bordered the suborbital fenestrae medially, the right element being partially preserved in AMNH 22555.

Comentario [GP5]: Could you please refer to a figure? Because this interpretation about the palatine is not shared by other researchers, and so, it is important to support well the new inferred condition.

Pterygoid. Although most of the posterior palatal bones were lost, part of the left pterygoid lies in dorsal view inside the nasoantorbital fenestra. This bone shows a very long and acute rostral process, connected to a concave surface, which is followed posteriorly by a transversal ridge. This ridge can be interpreted as part of a vestigial ectopterygoid, already reported for other specimens of *Anhanguera* (Pinheiro & Schultz, 2012). In close association, there is a flat, triangular bone of uncertain affinities. It is possible that it represents the posterior extension of the pterygoid, which would contact the basipterygoid caudally.

Vomers. The fused vomers form a slim element that partially divides the choanae medially. There is no sign of sutures between the two vomers or between them and other elements of the palate.

Dentition. Only the dentition pattern of the upper jaw of AMNH 22555 can be assessed, and is reminiscent of that seen in other species of *Anhanguera*. The 1st pair of teeth is located at the tip the rostrum, slightly higher than the 2nd pair, facing anteriorly, as is usual in anhanguerians (Rodrigues & Kellner, 2013). The alveoli grow in width until the 3rd pair. As is usual in the genus *Anhanguera*, the 4th and 7th pairs of alveoli are larger than the 5th and 6th. From the 8th onwards, the alveoli tend to gradually decrease in width. The distances between the alveoli increase gradually, but are most notably larger from between the 7th and 8th alveoli onwards. As noted above, the maxillary margin is not well preserved and most posteriormost alveoli cannot be assessed, but the dentition would continue until at least the beginning of the nasoantorbital fenestra. Some teeth are preserved, showing a curved and pointed shape and longitudinal ridges where the enamel is present, as typical of anhanguerids (Rodrigues & Kellner, 2010).

Discussion

Patterns of premaxillary crest growth in Anhanguera *and their taxonomic significance*

Morphology of cranial crests was invariably used as a crucial character in~~on~~ the diagnosis of every single species of *Anhanguera* proposed thus far. Among crest features suggested to distinguish *Anhanguera* species, the most common ~~are~~ is its height and the antero-posterior extension. The first description of *Anhanguera blittersdorffi* by Campos & Kellner (1985) mention a “large sagittal crest on the anterior part of the skull, situated on the premaxillas (sic), which ends almost at the beginning of the external naris” (Campos and Kellner, 1985, p. 459). Similarly, *Anhanguera spielbergi* would differ from other species for having a “large premaxillary sagittal crest, in ratio length-total length skull (sic), which extends dorsally from the anterior aspect until the anterior border of the nasoantorbital fenestra” (Veldmeijer, 2003, p. 43). Also, following the taxonomic revision provided by Kellner and Tomida (2000), the only feature that would distinguish "*Anhanguera robustus"* from other species of the~~is same~~ genus would be a large dentary crest with an anterior margin forming an angle of about 50º with the dorsal margin of the lower jaw (Kellner and Tomida, 2000, p. 117).

At least one species of *Anhanguera* would be diagnosed by a small, rather than a large premaxillary crest: according to Kellner and Tomida (2000), *Anhanguera piscator* would differ in having the "bony part of the premaxillary crest comparatively long but low, not reaching the highest point of the skull" (Kellner and Tomida, 2000, p. 7). The two remaining proposed species of the genus would be distinguished by the antero-posterior extension of the premaxillary crest: also following the taxonomic background of Kellner and Tomida (2000), "*Anhanguera araripensis*" would be distinguished by a sagittal crest positioned "right in front of the nasoantorbital fenestra" (p. 105), whereas "*Anhanguera santanae*" would have a "sagittal crest confined to the anteriormost portion of the skull" (p.109).

Con formato: Resaltar

Comentario [GP6]: I think that this paragraph is too much complicated to follow, and needs to be rephrased. Maybe it could be better that you don´t use direct, textual references but your own interpretations about the morphology of the crests in those species.

Con formato: Resaltar

Our regression analysis, however, deeply challenges the use of height and anteroposterior extension of the premaxillary crest as robust characters on the diagnosis of anhanguerids. As demonstrated here, anhanguerid skulls show statistically significant positive allometric growth of the premaxillary crest (see also the work of Bantim et al., 2015). Besides a simple increase in height, the detected pattern of allometric growth also indicates an anteroposterior development of the crest following the increase in total skull size (a pattern also corroborated by the analyses of Bantim et al., 2015).

Comentario [GP7]: But, you also found some variability in the behavior of this structure concerning growth patterns, right? And as you probably have analyzed just one individual per species, maybe you have to be less categorical with respect to this result.

Following the recent discovery of crested pterosaur assemblages preserving a ~~with~~ large number of individuals belonging to ~~of~~ a single species (Manzig et al., 2014; Wang et al., 2014), it was verified that pterosaur cranial crest development may indeed be strongly controlled by ontogeny and/or sexual dimorphism, as suggested before (for instance, Bennett, 1992). The strong positive allometric growth of the premaxillary crests of pterosaurs such as *Caiuajara dobruskii* (Manzig et al., 2014) and the sexual dimorphism related to the cranial crest observed in *Hamipterus tianshanensis* (Wang et al., 2014) are strong evidences to postulate that pterosaur cranial crests evolved by sexual selection, as was already proposed by several authors (e.g. Hone et al., 2012; Knell et al., 2013). As is characteristic of display structures, it is expected that cranial crest size and morphology had strongly intraspecific variation in pterosaurs. On these grounds and in agreement with our analyses, we propose that cranial crest characters should be excluded as diagnostic of pterosaur nominal species, at least when the variation does not imply deep changes on the skull architecture, what is not the case for *Anhanguera*.

Comentario [GP8]: I insist into the availability of specimens of the same species that can prove this statement as to be confident. You don´t have the same situation here as in Wang et al., doesn't you?. Your point is a valid hypothesis to test, but needs to be proved in Anhanguera species. You don't know if the variation of all the skull crests is an ontogenetic or a sexual character for these taxa unless you have evaluated it in several individuals of the same species. Thus, the morphology of the crests is still a valid character that deserves continue to be evaluated as a possible taxonomic feature. I would suggest that you don´t need to be so categorical at this stage of your study.

The taxonomy of Anhanguera

On the diagnosis of Anhanguera

Kellner (2003) listed as synapomorphies of the genus *Anhanguera* (1) the presence of an elongate and medially placed nasal process, (2) a foramen on the nasal process, (3) a characteristic size difference in the rostral teeth (in which the 5th and 6th tooth pairs are smaller than the 4th and 7th ones); (4) scapulae length at most 80% of that of the coracoids, (5) a coracoidal articulation surface with the sternum oval and with a posterior expansion, and (6) a pneumatic foramen on the proximal dorsal surface of the humeri. However, more recently described specimens challenge some of these features and show that they are more widespread among pterosaurs?. Characters (1) and (2) are present on *Ludodactylus sibbicki* from the Crato Formation (Frey, Martill & Buchy, 2003), and characters (4), (5) and (6) are also found in *Brasileodactylus* sp. (SNSB-BSPG 1991 I 27; Veldmeijer, Meijer & Signore, 2009) and in *Istiodactylus* (Hooley, 1913; Andres & Ji, 2006). Therefore, from these, only character (3) would be synapomorphic for *Anhanguera*.

Naturally, these are characters used in a cladistic sense but others have been proposed as diagnostic of the genus. While comparing *Anhanguera* and *Coloborhynchus*, Fastnacht (2001) stated that *Anhanguera* presents (1) a premaxillary crest beginning more posteriorly instead of at the anterior tip of the rostrum, (2) a premaxillary crest lower than in *Coloborhynchus* with its height about one third of its length, (3) a thin crest, (4) the anterior end of the rostrum inclined at an angle of about 45 degrees, and (5) the absence of a spoon-shaped distal expansion of the rostrum. From these, our analyses demonstrate that characters (1) and (2) could be attributed to ontogenetic development in the genus *Anhanguera*. Character (5) is a misinterpretation since the type species, *Anhanguera* blittersdorffi, has a distal expansion with this morphology (see Rodrigues & Kellner, 2008). Characters (3) and (4), although useful to distinguish *Anhanguera* from *Coloborhynchus*, are also present in *Liaoningopterus* and *Caulkicephalus* (Wang & Zhou, 2003; Steel et al., 2005; Rodrigues et al. 2015) and therefore are more widespread within anhanguerids. A very similar set of characters was also discussed by

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Comentario [GP9]: There is no possibility that this species does not belong to the genus Anhanguera?

Veldmeijer (2003). This author suggests that AMNH 22555 is a juvenile *Coloborhynchus*. However, some of the characters used by him to separate *Anhanguera* and *Coloborhynchus*, such as the position of the premaxillary crest, are also listed by him as possibly explained by ontogenetic variation, a view that is supported by our results. Veldmeijer (2003) suggests that features present at the posterior part of the skull of AMNH 22555 are more similar to *Anhanguera spielbergi* (regarded by him as belonging to ~~in~~ the genus *Coloborhynchus*) thae~~e~~n to the holotype of "*Anhanguera santanae*". However, the diagnostic value of these minor differences is dubious. Therefore, it seems that *Anhanguera* remains diagnosed by a single unambiguous character, the 5th and 6th tooth pairs being smaller than the 4th and 7th ones, and by combinations of characters.

Here we suggest the following revised diagnosis ~~of~~ for *Anhanguera*, which includes the ontogenetic changes discussed above: anhanguerid pterosaurs with premaxillary and dentary median crests; premaxillary crest thin; premaxillary crest largely asymmetric; premaxillary crest begins near but not at the tip of the skull; premaxillary crest not confined to the anteriormost tip of the skull; premaxillary crest grows allometrically in height and length during ontogeny; 5th and 6th upper dental alveoli smaller than the 4th and 7th ones; parietal crest blade-like and thin; palatal ridge modest in depth.

Comentario [GP10]: Above, you recommended that cranial crest characters should be excluded from the list of diagnostic characters! Consistence needed.

AMNH 22555 cannot be confidently referred to what is known as "Anhanguera santanae"

Con formato: Fuente: Cursiva

When first described by Wellnhofer (1991), AMNH 22555 was referred to "*Anhanguera santanae*", a pterodactyloid pterosaur described a few years before by the same author and from the same formation (Wellnhofer, 1985). The assignment of AMNH 22555 to "*A. santanae*" (then regarded as "*Araripesaurus*"; see Introduction) *was* made mainly on the basis that both specimens share the same number of bones in the carpals, besides possessing similar sized skulls, even though the position of their premaxillary crests would differ (Wellnhofer, 1991). A close examination of "*A. santanae*" holotype (SNSB-BSPG 1982 I 90) and comparison to other skulls now known, however, revealed to us that AMNH 22555 cannot be confidently referred to this species more than to any other proposed species of *Anhanguera*.

Although AMNH 22555 is indeed similar to the “*Anhanguera santanae”* holotype in size and overall skull morphology, the two specimens differ in a series of features (Figure 5). First of all, the frontoparietals of “*A. santanae”* are narrower and project posterodorsally as a thick frontoparietal crest. On the other hand, the frontoparietals of AMNH 22555 are broader and form a much more delicate crest, mostly posteriorly extended. The two specimens also differ in the morphology of the jugal: the lacrimal process of this bone is much broader in *A. santanae* than in AMNH 22555.

Differences between AMNH 22555 and “*A. santanae”* also extend to the occipital and palatal regions. In occipital view, it is notable that the supraoccipital crest is much more conspicuous in “*A. santanae”* than in AMNH 22555. Also, although the occiput of AMNH 22555 is not well preserved, the dorsal margin of the posttemporal fenestra is well marked and reveals that this opening was probably directed downwards, unlike the condition observed in “*A. santanae”* holotype. As a consequence of the bad preservation, however, this character must be regarded with caution. In palatal view, it is remarkable that in AMNH 22555 the fusion of the palatal plates of the maxillae forms a strong palatal ridge (although not as deep as in *Tropeognathus*) that is followed posteriorly by a slight convexity of the palatal surface. “*A. santanae”* also bears a palatal ridge, but this structure is much lower and extends posteriorly to a region closer to the choanae than that seen in AMNH 22555. In addition, the choanae morphology is also different between the specimens, those of AMNH 22555 being distinctly rounder and lateromedially expanded.

Comentario [GP11]: Some of the characters that you describe could be taphonomically constrained and other could be sexual differences. Most may be also subjective.

In spite of the remarkable differences between AMNH 22555 and *“Anhanguera santanae”* holotype (SNSB-BSPG 1982 I 90), none of the characters listed above has its distribution well mapped for *Anhanguera*, and may fall within the range of intraspecific variation of this genus. In addition, it is noteworthy that allegedly diagnostic features of *Anhanguera* nominal species are, in most cases, subtle, poorly defined traits, especially related to the presence and morphology of the premaxillary crest. As discussed, premaxillary crest shows significant allometric growth within *Anhanguera*-like pterodactyloids, demonstrating that this structure is size-dependent and has limited use for taxonomic purposes. Bearing this in mind, we reassess here the significance of anatomical features traditionally thought to support *Anhanguera* species, with impact on the taxonomy of this genus.

Con formato: Resaltar

Comentario [GP12]: This is not reflected in the suggested diagnosis for Anhanguera presented above.

Con formato: Resaltar

*On the validity of "*Anhanguera santanae*" and other species of* Anhanguera

A reappraisal of the supposedly diagnostic features of *Anhanguera* species revealed that most, if not all of the characters that are currently used to define species are probably well inside the range of intraspecific variation. Considering this, it is pertinent to inquire about the validity of each one of the species attributed to this genus.

When first described, *"Anhanguera santanae"* was differentiated from other pterosaurs on the basis of characters that are today known to be well distributed on other Santana Group ornithocheiroids. A complete discussion of the validity of the diagnostic features originally proposed for *"A. santanae"* was made by Kellner & Tomida (2000). As a conclusion, these authors stated that the only remaining diagnostic character for this taxon would be the position of the premaxillary crest, well anterior to the nasoantorbital fenestrae. It is noteworthy that the crest itself is not preserved on *"A. santanae"* holotype, and its presence is inferred by the acute dorsal margin of the premaxillae close to the anterior extremity of the specimen, as preserved. One of the specimens analyzed in the present allometric regression, SMNK PAL 1136, presents a crest that can be presumed to be positioned as far from the nasoantorbital opening as in the holotype of "*A. santanae*". As discussed, cranial crest characters are here regarded as unfit for the diagnosis of nominal anhanguerid species, what means that *"A. santanae"* holotype lacks unambiguous diagnostic features and should be considered as a *nomen dubium.*

Anhanguera blittersdorffi, the type species of *Anhanguera*, was first diagnosed by characters that later proved to be diagnostic of more inclusive clades, such as the presence and morphology of the premaxillary and frontoparietal crests and the presence of a distal expansion and of larger teeth at the tip of the rostrum (Campos & Kellner, 1985). Actually, *A. blittersdorffi* has the standard morphology of *Anhanguera* and, after the description of other anhanguerids, it became difficult to recognize unique characters for this species. A more or less recent revision (Kellner & Tomida, 2000) proposed as diagnostic of the species a "lower skull with a proportionally shorter quadrate". Those characters, however, are subjective and lack a morphometric definition. Besides the holotype, only one more specimen was formally attributed to *A. blittersdorffi* (Pz-DBAV-UERJ 40) (Kellner and Tomida, 2000), though the later still lacks an anatomical description. Remarkably, the number of alveoli on *A. blittersdorffi* upper jaws (52) is higher than in any other proposed *Anhanguera* species and this might be a more suitable diagnostic character for this taxon.

“*Anhanguera araripensis*” was described based on a very incomplete skull with associated postcranial bones by Wellnhofer (1985). As was the case for *A. blittersdorfii*, “*A. araripensis*” was first diagnosed by characters that later were demonstrated to be widespread among anhanguerids or ontogeny dependent. After the revision of Kellner & Tomida (2000), only two characters remained as diagnostic for this species: the dorsal margin of the premaxillae is “keel shaped” up to the anterior end of the nasoantorbital fenestrae (a character described as being related to the position of the premaxillary crest, which is not preserved at the holotype), and the presence of small lateral projections on the basioccipital processes of the pterygoids (Kellner, 1991) (Figure 6, D). Based on this character, other specimens have been referred to this species, such as MN 4735-V (Kellner & Tomida, 2000) and SAO 16494 (Veldmeijer, 2003; Veldmeijer, 2006). We agree that the “keel shaped” dorsal margin of the premaxillae is probably related to the presence and morphology of the premaxillary crest and, for the reasons mentioned above, challenge the taxonomic value of this character. Regarding the lateral projections of the pterygoids inside the subtemporal fenestrae, we consider this character as problematical, because it is probably related to the bone outgrow between different elements of the adductor musculature that crossed the subtemporal openings. Also, these projections are exceptionally delicate and were probably abraded on not so well preserved skulls. Remarkably, specimens such as the holotype of *Tropeognathus mesembrinus* (SNSB-BSPG 1987 I 46) and *A. blittersdorffi* (MN 4805-V) have very discrete bulges at this same location (Figure 6, E). Thus, we here regard the holotype of “*A. araripensis”* as nondiagnostic and, for this reason, “*Anhanguera araripensis”* shall also be considered as a *nomen dubium*.

“*Anhanguera robustus”*, at its first description referred to the genus *Tropeognathus* by Wellnhofer (1987) and later assigned to *Anhanguera* (Kellner & Campos, 1988) was originally diagnosed by the presence of a well-developed dentary crest, with a straight anterior margin; and by a spoon-like anterior expansion of the dentaries and long anterior teeth. As was already observed by Kellner & Tomida (2000), strong anterior teeth associated to a lateral expansion of the dentaries are widespread among anhanguerids. The other supposedly diagnostic characters are related to the dentary sagittal crest and are probably associated to the apparently advanced ontogenetic stage of the specimen (SNSB-BSPG 1987 I 47). Thus, we also consider “*Anhanguera robustus”* as a *nomen dubium*.

Despite its large size, the holotype of *Anhanguera piscator* presents clear evidences of an early ontogenetic stage, which~~at~~ partially explains the presence of the low premaxillary crest that was regarded by Kellner and Tomida (2000) as diagnostic of the species. Our analysis demonstrates that crest height in this species cannot be explained on allometric growth~~und~~ alone, but nonetheless considers this character as inappropriate for the diagnosis of anhanguerids. Kellner and Tomida (2000) indicated another cranial character as diagnostic ~~of~~ for this taxon: a “basisphenoid constricted in the middle part” (Kellner & Tomida, 2000, p. 7). This feature cannot be accessed in SNSB-BSPG 1982 I 89 (“*Anhanguera araripensis”*) or SNSB-BSPG 1987 I 47 (“*Anhanguera robustus”*). Although this character still lacks an unambiguous morphometric definition, basisphenoid morphology in *A. piscator* holotype is indeed different from what is observed in *Anhanguera blittersdorffi* and SNSB-BSPG 1982 I 90 (“*Anhanguera santanae*”), resembling the condition of *Anhanguera spielbergi*. Other proposed diagnostic features of *A. piscator* are associated to the postcranial skeleton, which is poorly preserved or absent in most other *Anhanguera* holotypes. *A. piscator* is here regarded as a valid taxon, at least until more information about the distribution of these postcranial characters and basisphenoid morphology becomes more clear within Anhangueridae.

Veldmeijer (2003) considered *Anhanguera spielbergi* as a representative of *Coloborhynchus*, including on the diagnosis of this species an “ill-defined, almost absent (…) palatinal ridge and corresponding mandibular groove; mandibular groove not extending onto spoon-shaped expansion; slight, almost absent, ventrolaterally extending tooth-bearing maxillae; large premaxillary sagittal crest, in ratio length-total length skull, which extends dorsally from the anterior aspect until the anterior border of the nasoantorbital fenestra; strongly medial bended rami; sternum with rounded triangular posterior plate of which the length is as long as the width” (Veldmeijer, 2000, p. 43). Although the palatal ridge of *A. spielbergi* is indeed weaker than what is observed in other *Anhanguera* holotypes, it is still not clear how this character is affected by ontogeny, the same being valid for the mandibular groove. As discussed, premaxillary crest morphology is here regarded as inappropriate for species diagnosis, whereas a medial bending of mandibular rami cannot be assessed in most of the other holotypes, but is present in other complete anhanguerid mandibles (for instance, “*Anhanguera robustus*”). Although the intrageneric variation of the remaining characters is still nebulous, we regard *A. spielbergi* as a valid taxon, a taxonomic statement that may be tested through a better sampling within the genus.

A highly diverse genus or an exceptionally biased record?

Specimens attributable to *Anhanguera* often present slight differences on their skull anatomies, especially with respect to the size and morphology of the premaxillary crest. Historically, these different morphotypes were used to base the definition of new taxa, what is not reprehensible, considering the fact that the knowledge about ontogenetic and sexual variability connected to crest morphology was (and still is) incipient. Nowadays, however, this practice led to an abundance of nominal species with, as we demonstrate, continuous morphologies. As a result, it is considerably difficult to attribute with a proper degree of certainty any new material to a previously described species. This same issue was detected before in other fossil localities that have, historically, yielded pterosaur fossils, such as the Niobrara and Pierre Shale formations of the USA (*Pteranodon* and *Nyctosaurus* sites) and the Solnhofen limestones of Bavaria, Germany. Similarly to what we discuss for *Anhanguera*, the diversity of taxa found in those sites were reassessed taking into account that ontogeny, sexual dimorphism, individual differences and time may have strong influences in a morphological disparity previously considered of taxonomic significance (e.g. Bennett, 1992; Bennett, 1994; Bennett, 1995).

A possible overestimation in the anhanguerid diversity of the Romualdo Formation was already pointed out by Kellner and Tomida (2000). These authors commented on the lack of comparable elements between some of the taxa and on potential intraspecific variations for the taxonomic inflation, although not making reference to other potential biases.

As the relation between morphological disparity and speciation is vague, the application of the prevailing definition of biological species (growing~~unded~~ in~~on~~ reproductive isolation) to the fossil record is exceedingly challenging (e.g. Gingerich, 1985; Bennett, 1994; Kellner, 2010). This is even more delicate when one is dealing with lineages that lack extant analogues, as is the case for pterosaurs. In order to distinguish fossil and extant species, the amount of morphological variation among studied specimens is less important than the presence of morphological discontinuities (Gingerich, 1985).

Disparate morphologies that show continuous intermediates in the sample are, thus, better explained by intraspecific variation or temporal evolutionary effects (this later only recognizable in the fossil record).

As we demonstrated, most of the allegedly diagnostic characters traditionally used to distinguish proposed *Anhanguera* species, display continuous variation in the available sample and are correlated to skull size, being, thus, unfit for taxonomic purposes. The detected residual variation (not attributable to the allometric growth of the skull) is, in most of the times, characterized by disparate conditions linked by intermediate morphologies. However, in some other cases, as the crest morphology of specimen MN 4735-V and *Anhanguera piscator* holotype, the residual variation is well beyond the condition expected for animals of their sizes, maybe reflecting taxonomic discrepancies. We discuss, here, possible explanations for this peculiar pattern of morphological disparity of *Anhanguera*-like pterosaurs.

A natural ecological question that follows the assumption that Romualdo Formation pterosaur taxa were sympatric and coeval is how a large number of taxa with supposedly overlapping ecological niches may coexist. However, competitive exclusion of species happens only when the resources are scarce to the point of limiting population growth. If we assume, as is likely, that *Anhanguera* species competed for prey, sufficiently high fish populations could sustain several piscivorous species. This, however, would result in an apparently aberrant community structure, and the pattern observed in the fossil record may be better explained by the influence of biological and stratigraphic bias.

Although our allometric regressions are not *per se* direct evidence that premaxillary crests grew with age, the strong correlation of crest development with respect to skull size makes it very likely that the patterns observed here indeed reflect ontogeny. Allometric growth of skull ornaments in pterosaurs was recently confirmed by the discovery of monospecific bonebeds with fairly complete growth series (e.g. Manzig et al., 2014). The strongly positive allometry demonstrated here (as in pterosaurs like *Caiuajara dobruskii*) is characteristic of sexually selected traits (Tomkins et al., 2010), which are exceptionally variable within species. Thus, it is likely that a considerable amount of the morphological disparity observed in anhanguerids is attributable to intraspecific variation. Sexually selected characters tend also to be sexually dimorphic, and sexual dimorphism related to cranial crests was present in pterosaurs (e.g. Wang et al., 2014). It is possible that anhanguerid cranial crests were also sexually dimorphic, what would explain at least some of the residual variation recovered by our analyses. However, small sample size and the probable effect of stratigraphic biases (as we discuss below) makes it impossible to assess this hypothesis at the time. It is consensual that robust synecological inferences based on Romualdo Formation fossils are impossible to be done based on museum specimens. The reason for this hindrance is that the commercial exploitation of Romualdo Formation fossil bearing strata disregard elemental field data, such as those concerning the stratigraphic distribution and abundance of species. Virtually all the Romualdo Formation specimens deposited in museums and universities throughout the world (i. e., those available for scientific research) fall in this scenario. The high commercial value of complete specimens or specific taxa, such as pterosaurs, created a strong collection bias and, as a result, museum specimens are not representative of the actual Romualdo Formation diversity (Fara et al., 2005; Vila Nova et al., 2011). Stratigraphically controlled excavations on Romualdo Formation are still incipient (Fara et al., 2005; Vila Nova et al., 2001). The few works dealing with the results of these enterprises, however, already demonstrated strong geographic and stratigraphic biases, which may have impact on our understanding of Romualdo Formation pterosaur taxonomy and diversity.

The yet incipient results derived from controlled excavations on the Romualdo Formation already demonstrate clear evidence for faunal turnover, through the substitution of a basal fish assemblage dominated by the gonorynchiform *Tharrhias* by upper strata where the most abundant taxon is the aspidorhynchid *Vinctifer* (Fara et al., 2005). Possible reasons for this faunal interchange have still not been investigated. However, considering the presumable low deposition rate of the shales that embed Romualdo Formation fossil concretions, it is likely that a substantial time interval was associated with this turnover.

The temporal resolution of Romualdo Formation fossils was never estimated and several events of mass mortality probably took place (Fara et al., 2005; Vila Nova et al., 2001). Thus, based on the present stage of knowledge, it is likely that some of the Romualdo Formation pterosaurs were not coeval, which could also be an explanation for the high number of similar species of anhanguerians in the same geological unit. Thus, it is possible that different *Anhanguera*-like morphotypes may represent subtle morphological changes in a lineage undergoing anagenetic evolution. A similar pattern

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Comentario [GP13]: This sentence should be revised, maybe rephrase it for clarification.

Con formato: Resaltar

Comentario [GP14]: And what are the main characters that diagnose these Anhanguera-like morphotypes? I think that the manuscript needs a table to show the species of Anhanguera that you consider valid, a character that may be useful to diagnose them and a specification of the number of specimens of each valid species that are available for revision.

was proposed by Bennet (1994) for different *Pteranodon* species (but see Kellner, 2010). Stratigraphically controlled excavations, such as the ones reported by Fara et al. (2005) and Vila Nova et al. (2001) hopefully will shed light on this issue.

Conclusions

Even though more than a dozen relatively complete skulls referable to the Anhangueridae and closely related taxa are nowadays held in public collections, this is the first study to perform a more comprehensive morphometric analysis of continuous traits seen in skulls of this clade. As a result, characters related to both height and anteroposterior extension of the premaxillary crest are found to be statistically correlated to skull size. The observation that anhanguerid crest morphology is size-dependent makes it unfit to be used as diagnostic for the genus ~~species~~, as has been commonly proposed for this group. A taxonomic review excluding these characters reveals that as few as three *Anhanguera* species are potentially valid: *A. blittersdorffi*, *A. piscator* and *A. spielbergi*. The significance of the minor, continuous differences between specimens is still not entirely clear, though. Controlled stratigraphic studies on the Romualdo Formation demonstrate faunal turnover in fishes, and the same could be true ~~regarding~~ also for pterosaurs. Thus, the seemly continuous morphological changes observed in anhanguerids could be explained by anagenetic evolution. However, as virtually all pterosaur specimens from this unit lack fundamental stratigraphic information, it is impossible to assert this hypothesis at this point.

Comentario [GP15]: If you revised Just one single specimen representing each species of Anhangurea, then you Just found results for the genus.

Acknowledgments

For granting access to AMNH 22555 and other pterosaur specimens, the authors are particularly indebted to Mark Norell and Carl Mehling (AMNH). Also, we would like to thank the following people for allowing the study of specimens under their care and for kind help during visits: Álamo Saraiva and João Kerensky (MPSC); Oliver Rauhut and Markus Moser (SNSB-BSPG); Alexander Kellner and Helder Silva (MN); Eberhard Frey (SMNK); Rainer Schoch (SMNS); Sandra Chapman and Lorna Steel (NHMUK); Dan Pemberton and Matt Riley (CAMSM); Stephen Hutt (IWCMS); David Gelsthorpe (MANCH); Urs Oberli (SAO); Jon de Vos (Naturalis); Mauro Bon (MSN); and Wang

Xiaolin (IVPP). FLP thanks Cesar Schultz for advisement on pterosaurs, TR thanks Alexander Kellner for advisement and support. We also acknowledge Pedro Godoy (University of Birmingham) for comments and suggestions on the methodology applied here, as well as Renan Bantim and an anonymous referee for valuable comments on an early version of this paper.

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Legends to the figures

Figure 1. Location map of the Araripe Basin, northeastern Brazil and simplified stratigraphic chart of the Santana Group. Levels where pterosaur fossils are found are indicated. Modified from Pinheiro & Schultz (2012).

Figure 2. Specimen AMNH 22555, a partial anhanguerid skeleton. Some selected elements are figured in detail. A, pelvic region in dorsal view; B, torso in dorsal view; C, D, E, sixth cervical vertebrae in, respectively, anterior, dorsal and right lateral views; F, G, right mandibular ramus in, respectively, medial and lateral views; H, left scapula in dorsal view; I, left coracoid in lateral view; J, distal carpals in distal view; K, proximal carpals in distal view. Scale bars equal to 50 mm. Line drawings of some bones were modified from Witton (2013).

Figure 3. Geometric morphometric analysis of twelve skulls referable to *Anhanguera* (red dots) and closely related taxa (blue dots) of the regression score on centroid size log. Used landmarks are plotted in the skull of *Anhanguera blittersdorffi* holotype. Deformation grids and wireframe graphs display morphological components predicted by allometry in *Barbosania* (red) and *Tropeognathus* cf. *mesembrinus* (blue).

Figure 4. Interpretative drawings of AMNH 22555 skull in A, right lateral, B, dorsal and C, palatal views. Abbreviations: ch, choanae; ec, ectopterygoid; fp, frontoparietal; j, jugal; l, lacrimal; m, maxilla; n, nasal; naof, nasoantorbital fenestra; op, opisthotic; pf, prefrontal; pl, palatine; po, postorbital; pm, premaxilla; pt, pterygoid; q, quadrate; so, supraorbital; sq, squamosal; v, vomers. Scale bar equals 100 mm.

Figure 5. Comparison between the skulls of AMNH 22555 and *Anhanguera santanae* holotype (SNSB-BSPG 1982 I 90). A, AMNH 22555 skull in lateral view; B, Interpretative drawing of the photo in A. C, *Anhanguera santanae* (SNSB-BSPG 1982 I 90) skull in lateral view (mirrored); E, F, G, H, palatal views and interpretative drawings of, respectively, AMNH 22555 and *A. santanae* (SNSB-BSPG 1982 I 90) skulls; I, J, interpretative drawings of the occipital views of, respectively, AMNH 22555 and *A. santanae* (SNSB-BSPG 1982 I 90) skulls. Scale bar equal to 100 mm in A, B, C, D, E, F, G, H, and 50 mm in I, J. Abbreviations: ch, choanae; fpc, frontoparietal crest; lpj, lacrimal process of jugal; pr, palatal ridge; ptf, posttemporal fenestra; soc, supraoccipital crest.

Figure 6. Overview of the holotypes of several *Anhanguera* species. A, *Anhanguera blittersdorffi* (MN 4805-V) in lateral view. B, C, F, “*Anhanguera araripensis*” (SNSB-BSPG 1982 I 89) in dorsal, ventral, and lateral views, respectively. D, detail of C; arrow points a lateral projection of the pterygoid. E, detail of the *Tropeognathus mesembrinus* (SNSB-BSPG 1987 I 46); arrow points a bulge laterally on the pterygoid. G, H, holotype of “*Anhanguera robustus*”(SNSB-BSPG 1987 I 47) in dorsal and lateral views, respectively. I, holotype of *Anhanguera spielbergi* (RGM 401 880) in lateral view.