



A new pterosaur mandible from the Lower Cretaceous of Brazil, and its implications on the taxonomy of the genus *Anhanguera* (Pterosauria, Anhangueridae)

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ABSTRACT

Pterosaurs are extinct archosaurs specialized in an active flight lifestyle, with more than half of the species described classified as pterodactyloids. Much of the anatomical knowledge on pterodactyloids originated from specimens collected in the Cretaceous deposits of South America. The Araripe Basin in Northeastern Brazil holds a remarkable record, particularly within the Aptian–Albian Crato and Romualdo formations, from which numerous specimens have been assigned to the genus *Anhanguera*. To date, three species from this unit are recognized as valid based on relatively complete specimens: *A. blittersdorffi*, *A. piscator*, and *A. spielbergi*. Here, we describe a new anhanguerid specimen from the Romualdo Formation, comprising an almost complete lower jaw and elements of the hyoid apparatus. MZSP-PV 368 is assigned to *Anhanguera* based on the presence of a well-developed ventral mandibular crest, specific alveoli count, and tooth morphology. The specimen has an overall shape of the crest that is unique among ornithocheiromorphs and supports its referral to *A. robustus*, a species recently considered a *nomen dubium*. Phylogenetic and morphometric analyses of MZSP-PV 368 further support its affinity with *A. robustus*, highlighting the diagnostic value of mandibular crest morphology in anhanguerid taxonomy. These findings indicate that *A. robustus* represents a diagnosable taxon, herein recognized as a valid species. However, the taxonomy of the genus *Anhanguera* remains unresolved and will require additional specimens with a greater degree of anatomical overlap for further clarification.

1. Introduction

Pterosauria represents the earliest known group of vertebrates to have evolved powered flight (Alexander, 2015). Of the approximately 200 species described, more than half are assigned to the clade Pterodactyloidea (Andres, 2021), with some of the most significant fossil records being known from Cretaceous deposits of South America (Pentland and Poropat, 2023). In Brazil, pterosaurs are particularly well represented in the Lower Cretaceous Araripe Basin, where the abundance and exceptional preservation of specimens have facilitated extensive research on pterosaurian anatomy, paleobiology, and paleoecology (e.g. Chatterjee and Templin, 2004; Costa et al. 2014).

Within the Araripe Basin, anhanguerids are the most abundant tetrapods recovered from the Lower Cretaceous (Aptian–Albian) Romualdo

Formation (Bom et al. 2023). This assemblage includes well-known genera such as *Anhanguera* Campos and Kellner, 1985, *Tropeognathus* Wellnhofer, 1987, and *Maaradactylus* Bantim, Saraiva, Oliveira & Sayão (2014), as well as closely related taxa like *Santanadactylus* de Buissonjé, 1980; *Cearadactylus* Leonardi and Borgomanero, 1985, alongside numerous referred specimens (e.g. Wellnhofer, 1985; Frey and Martill, 1994; Veldmeijer et al. 2006; Duque and Barreto, 2018; Duque et al. 2023). Although anhanguerids have been documented from multiple localities worldwide (e.g., Rodrigues and Kellner, 2013; Holgado and Pêgas, 2020; Pêgas et al. 2021a; Pentland et al. 2024; Pêgas, 2025), the Romualdo Formation remains exceptional for yielding an extensive number of nearly complete and three-dimensionally preserved specimens (Kellner and Tomida, 2000; Veldmeijer, 2003).

The genus *Anhanguera*, originally described based on a complete

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skull (Campos and Kellner, 1985), has a complex and debated taxonomic history. Over time, six species have been proposed as valid, primarily distinguished by subtle variations in the morphology of the premaxillary crest (Rodrigues and Kellner, 2008). However, Pinheiro and Rodrigues (2017) challenged this classification through a geometric morphometric analysis, demonstrating that premaxillary crests in anhanguerids should be evaluated cautiously as a source of autapomorphic characters due to the potential influence of sexual dimorphism and ontogenetic variation (see Bennett, 1992; Manzig et al. 2014; Wang et al. 2014a). Since the study by Pinheiro and Rodrigues (2017), only three species are considered valid. The type species, *Anhanguera blittersdorffi* Campos and Kellner (1985), is represented by the holotype MN 4805-V, a relatively complete, three-dimensionally preserved skull. Two additional species are recognized based on nearly complete skeletons with skulls and lower jaws: *Anhanguera piscator* Kellner and Tomida (2000), with the holotype NSM-PV 19892, and *Anhanguera spielbergi* (Veldmeijer, 2003), with the holotype RGM 401 880 originally described as a new species of *Coloborhynchus* Owen (1874). In contrast, three species are considered dubious: '*Anhanguera araripensis*' (Wellnhofer, 1985), originally described in the genus '*Santanadactylus*' Buisonjé (1980), and '*Anhanguera santanae*' (Wellnhofer, 1985), originally described in the genus '*Araripesaurus*' Price, 1971, were both based on incomplete skulls associated with appendicular elements (BSP, 1982 I 89 and BSP, 1982 I 90, respectively), while *Anhanguera robustus* (Wellnhofer, 1987), originally described as a species of *Tropeognathus* (Wellnhofer, 1987), is based on a complete lower jaw (BSP, 1987 I 47), and was later reassigned to *Anhanguera* (Kellner and Campos, 1988).

Here, we describe a new pterosaurian specimen from the Aptian–Albian Romualdo Formation, MZSP-PV 368, which comprises an almost complete lower jaw and elements of the hyoid apparatus, identified as ceratobranchials. This specimen exhibits a combination of morphological traits that support its assignment to the genus *Anhanguera*. Additionally, we conducted a geometric morphometric analysis using a dataset that includes crested mandibles of pteranodontoid pterosaurs to assess the morphological variation and its implications for the taxonomic affinities of MZSP-PV 368. Furthermore, a phylogenetic analysis was performed, incorporating all *Anhanguera* specimens with preserved lower jaws as operational taxonomic units (OTUs), aiming to explore systematic patterns in mandibular morphology and clarify the relationships of the new specimen within *Anhanguera*.

2. Geological settings

The breakup of the supercontinent Gondwana, which led to the separation of South America and Africa and the opening of the Atlantic Ocean, had varying geological effects across northeastern Brazil (Assine, 1992, 2007). Among the resulting sedimentary basins in the region, the Araripe Basin is the most extensive and possesses a complex geological history (Fig. 1A and B). The Aptian–Albian deposits of northeastern Brazil reflect transgressive and regressive marine cycles, driven by thermal subsidence and global eustatic sea-level fluctuations (Fabini et al. 2018). These processes facilitated the deposition and preservation of marine sediments, forming an almost complete sedimentary cycle, though truncated at the top, lacking high-sea alluvial system facies at its uppermost levels (Assine, 2007).

The rift sequence of the Araripe Basin (Aptian–Albian) marks the initial phase of the continental post-separation, influenced by thermal flexural subsidence (Assine, 2007). This sequence corresponds to the Santana Group (Valença et al. 2003), which encompasses the Rio da Batateira, Crato, Ipupi, and Romualdo formations. The upper section of the Romualdo Formation is predominantly characterized by a transgressive sequence of green and black shales (Bom et al. 2023). Within the black shales, multiple layers rich in carbonate concretions exhibit lateral continuity throughout the Basin (Fara et al. 2005; Saraiva et al. 2007; Vila Nova et al. 2011).

These concretions played a crucial role in the exceptional

preservation of the Romualdo Formation biota (see Maisey, 1991). The fossil record includes several palynomorphs and plant remains (e.g. Arai and Assine, 2020; Batista et al. 2021), along with a diverse assemblage of metazoan remains, including coquinas of echinoderms and mollusks (e.g. Prado et al. 2018), and rare specimens of fossil crustaceans (e.g. Lima et al. 2023). Among the vertebrate fauna, fishes represent the most abundant specimens recovered (e.g. Brito and Yabumoto, 2011; Barbosa et al. 2022; Barreto et al. 2022), but turtles (e.g. Scheyer et al. 2023) and crocodilians (e.g. Kellner, 1987) are also recorded, including an exceptionally rare occurrence of an egg with crocodilian affinities (Abreu et al. 2020). Dinosaur remains are less commonly recovered from this unit, but comprises well-preserved specimens (e.g. Sales and Schultz, 2017; Sayão et al. 2020; Schade et al. 2023). Nevertheless, the most abundant tetrapods recovered from the Romualdo Formation are pterosaurs, particularly anhanguerids (Maisey, 1991; Kellner and Tomida, 2000; Pentland and Poropat, 2023; Bom et al. 2023).

3. Material and methods

3.1. Curatorial history

The exact provenance and collection date of MZSP-PV 368 is uncertain, as it belonged to the historical collection formerly housed at the Museu do Estado (currently the Museu Paulista da Universidade de São Paulo), established in 1890. With the foundation of the Department of Zoology of the Secretariat of Agriculture, Industry and Commerce of the State of São Paulo, in the beginning of the 1940's, all natural history collections housed at the Museu Paulista were transferred to this new repository. Finally, in 1969, the collections were integrated to the current Museu de Zoologia da Universidade de São Paulo (MZUSP). Although the specimen lacks any detailed information about its provenance in the old inventory books, its carbonate concretion surrounding matrix and mostly uncrushed and tridimensional state of preservation indicates that it comes from the Lower Cretaceous (Aptian–Albian) Romualdo Formation of the Araripe Basin in northeastern Brazil (Fig. 1).

3.2. Chemical preparation

The new specimen underwent chemical preparation, following the protocols established by Grant (1989). MZSP-PV 368 was subjected to formic acid (Methanoic acid, HCOOH or HCO₂H) treatment at concentrations ranging from 1 % to 3 %, buffered with tribasic calcium phosphate to minimize matrix dissolution. When necessary, mechanical preparation techniques were applied in accordance with the protocols of Chaney (1989), May et al. (1994), Palmer (1989), and Sohl (1989). To consolidate the specimen and reattach fractured elements, a cyanoacrylate-based adhesive (Paraloid B72) was applied, following the procedures outlined by Wolberg (1989). All preparation work was carried out at the Paleontology Laboratory of the MZUSP, where the specimen is housed and fully accessible for scientific research. All images produced upon completion of the preparation process were processed and edited using Krita v5.2.3 (Ettrich, 1998).

3.3. Morphometric analyses

Two two-dimensional geometric morphometrics analyses were conducted to assess the significance of size, shape, and position of the mandibular crest relative to the tooth row, as well as to evaluate their implications for the characterization and diagnosis of anhanguerids and closely related taxa that possess such crests. Additionally, both analyses tested the morphological congruence between MZSP-PV 368 and other anhanguerid specimens.

A total of 10 specimens were included in the analysis, selected based on the preservation status of the anterior portion of the symphysis and the mandibular crest. Specimens with significant missing or poorly preserved regions of interest, such as Pz-DBAV-UERJ 40 and SAO 16494,

were excluded. The dataset included holotypes of *A. piscator* (NSM-PV, 19892), *A. spielbergi* (RGM 401 880), and *A. robustus* (BSP, 1987 I 47), along with the referred specimens SMNK PAL 2302, SAO 200602, and the newly described MZSP-PV 368. Additionally, the analysis incorporated other anhanguerids such as the holotype of *Tropeognathus mesembrinus* Wellnhofer (1987); BSP 1987 I 46) and a referred specimen with a complete lower jaw (SMNS 56994). Closely related taxa were represented by the holotype (IVPP V18199) and the referred specimen (IVPP V18406) of *Ikrandraco avatar* Wang, Rodrigues, Jiang, Cheng &

Kellner (2014b).

Using standardized lateral-view photographs of the specimens, a total of 19 landmarks were defined and plotted for each specimen (Fig. 2). Eleven of these landmarks correspond to the anterior-most margin of each of the first eleven alveoli relative to the dorsal margin of the jaw. Landmarks 12 and 13 represent, respectively, the ventral-most tip and the posterior-most limit of the dentary crest. Additionally, six semi-landmarks were added in order to quantify the curvature of the anterior half and the posterior half of the crest (Gunz and

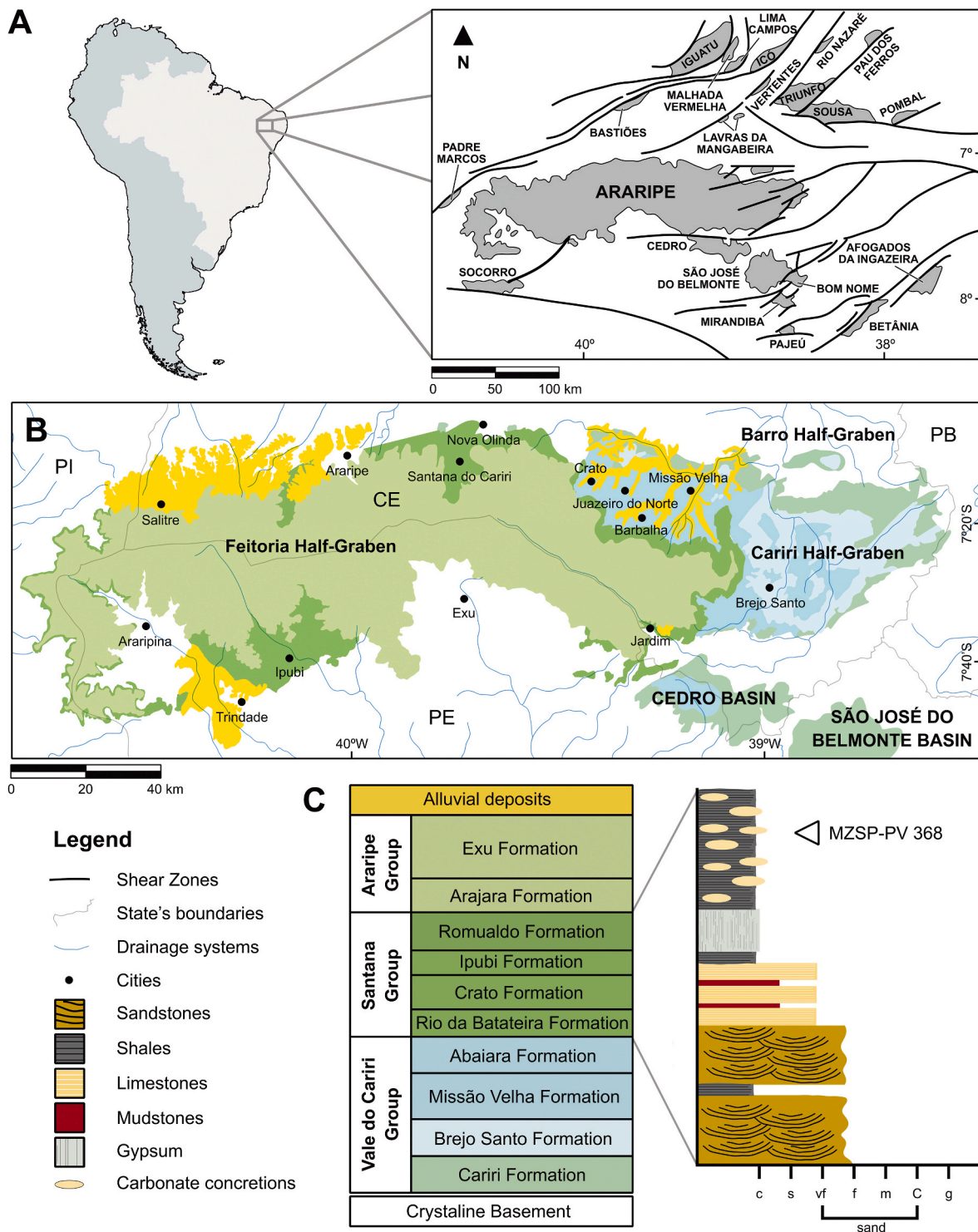


Fig. 1. Geographic and geologic provenance of the new *A. robustus* lower jaw (MZSP-PV 368): (A) Map of South America highlighting the Araripe Basin and adjacent basins; (B) Geological section of the rift sequence (Santana Group); (C) Stratigraphic position of MZSP-PV 368. Modified from Pinheiro and Rodrigues (2017).

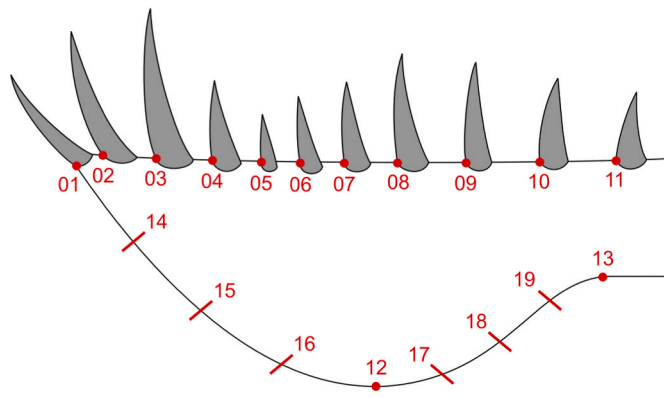


Fig. 2. Used landmarks plotted and numbered in the drawing of a hypothetical lower jaw of *Anhanguera*, with landmarks represented as dots and semi-landmarks represented as lines. The hypothetical lower jaw of *Anhanguera* was redrawn based on all specimens shown in Fig. 8.

Mitteroecker, 2013). In this manner, three semi-landmarks were positioned between landmarks 1 and 12, and the remaining three between landmarks 12 and 13, dividing both the anterior and posterior halves of the crest into three segments of comparable proportions, each. This configuration ensures that the first 11 landmarks capture the position of the teeth along the jaw, while landmarks 12 and 13, together with the six semi-landmarks, reflect the size, shape, curvature, position, and orientation of the mandibular crest relative to the tooth row and the overall jaw morphology. Landmarks were digitized using TPSDig2 v2.16 (Rohlf, 2010), and all analyses were performed in PAST v4.1 (Hammer, 2001; Hammer et al. 2001). Following Procrustes superimposition, Principal Component Analysis (PCA), and Linear Discriminant Analysis (LDA) were conducted to investigate morphometric variation, facilitating comparisons between the two methodologies (see Supplementary Material).

3.4. Phylogenetic analyses

The specimen MZSP-PV 368 was included in a phylogenetic analysis to evaluate its affinities within Pterosauria. We used a modified version of the data matrix from Pêgas (2024), which currently represents the most comprehensive phylogenetic dataset available for pterosaurs. To improve the representation of mandibular morphology within the genus *Anhanguera*, we incorporated four OTUs at specimen level: MZSP-PV 368, SMNK PAL 2302 (originally assigned to *A. robustus*; Fastnacht, 2001), SAO 200602 (originally considered an indeterminate specimen of *Anhanguera*; Veldmeijer et al. 2005; BSP 1987 I 47, the holotype of *A. robustus* (Wellnhofer, 1987). Additionally, we introduced a new character (character 520) to account for variation in the shape of the anterior margin of the dentary crest, distinguishing between a curved (state 0) and a straight (state 1) morphology. The final dataset (see Supplementary Material) comprises 521 characters and 196 terminal taxa. The phylogenetic analysis was conducted using TNT v1.5 (Goloboff, 1999; Goloboff and Catalano, 2016), following the same search parameters as in Pêgas (2024).

3.5. Computed tomography (CT) scanning

The specimen MZSP-PV 368 was X-ray CT-Scanned using a medical tomograph Siemens Emotion 16, in a partnership with the Departamento de Radiologia e Oncologia of the Instituto de Radiologia (InRad), by the Plataforma de Imagem na Sala de Autópsia (PISA) at Hospital das Clínicas da Faculdade de Medicina da Universidade de São Paulo (HCFMUSP). The slice thickness of the scans is 0.75 mm and the data was reconstructed with layer thickness between 0.75 GD at 130 kVp, and image size of 512x512 pixels. The resulting tomographic slices were

processed and segmented using VGStudio MAX v2024.4 64 bits, available at the Multi-User Laboratories of the MZUSP. The raw 3D data is available at MorphoSource (ark:/87602/m4/757259). The rendered images were treated and edited using Krita v5.2.3 (Ettrich, 1998).

3.6. Institutional abbreviations

- AMNH, American Museum of Natural History, New York, USA.
- BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.
- CP, Centro de Pesquisa Paleontológica da Universidade do Contestado, Mafra, Brazil.
- DGEO, Universidade Federal de Pernambuco, Recife, Brazil.
- DBAV, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil.
- DGM, Museu de Ciências da Terra, Rio de Janeiro, Brazil.
- IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.
- MN, Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.
- MPSC, Museu de Paleontologia de Santana do Cariri, Santana do Cariri, Brazil.
- MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
- NHMUK, Natural History Museum, London, UK.
- NSM, National Science Museum, Tokyo, Japan.
- 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.
- SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

4. Description and comparisons

4.1. General description and preservation state

MZSP-PV 368 consists of an almost complete lower jaw associated with fragments of hyoid bones. The lower jaw is elongated, laterally compressed, and straight in lateral view (Fig. 3). As with other anhanguerid symphysis, MZSP-PV 368 presents an extended symphysis with diverging rami in both dorsal and ventral views (Fig. 4A and B). Anteriorly, a ventral dentary sagittal crest is present, while the posterior half of the rami exhibits a subtle posteromedial curvature. This lower jaw closely resembles BSP 1987 I 47, the holotype of *A. robustus* (Wellnhofer, 1987), regarding gross morphology, the configuration of the alveoli, and most aspects of the crest (Figs. 5 and 6). A small and long bone is associated ventrally with the left mandibular ramus, alongside additional elements that were originally disarticulated from the jaw. All bones are preserved three-dimensionally, allowing for the identification of sutures where present, although these are generally difficult to discern. The fossil was originally encased within a concretion that was broken into six pieces. Most of these fragments remained largely intact, containing the symphysis along with the crest, and the right mandibular ramus. The piece which comprises nearly the entire left mandibular ramus lost its contact surface with the symphysis due to erosion. This region suffered significant alveolar damage, primarily due to extensive crystallization of an unknown mineral, possibly calcite, though remnants of some alveoli are still recognizable. Restoration work was required to reassemble the fragments before chemical preparation. Additionally, associated material — including small fish vertebrae and disarticulated hyoid bones — was separated from the jaw during the final stages of preparation.

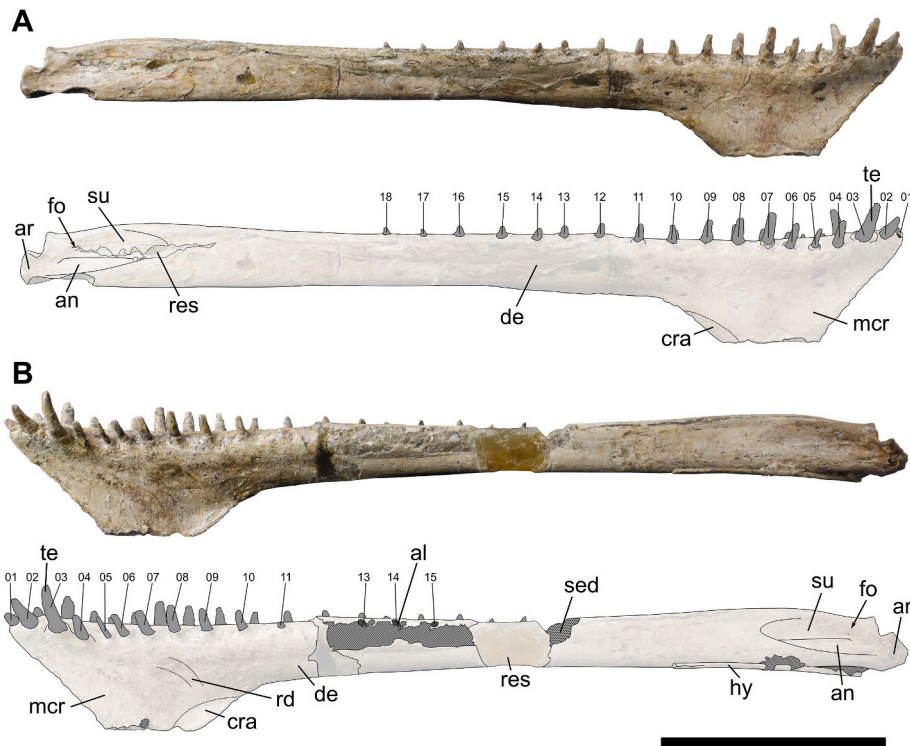


Fig. 3. New *A. robustus* lower jaw (MZSP-PV 368): (A) right lateral view and interpretative drawing; (B) left lateral view and interpretative drawing. Teeth and alveoli are numbered alongside the jaw starting from the anterior-most pair. The mandibular crest anomaly is indicated by a dotted line. Anatomical abbreviations: al, alveolus; an, angular; ar, articular; cra, crest anomaly; de, dentary; fo, foramen; hy, hyoid; mcr, mandibular crest; rd, ridge; res, resin; sed, sediment; su, surangular; te, teeth. Scale bar equals 10 cm.

4.2. Mandible

4.2.1. Dentary

Both dentaries are elongated bones that comprise the majority of the lower jaw (Fig. 3). Anteriorly, they are fused into a symphysis, though the sutures are difficult to distinguish. A sagittal crest, formed by the dentaries, is present on the anteroventral surface of the symphysis, with its boundaries defined by the limits of the symphysis itself.

The rostral tip is rounded and, in anterior view, this region provides the clearest view of possible suture scars from the symphysis (Fig. 7A). Posterior to the tip, the rostrum expands laterally in a spoon-shaped morphology, a feature characteristic of anhanguerians (Rodrigues and Kellner, 2013) that may be absent in rare exceptions, which is the case in Australian taxa (Pentland et al. 2019, 2024). The expansion in MZSP-PV 368 reaches its greatest width between the second and third pairs of alveoli (Fig. 4A and B). A few small foramina are scattered across the rostral tip in anterior view (Fig. 7A). The symphysis gradually narrows along the mandible until the eleventh alveolar pair, where it then expands again before the rami separate. Just before this division, the symphysis forms a symphyseal shelf at its posterior limit, though no symphyseal cavity is present. Notably, the symphysis is exceptionally long, accounting for nearly half of the mandible's total length (Table 1).

A shallow longitudinal sulcus, flanked by two low ridges, extend along most of the symphysis (Fig. 4A). Despite this, the occlusal surface is predominantly flat to slightly concave, with rounded occlusal margins throughout the jaw. The overall morphology of the symphysis is remarkably similar to that of *A. robustus* (BSP, 1987 I 47), including the presence of a dorsal shallow groove, (Fig. 6A). Some damage in the central region has allowed for infiltration of sediment during fossilization. In the posterior portion of the symphysis, between the alveolar rows, a pair of short, shallow sagittal grooves extend across the symphyseal shelf from alveoli 13 to 17, a feature that in BSP 1987 I 47 extends from alveoli 12 to 17 (Fig. 6A).

The dentary crest is well developed, positioned ventrally along the symphysis (Fig. 3), and accounts for nearly one-third of the mandible's length (Table 1). Anteriorly, it begins at the rostrum, following the natural curvature of the symphysis, and posteriorly, it merges with the ventral margin of the mandible between the tenth and eleventh alveolar pairs. Laterally, the crest exhibits a blade-like, trapezoidal shape, with the ventral surface forming the smaller base, while the anterior and posterior surfaces are straight and nearly perpendicular to one another. However, this trapezoidal shape is because of the ventral surface being damaged, with the apex missing, which causes this region to appear straightened. The anterior and posterior surfaces form an angle of approximately 45°–50° relative to the dorsal margin of the jaw, a feature also observed in BSP 1987 I 47 (Fig. 5) and other specimens related to *A. robustus* (Wellnhofer, 1987; Kellner and Tomida, 2000). Extrapolating the results of Pinheiro and Rodrigues (2017) regarding mandibular crests, the pronounced height of this crest suggests that MZSP-PV 368 represents at least a subadult individual (estimated wingspan $\approx$ 4 m), despite being significantly smaller in overall mandibular length compared to most known specimens of *Anhanguera* (Fig. 8).

Several aspects of the crest show indications of taphonomic distortion. On the left lateral side, a large, curved, shallow and broken concavity is present (Fig. 7C), and the posteroventral region of the crest exhibits a subtle leftward twist. No bony calluses, cracks, or other indicators of postmortem damage are present in these areas (Fig. 7A and C), suggesting that this concavity may have occurred during the specimen's life, being possibly a pathology, though this interpretation remains tentative. The lateral surfaces of the ventral portion of the crest displays a rugose texture, indicative of a keratinized covering, such as a rhamphotheca, or the presence of overlying soft tissue (Kellner and Tomida, 2000). Additionally, deep channels resembling blood vessel scars are present (Fig. 7C), similar to those observed on the cranial crest of the anhanguerid specimen MN 6594-V, attributed to *Tropeognathus* cf. *mesembrinus* (Kellner et al. 2013), as well as DGM 1476-R, the holotype

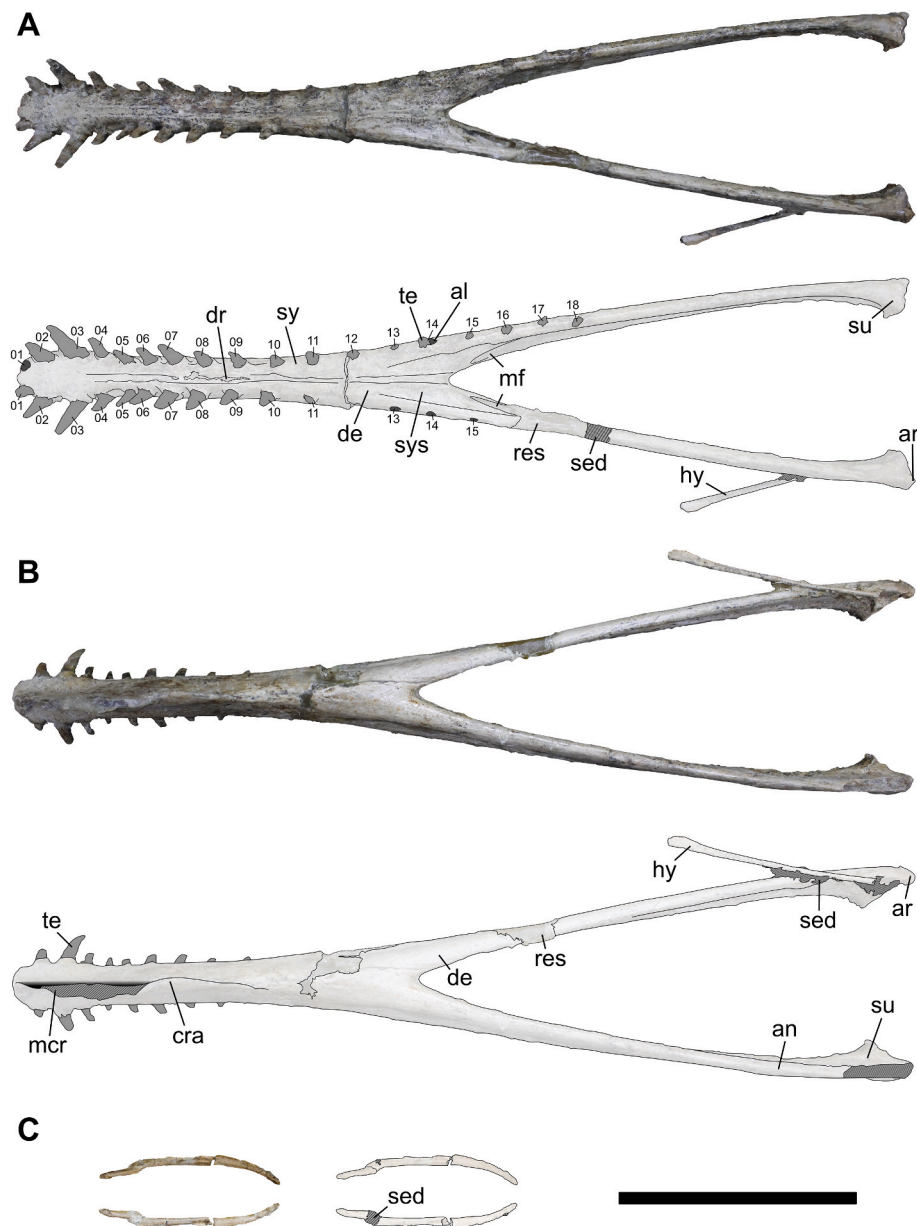


Fig. 4. New *A. robustus* lower jaw (MZSP-PV 368): (A) dorsal view and interpretative drawing; (B) ventral view and interpretative drawing; (C) the two hyoid elements associated with MZSP-PV 368, and interpretative drawing. Teeth and alveoli are numbered alongside the jaw starting from the anterior-most pair. Anatomical abbreviations: al, alveolus; an, angular; ar, articular; cra, crest anomaly; de, dentary; dr, damaged region; hy, hyoid; mcr, mandibular crest; mf, meckelian fossa; res, resin; sed, sediment; su, surangular; sy, symphysis; sys, symphyseal shelf; te, teeth. Scale bar equals 10 cm.

of *Thalassodromeus sethi* Kellner and Campos 2002; Pêgas et al. 2018). Although this pattern is common among anhanguerids, some specimens, such as BSP 1987 I 46, the holotype of *Tropeognathus mesembrinus* (Wellnhofer, 1987), appear to have smooth crests lacking rugose surfaces or vascular impressions. However, in the case of BSP 1987 I 46, surface damage to the cortical bone may have obscured such features, highlighting the need for further studies to clarify crest variability among anhanguerids of the Santana Group.

The dentaries also form the majority of the mandibular rami, which exhibit an overall convex dorsal surface. Laterally, the symphysis runs subparallel to the mandibular rami, which themselves are straight. The dentaries extend into the posterior half of the mandibular ramus, lying beneath the dorsal portion of the surangular and effectively separating most of the surangular from the angular. This contact pattern is observable on both rami, though the right mandibular ramus is significantly damaged in this region (Fig. 3A). A similar pattern is seen in BSP

1987 I 47, the holotype of *A. robustus* (Fig. 5) and is comparable to the right lateral view of NSM-PV 19892, the holotype of *A. piscator* (Kellner and Tomida, 2000). Medial boundaries between the dentaries and other elements of the lower jaw are challenging to determine due to extensive fracturing of both rami, particularly on the left side.

4.2.2. Meckelian fossa

Both Meckelian fossae are well preserved, with their anterior margins clearly delineated (Fig. 9). They begin posterior to the symphyseal shelf, situated medially in the rami, and have an anteroposteriorly elliptical shape, similar to that observed in BSP 1987 I 47 (Fig. 6A). While the posterior margin of the left fossa is missing, the right fossa remains largely intact, with its posterior border extending between the alveolar pairs 16 and 17.

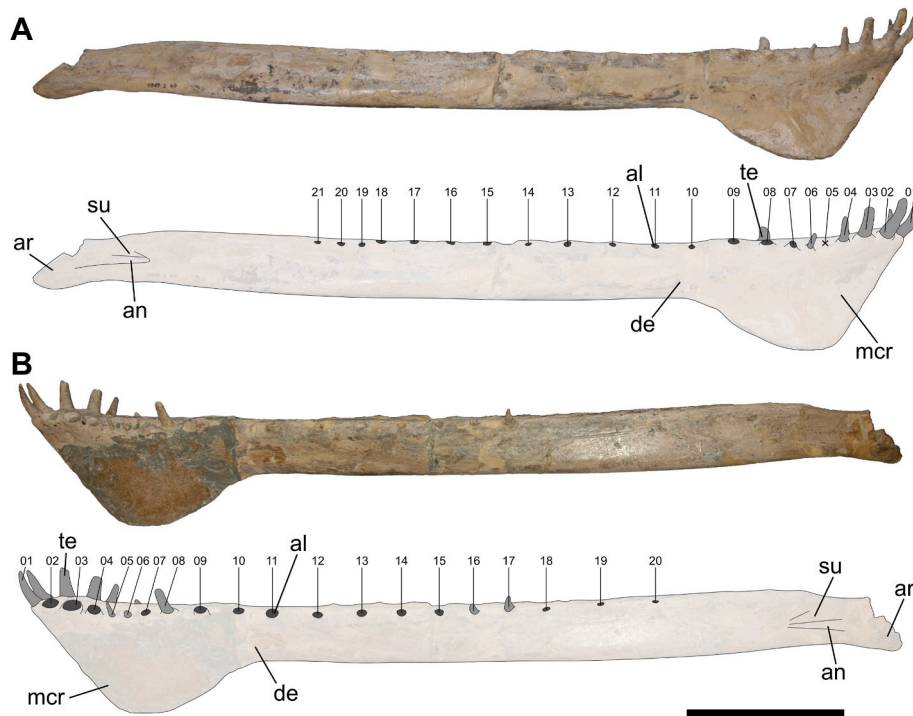


Fig. 5. The holotype of *A. robustus* (BSP, 1987 I 47): (A) right lateral view and interpretative drawing; (B) left lateral view and interpretative drawing. Teeth and alveoli are numbered alongside the jaw starting from the anterior-most pair. Anatomical abbreviations: **al**, alveolus; **an**, angular; **ar**, articular; **de**, dentary; **mcr**, mandibular crest; **su**, surangular; **te**, teeth. Scale bar equals 10 cm.

4.2.3. Splenial

The splenial comprises most of the medial surface of the mandibular ramus (Fig. 9). It extends posteriorly from the Meckelian fossa, positioned dorsal to the angular and ventral to both the dentary and surangular, reaching as far as the adductor fossa. However, a combination of extensive damage, during fossilization, and possible fusion between the splenial bones and other elements of the lower jaw, in both rami, has obscured most of the bone's boundaries, making it difficult to determine its precise contacts. Small foramina, possibly representing neurovascular foramina, are visible in some regions of the left ramus (Fig. 9B).

4.2.4. Adductor fossa

Both adductor fossae are well preserved, with most of their shape exposed on both rami (Fig. 9). These structures are elongate and narrow, occupying approximately one-sixth of the mandibular length. The surangular forms the posterior and dorsal margins of the fossa, while the anterior and ventral margins remain indeterminate due to extensive fusion and cracking of the sutures.

4.2.5. Angular

The angular is a relatively elongated bone that, in lateral view, contacts the surangular dorsally and the dentary anteroventrally (Figs. 3 and 9). In ventral view, it extends anteriorly, forming the posterior portion of the medioventral surface of the rami. Its ventral limits and contacts with adjacent bones are difficult to establish because of their poor preservation. While the right ramus has lost its angular and articular contact, this connection is well preserved on the left side, where the articular meets the angular posterodorsally.

4.2.6. Surangular

In both mandibular rami, the lateral portion of the surangular is clearly visible, bordered anterodorsally by the dentary and ventrally by the angular (Figs. 3 and 4B). The contact between the surangular and the angular forms a straight suture, a morphology also observed in NSM-PV 19892, the holotype of *A. piscator* (Kellner and Tomida, 2000), as well as

on both sides of BSP 1987 I 47, the holotype of *A. robustus* (Fig. 5). A very small foramen, possibly a neurovascular foramen, is present immediately dorsal to the surangular-angular suture and remains discernible on both rami (Fig. 3), even though the right ramus is damaged in this region. In dorsal view, the surangular extends posteriorly over the glenoid fossa, forming the dorsal portion of the concave cotyles that articulate with the condyloid processes of the skull. Anteriorly, the surangular extends along the posterior portion of the dorsal surface of the ramus. However, due to preservation bias, the exact dorsal boundary between the dentary and surangular is difficult to determine. Additionally, crushing artifacts obscure the medial limits of the surangular on both rami, making precise identification challenging.

4.2.7. Prearticular

In medial view, a bone positioned anterior to the articular and ventral to both the surangular and the adductor fossa is interpreted as the prearticular (Fig. 9). It is a long, slender element that extends posteroventrally in medial view. Following Veldmeijer (2003) for *A. spielbergi* and Bennett (2001) for *Pteranodon Marsh, 1876*, it reaches the concave surface of the articular and partially contributes to the composition of the retroarticular process, however the contact between the prearticular and the articular appears to be fused and obliterated on the right ramus, while the putative contact region on the left ramus is covered in sediment. In both rami, the prearticular maintains contact anteriorly with the splenial, though these contacts are very fragmented.

4.2.8. Articular

The articular is the smallest bones in the lower jaw, yet it remains relatively elongated. The regions that are damaged in one ramus are preserved in the other ramus, allowing for comparative description between both rami. Along with the surangular, the articular contributes to the formation of the concave glenoid fossa, which articulates with the condyloid process of the skull (Fig. 9). The articular forms the medial and lateral cotyles of the glenoid fossa, while the surangular composes the lateral and medial ridges dorsal to the cotyles (Fig. 10).

The posteroventral extension of the articular, together with the posterior extension of the angular, forms the retroarticular process, which is positioned posteroventral to the glenoid fossa and constitutes the posterior-most portion of the lower jaw (Fig. 10). In lateral view, this process is anteroposteriorly short, relative to the length of the mandibular rami (Fig. 3), with a sub-horizontal orientation and a subtriangular shape, featuring acute angles formed by the straight dorsal, posterior and ventral margins, and a continuous axis without a constricted posterior expansion. The process, in this manner the dorsal margin, forms a right angle with the articular facet of the glenoid fossa in lateral view (Fig. 3). A distinct oblique ridge separates the glenoid fossa from the retroarticular process, running in a posterolateral-to-anteromedial direction (Fig. 10). The medial surface of the process is concave, and within this concavity, ventral to the medial cotyle, a large pneumatic foramen with an oval shape is present in both rami.

4.3. Dentition

The mandible of MZSP-PV 368 preserves a total of 18 alveoli on the right side and 14 on the left. Although the alveolar positions mirror each other, the four posterior-most left alveoli are located in a region severely damaged. Given this, it is inferred that the mandible originally contained a total of 36 teeth, corresponding to 18 pairs. Most teeth are preserved in the right series, though the first is broken (Figs. 3 and 4A). On the left side, 11 teeth remain intact. Despite tooth loss, the left alveoli 13, 14, and 15 are still visible within the damaged region, confirming that dentition extends to approximately half the length of the mandible.

All alveoli exhibit an elliptical shape and are positioned latero-odorsally, except for the first pair, which are circular and directed

anteriorly at the rostrum. The elliptical alveoli are oriented anteromedially and posterolaterally. The teeth are all curved posteromedially, with the curvature offset by at least the diameter of each tooth. The orientation of the alveoli influences the direction of the teeth, making their curvature more medially directed rather than purely posterior. Only the first pair of teeth projects anteriorly. In lateral view, all preserved teeth are unidirectional and subvertical relative to the margin of the jaw, except for the procumbent first pair. The teeth have a conical shape, with varying degrees of taper, and a disparity in size between the mesial teeth (anteriorly, mostly at the symphysis) and cheek teeth (posteriorly, mostly at the rami).

The first left tooth is preserved, and it is small. This region shows no signs of an odontoid process, as observed in *Istiodactylus latidens* Seeley (1901); Martill (2014). The second teeth are larger and conical, while the third teeth are the longest and most robust in the jaw, resembling elongated, recurved spikes. The right third tooth is damaged at the tip. The fourth teeth are smaller than the second, and the fifth are smaller than the fourth. The sixth teeth are slightly larger than the fifth but remain subequal in size, being smaller than the fourth. The seventh teeth are nearly as large as the second. The alveolar size somewhat reflects this variation in the size and thickness of the teeth (Table 2).

From the seventh to the twelfth pairs, the teeth gradually decrease in size, with the ninth teeth being comparable in length to the fourth. The size of the alveoli also decreases gradually (Table 2). The eleventh tooth pair is the only asymmetrical pair, as the left tooth is significantly smaller than its right counterpart, and it lacks wear or damage, closely resembling the first left tooth. From the twelfth to the last and posterior-most tooth, only the right teeth can be described. Until the last tooth, they decrease in size, with the last cheek tooth being the smallest,

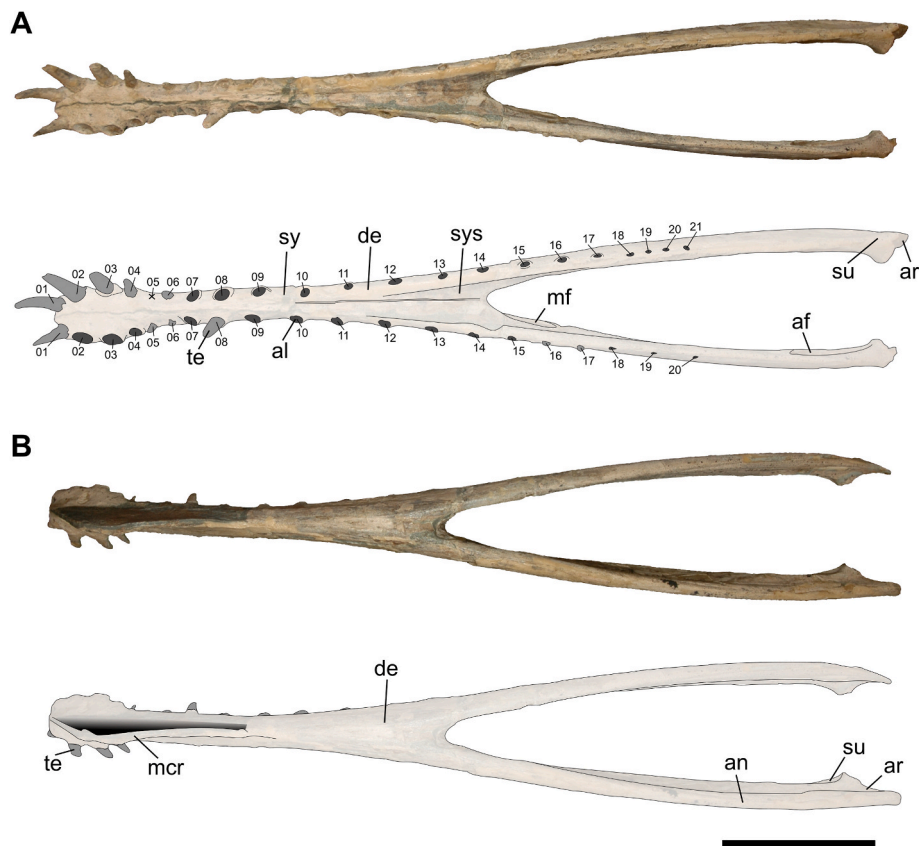


Fig. 6. The holotype of *A. robustus* (BSP, 1987 I 47): (A) dorsal view and interpretative drawing; (B) ventral view and interpretative drawing. Teeth and alveoli are numbered alongside the jaw starting from the anterior-most pair. Anatomical abbreviations: af, adductor fossa; al, alveolus; an, angular; ar, articular; de, dentary; mcr, mandibular crest; mf, meckelian fossa; su, surangular; sy, symphysis; sys, symphyseal shelf; te, teeth. Scale bar equals 10 cm.

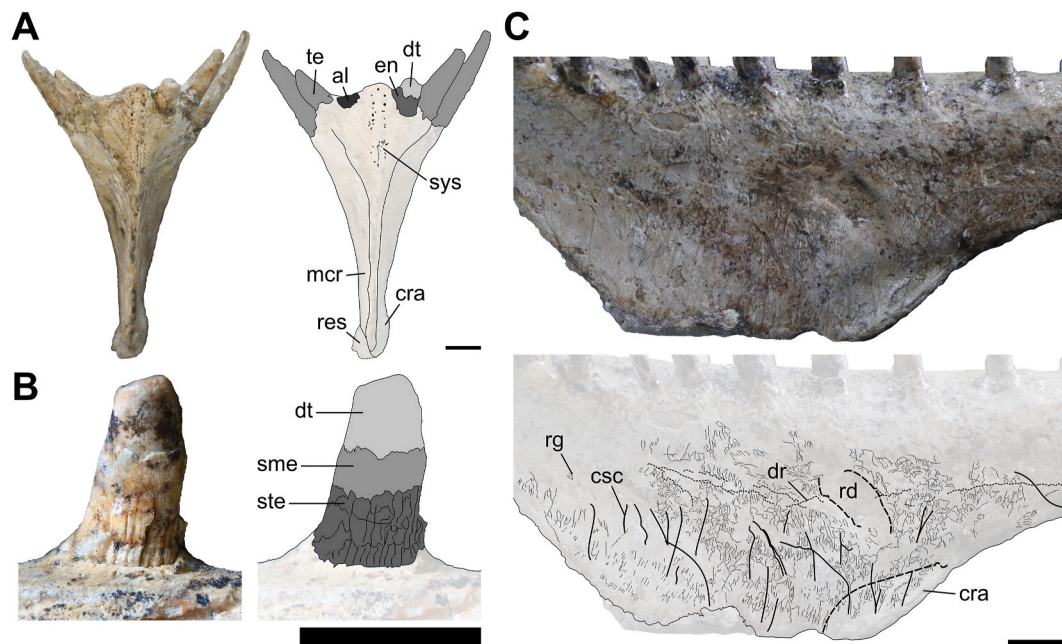


Fig. 7. New *A. robustus* lower jaw (MZSP-PV 368): (A) anterior view and interpretative drawing; (B) details of the left ninth tooth in medial view, and an interpretative drawing indicating the layers that compose it; (C) mandibular sagittal crest in left lateral view, and an interpretative drawing indicating the main structures. Anatomical abbreviations: al, alveolus; cra, crest anomaly; csc, channel sulcus; dr, damaged region; dt, dentine; en, enamel; mcr, mandibular crest; rd, ridge; res, resin; rg, rugosities; sme, smooth enamel; ste, striated enamel; sys, symphyseal scars; te, teeth. Scale bars equal 1 cm.

Table 1

Selected measurements (in millimeters) of MZSP-PV 368.

Maximum anteroposterior length	412
Symphysis, anteroposterior length	189
Symphysis, dorsoventral height (with crest)	52
Symphysis, dorsoventral height (without crest)	30
Crest, anteroposterior length (upper base)	113
Crest, anteroposterior length (lower base)	46
Crest, dorsoventral height	22
Mandible, tooththrow length	247
Mandibular ramus, mid-depth	69

something also reflected on the size of the alveoli (Table 2). All teeth from the thirteenth to the posterior-most have a conical, almost triangular shape, resembling elongated and recurved spikes. All alveoli have raised rims, which are particularly prominent around the cheek teeth (Figs. 7B and 9). The teeth generally fit well within their respective alveoli, except for tooth 14, which has a noticeable posterior gap within its socket, creating the impression that the tooth is smaller than the alveolus that houses it (Table 2). Additionally, all teeth are relatively well-aligned along the tooth row, with the exception of tooth 17, which is positioned more laterally than the others.

Each tooth comprises up to three layers, which are best preserved and most visible in the left ninth tooth (Fig. 7B). The outermost layer, visible at the base of the well-preserved teeth, consists of an ornate, striated enamel with thin longitudinal ridges separated by fine grooves running parallel to the tooth axis. The second layer exhibits a smooth, continuous enamel surface. The innermost layer, visible at the tooth tip, consists of a smooth and continuous layer of dentin. Notably, while the maximum crown height is at least four times the basal width, the dentin layer remains confined to the tooth tip and does not extend halfway down the crown.

The first pair of alveoli are closely spaced but separated by a gap no larger than their diameter at the symphyseal contact. In contrast, the first and second alveolar pairs are nearly adjacent, with minimal spacing between them. The second and third pairs are set slightly farther apart, while the spacing between the third, fourth, and fifth pairs remains

consistent and slightly shorter than that between the second and the third pairs (Table 3). The fifth and sixth alveolar pairs are closely positioned, nearly in contact, similar to the first and second pairs. Beyond the sixth pair, the space between the alveoli gradually increases, with the cheek teeth positioned progressively farther apart (Table 3). The longest diastema is observed between the cheek teeth at the ramus, posterior to the symphysis. While the average spacing between successive mesial teeth is at most equivalent to the tooth diameter, the spacing between successive cheek teeth is consistently greater than the tooth diameter. The spacing between each alveolar pair, on the other hand, reflects the spoon-shape morphology of the symphysis and the almost perfect symmetry of the teeth (Table 4).

Regarding the number, position, and morphology of the teeth, the right alveoli generally mirror the left. However, a subtle asymmetry is apparent in dorsal view (Fig. 4A). Up to the fifth alveolar pair, the right teeth are positioned slightly anterior to their left counterpart. From the sixth pair onward, this pattern reverses, with the left teeth positioned anteriorly to the right. The preserved cheek alveoli on the left mandibular ramus suggest another shift of alignment, where the right teeth become more anteriorly placed than the left starting from the fourteenth alveolar pair. As far as comparisons are possible, the thirteenth pair appear to be the only perfectly symmetrical pair. In BSP 1987 I 47 (Fig. 6A), the holotype of *A. robustus* (Wellnhofer, 1987), an asymmetry is also observed; however, in this case, it may be influenced by the absence of the right fifth tooth.

Kellner and Tomida (2000) reported that the first tooth pair is typically the largest in anhanguerids. However, in MZSP-PV 368, the first left tooth is one of the smallest preserved. Interestingly, it closely resembles the eleventh left tooth, both exhibiting an unusual small size and lacking any signs of wear or damage. These teeth are interpreted as being in the process of replacement. In addition to these two, two other teeth display aberrant positioning. The fourteenth right tooth has an unusually large posterior space within its alveolus, seemingly large enough to accommodate a second tooth. Meanwhile, the seventeenth right tooth is the only one misaligned from the tooth row, positioned more laterally than all other teeth. While it is possible that these teeth were also undergoing replacement, the CT-scan revealed no evidence of

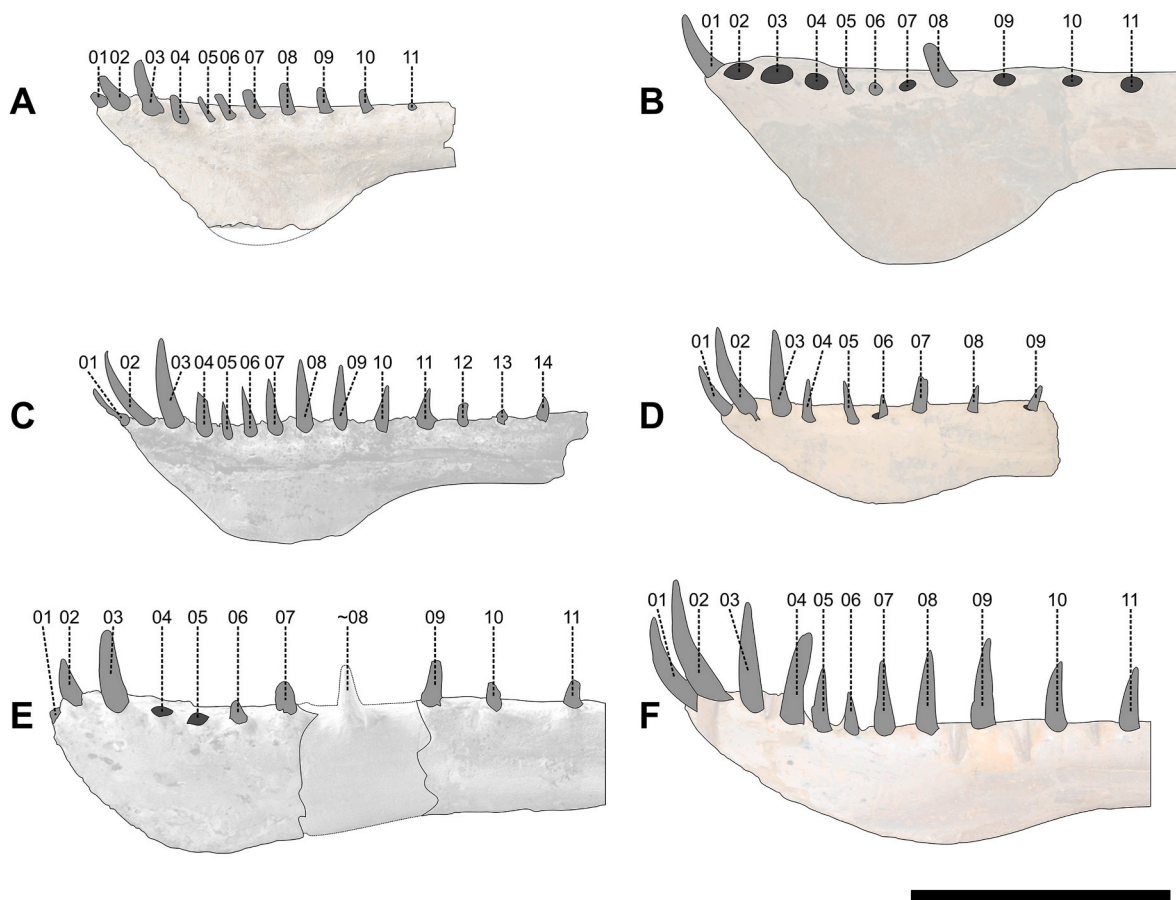


Fig. 8. Scaled interpretative drawings of lower jaws referred to *Anhanguera*: (A) MZSP-PV 368, the new specimen; (B) BSP 1987 I 47, the holotype of *A. robustus* (Wellnhofer, 1987); (C) SAO 200602 (Veldmeijer et al., 2005); (D) SMNK PAL 2302 (Fastnacht, 2001); (E) RGM 401 880, the holotype of *A. spielbergi* (Veldmeijer, 2003); (F) NSM-PV 19892, the holotype of *A. piscator* (Kellner and Tomida, 2000). Teeth and alveoli are numbered alongside the jaw starting from the anterior-most pair. Scale bar equals 10 cm.

replacement teeth in their vicinity (Fig. 11). Consequently, their unusual positioning remains unexplained.

4.4. Hyoid apparatus

Three long slender elements were preserved in association with the mandible. Their shape and relative position suggest they represent fragments of the hyoid apparatus. The longest element remains articulated ventrally with the left mandibular ramus (Figs. 3, 4A and 4B), oriented oblique to the ramus, with its anterior portion directed posteromedially and its posterior portion directed anterolaterally. The anterior tip is broken revealing it is circular in cross-section. The posterior end is preserved, displaying an elliptical cross-section that is somewhat flattened and expanded. The two additional disarticulated elements exhibit a subtle curvature (Fig. 4C). The longer element has a circular cross-section, and is broken at both ends, with sediment filling the middle fracture. The shorter element has an elliptical cross-section, tapering to a thin, preserved tip, while the opposite end is broken.

Although hyoid bones are rare among pterosaur fossils, well-documented specimens exist. Brazilian pterosaurs preserving hyoid elements include *Caiuajara dobruskii* Manzig et al. (2014), from the “Pterosaur Graveyard” site (CP.V 1449; Manzig et al. 2014), *Ludodactylus sibbicki* Frey et al., 2003, from the Crato Formation (SMNK PAL 3828; Frey et al. 2003), and specimens from the Romualdo Formation, such as *Tapejara wellnhoferi* Kellner, 1987 (AMNH 24440; Wellnhofer and Kellner, 1991) and *A. spielbergi* (RGM 401 880; Veldmeijer, 2003), with the damaged element of RGM 401 880 being tentatively identified as a ceratobranchial. Hill et al. (2015) provided a comprehensive

discussion on the evolution of hyoid bones within Archosauria, while Li et al. (2018) examined the elongation and functional adaptations of fleshy and muscular tongues. Together, these studies offer valuable insights for identifying the hyoid fragments preserved in MZSP-PV 368. The longest hyoid element, which remains articulated with the jaw, closely resembles the left first ceratobranchial as illustrated by Hill et al. (2015) for the crocodilian *Caiman* Spix, 1825, the oviraptorid *Khaan* Clark et al. (2001), and the birds *Dromaius* Vieillot, 1816, and *Gallus* Brisson, 1760. Additionally, it bears a strong resemblance to the tip of the ceratobranchials preserved in *Ludodactylus sibbicki* (Frey et al. 2003: Fig. 1). In MZSP-PV 368, the ceratobranchial is positioned near its presumed natural position but appears slightly rotated and displaced. The remaining disarticulated elements are more difficult to identify with certainty and may represent additional fragments of the first ceratobranchial.

4.5. Ontogenetic status

Although larger body size is often associated with mature individuals, Kellner and Tomida (2000) highlighted studies on extant taxa demonstrating that intraspecific variation can result in substantial size differences among individuals, independent of ontogenetic stage. Several non-ontogenetic factors, including food availability, climate conditions, competitive interactions, and individual variation, influence growth. Consequently, for taxa lacking a complete ontogenetic series — such as pterosaurs — it is necessary to establish size-independent criteria that would allow recognition of ontogenetic stages. Various studies have identified sequential patterns in the emergence of

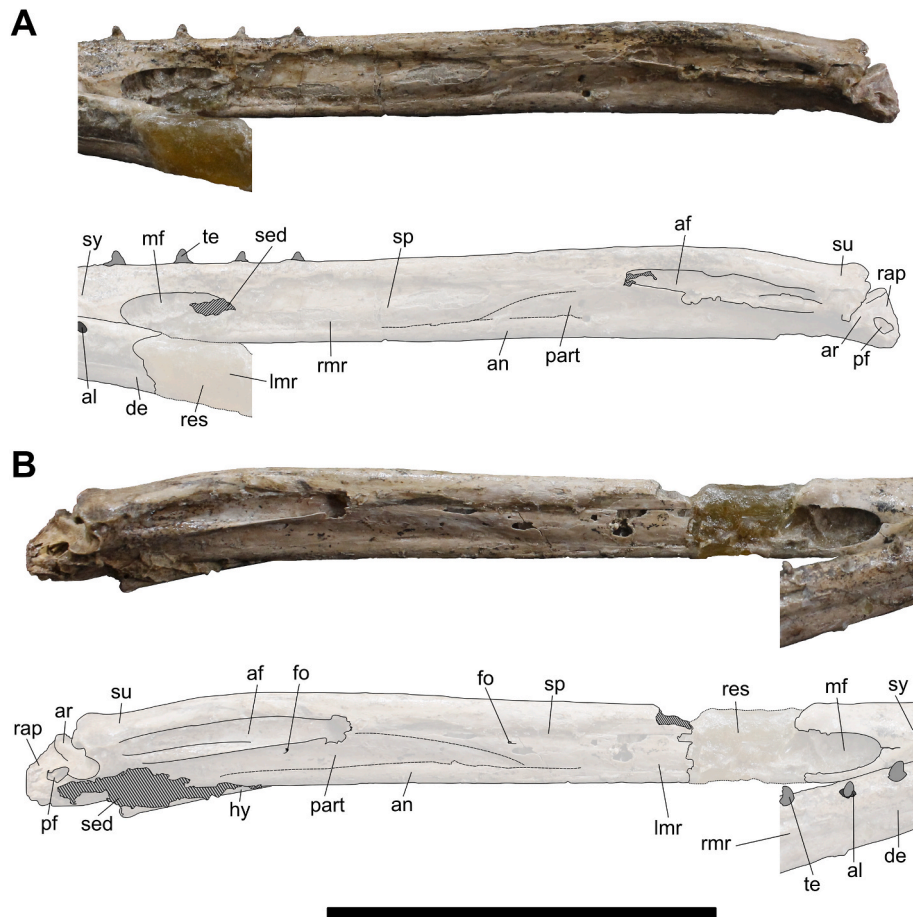


Fig. 9. New *A. robustus* lower jaw (MZSP-PV 368): (A) right ramus in oblique medial view and interpretative drawing; (B) left ramus in oblique medial view and interpretative drawing. Anatomical abbreviations: af, adductor fossa; al, alveolus; an, angular; ar, articular; de, dentary; fo, foramen; hy, hyoid; lmr, left mandibular ramus; mf, meckelian fossa; part, prearticular; pf, pneumatic foramen; rap, retroarticular process; res, resin; rmr, right mandibular ramus; sed, sediment; sp, splenial; su, surangular; sy, symphysis; te, teeth. Scale bar equals 10 cm.

ontogenetic features in pterosaurs (e.g. Wellnhofer, 1975; Bennett, 1993; Kellner and Tomida, 2000; Kellner, 2015; Araújo et al. 2024), which provide a basis for assessing the developmental stage of MZSP-PV 368.

In MZSP-PV 368, both dentaries are completely fused into a symphysis, and all other mandibular bones exhibit firm fusion. The early fusion of the dentary symphysis is a well-documented ontogenetic trait in pterosaurs (Kellner and Tomida, 2000). Further, MZSP-PV 368 cannot be classified as a juvenile, as it also possesses a fully developed mandibular crest — a feature indicative of more advanced ontogenetic stages (Pinheiro and Rodrigues, 2017; Duque et al. 2022). Pinheiro and Rodrigues (2017) proposed that the size and complexity of cranial crests in anhanguerids are ontogenetically influenced, while Duque et al. (2022) suggested that sexual selection also played a role in crest development. By extrapolating these findings from premaxillary crests to mandibular crests, the presence of a high and well-developed crest in MZSP-PV 368 can be interpreted as further support for the inference that this specimen had progressed beyond the juvenile stage. This contrasts with *A. piscator* (NSM-PV, 19892), which is presumed to be a subadult (Kellner and Tomida, 2000) and lack a fully developed crest, despite being significantly larger than MZSP-PV 368 (Fig. 8).

However, MZSP-PV 368 does not represent a fully mature individual either, as the sutures between the mandibular bones remain visible and have not yet undergone complete obliteration — like in certain cases such as DGM 1476-R, the holotype of *Thalassodromeus sethi* (Kellner and Campos, 2002; Pêgas et al. 2018). Based on these observations, MZSP-PV 368 is best classified as a subadult. It likely corresponds to

Ontogenetic Stage 4 (OS4) in the preliminary six-stage classification proposed by Kellner (2015), where OS1 represents hatchlings and OS6 denotes fully mature adults.

It is important to note that these ontogenetic stages, proposed by Kellner (2015) as universal for all pterosaurs, were primarily defined based on postcranial elements, which are unavailable for verification in MZSP-PV 368. Furthermore, the best framework for comparison with MZSP-PV 368 is Kellner and Tomida (2000), where *A. piscator* (NSM-PV, 19892) was compared extensively with other anhanguerid specimens, in order to identify its ontogenetic stage and also discern the sequence of bone fusion during ontogeny. However, the only mention of the lower jaw in this comparison is for the dentaries, fusing into a symphysis very early in ontogeny. Kellner and Tomida (2000) was one of the main studies used by Kellner (2015) to propose the ontogenetic stages. For Kellner (2015), the only mention of the lower jaw in the stages is again the dentaries, being both an ontogenetic condition and, for some non-pterodactyls, a possible phylogenetic signal. Nevertheless, as Araújo et al. (2024) discussed, the definition of ontogenetic categories in pterosaurs is a difficult approach, and it needs further investigation which is beyond the scope of this study.

5. Morphometric analyses

Our morphometric analyses revealed two distinct patterns: one at a broader scale and another at a finer scale (Fig. 12). On a broader scale, there is a clear separation between *Anhanguera* and non-*Anhanguera* specimens, forming three distinct clusters that correspond to the three

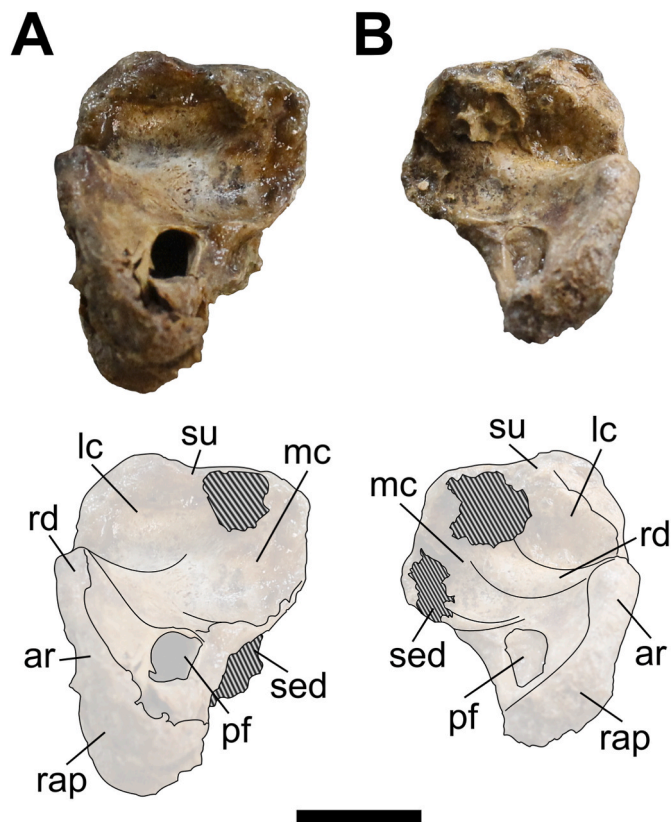


Fig. 10. New *A. robustus* lower jaw (MZSP-PV 368): (A) left and (B) right articular surfaces in posterior view, with an interpretative drawing indicating the main structures. Anatomical abbreviations: **ar**, articular; **pf**, pneumatic foramen; **lc**, lateral cotyle; **mc**, medial cotyle; **rap**, retroarticular process; **rd**, ridge; **sed**, sediment; **su**, surangular. Scale bar equals 1 cm.

Table 2
Measurements (in millimeters) of the alveolar diameters of MZSP-PV 368. All measurements were taken at the apex of alveoli.

Alveolus	Mesiodistal length	Labiolingual width
1	4	4
2	7	4 ^R , 5 ^L
3	7	5
4	3 ^R , 4 ^L	3
5	3	2
6	4	3 ^R , 2 ^L
7	5	3 ^R , 4 ^L
8	5	3
9	4	2
10	4	2
11	3	2
12	3 ^R	2 ^R
13	3	2
14	6 ^R , 3 ^L	2
15	3 ^R , 2 ^L	1 ^R , 2 ^L
16	3 ^R	1 ^R
17	2 ^R	1 ^R
18	2 ^R	1 ^R

Abbreviations: ^RRight; ^LLeft.

genera analyzed. While *Anhanguera* specimens are centrally distributed within the morphospace, *Tropeognathus* and *Ikrandraco* occupy opposite extremes. On a finer scale, within the *Anhanguera* morphospace, a subset of “*robustus*-like” specimens differentiates apart from the other *Anhanguera* specimens. Some specific details of these overall patterns vary between the PCA and LDA analyses.

In the PCA, the primary cluster includes all six analyzed *Anhanguera*

Table 3
Measurements (in millimeters) of the mesiodistal interalveolar spacing of MZSP-PV 368 for each side. All measurements were taken at the apex of alveoli.

Interalveolar space	Mesiodistal length
1–2	1
2–3	2 ^R , 3 ^L
3–4	3 ^R , 2 ^L
4–5	4
5–6	4 ^R , 2 ^L
6–7	3
7–8	5
8–9	7
9–10	9
10–11	8 ^R , 11 ^L
11–12	11 ^R
12–13	11 ^R
13–14	7 ^R , 9 ^L
14–15	7 ^R , 11 ^L
15–16	13 ^R
16–17	10 ^R
17–18	10 ^R
–	–

Abbreviations: ^RRight; ^LLeft.

Table 4
Measurements (in millimeters) of the labiolingual interalveolar spacing of MZSP-PV 368 between each sides. All measurements were taken at the apex of alveoli.

Interalveolar space	Labiolingual length
1–1	3
2–2	12
3–3	16
4–4	14
5–5	11
6–6	9
7–7	9
8–8	8
9–9	8
10–10	10
11–11	12
12–12	–
13–13	21
14–14	27
15–15	32
16–16	–
17–17	–
18–18	–

Abbreviations: ^RRight; ^LLeft.

specimens, which are clearly separated from *Tropeognathus* and *Ikrandraco*, both of which form distinct clusters of their own (Fig. 12A). Within the *Anhanguera* cluster, a smaller subgroup of three “*robustus*-like” specimens is observed, consisting of BSP 1987 I 47, MZSP-PV 368, and SAO 200602. Meanwhile, NSM-PV 19892 remains isolated, suggesting a unique “*piscator*-like” morphotype, irrespective of ontogenetic stage since it is presumed to be a subadult (Kellner and Tomida, 2000). Interestingly, SMNK PAL 2302 is positioned closer to RGM 401 880 than to other *Anhanguera* specimens, indicating the possible existence of a “*spielbergi*-like” morphotype.

In contrast, the LDA results suggest a different pattern. RGM 401 880 is positioned closer to *Tropeognathus* cluster rather than to other *Anhanguera* specimens, implying that the “*spielbergi*-like” morphotype may exhibit morphological similarities with *Tropeognathus*. Within *Anhanguera*, the “*robustus*-like” cluster expands to include four specimens — BSP 1987 I 47, MZSP-PV 368, SAO 200602, and SMNK PAL 2302 — suggesting a broader morphological cohesion within this subgroup (Fig. 12B). As in the PCA, NSM-PV 19892 remains isolated, reinforcing its distinct “*piscator*-like” morphotype as a presumed subadult (Kellner and Tomida, 2000). Meanwhile, both *Ikrandraco*

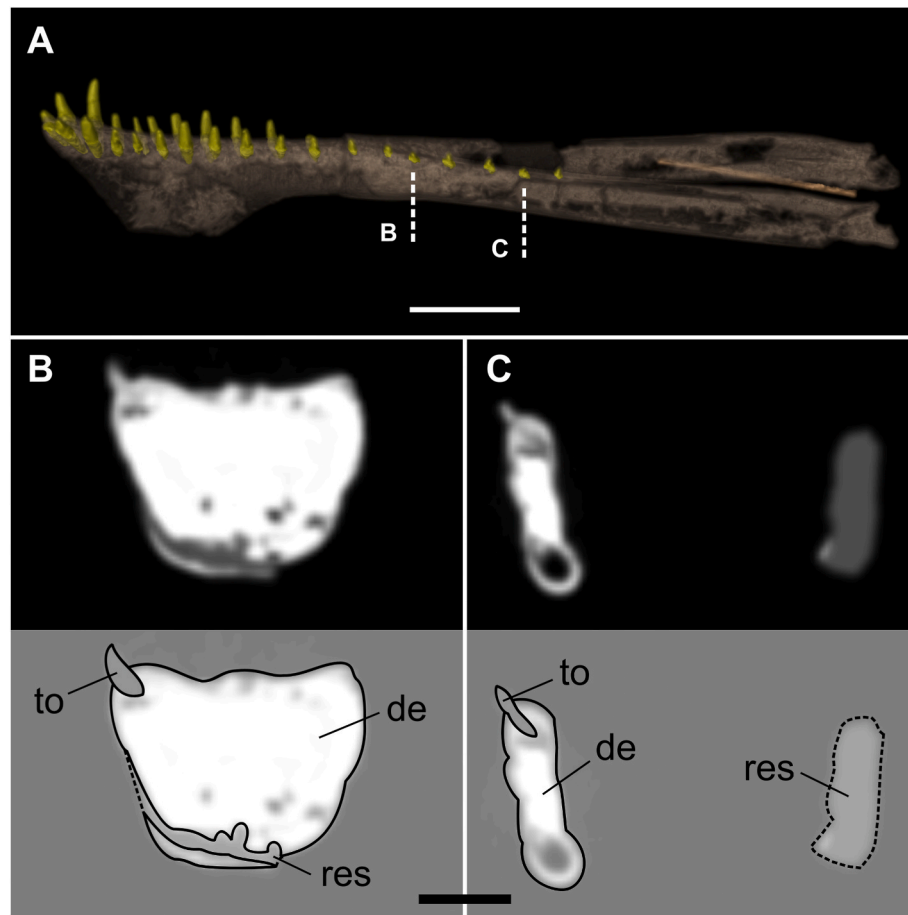


Fig. 11. New *A. robustus* lower jaw (MZSP-PV 368): (A) 3D model of the CT-scan, in oblique right lateral view (mirrored). The lower jaw is rendered at 10 % opacity, showing the root of the attached teeth and the articulated hyoid element. The dotted lines indicate the positions of the cross-sections of (B) and (C); Transversal slice of the CT-scan at the position where tooth 14 is implanted on the symphysis, with an interpretative drawing; (B) Transversal slice of the CT-scan at the position where tooth 17 is implanted on the mandibular ramus, with an interpretative drawing. Anatomical abbreviations: **de**, dentary; **res**, resin; **to**, tooth. Scale bar equals 10 cm (A) and 1 cm (B and C).

specimens form a well-defined and separate cluster.

6. Phylogenetic analyses

Our phylogenetic analysis resulted in 15 most parsimonious trees, with 2131 steps, a consistency index of 0.350, and retention index of 0.785. The variation from our analysis to that of Pégas (2024) is negligible, which reported 15 most parsimonious trees, with 2128 steps, a consistency index of 0.351, and retention index of 0.783. The topology of the strict consensus tree remains consistent with Pégas (2024), except for the internal relationships within the genus *Anhanguera*, which was recovered as monophyletic but with limited resolution (Fig. 13). Within *Anhanguera*, a trichotomy is formed, comprising the holotypes RGM 401 880, NSM-PV 19892, and a clade containing the remaining five specimens. This latter clade is unresolved and forms a polytomy that includes MZSP-PV 368, SAO 200602, SMNK PAL 2302, as well as the holotypes of *A. blittersdorffi* (MN 4805-V) and *A. robustus* (BSP, 1987 I 47). The internal node uniting *A. blittersdorffi* and *A. robustus* is supported by two ambiguous synapomorphies.

The first synapomorphy is a posteriorly restricted palatal keel (character 156, state 1), located posterior to the fifth pair of teeth. Bantim et al. (2014) considered a palatal ridge extending posteriorly autapomorphic to *A. blittersdorffi*, and in both MN 4805-V and SMNK PAL 2302 it is located posterior to the eighth pair of teeth. However, since this feature is restricted to the skull and the posterior portion of the palate, its condition remains unknown in BSP 1987 I 47, MZSP-PV 368,

and SAO 200602.

The second synapomorphy is a straight anteroventral margin of the mandibular crest (new character 520, state 1), which is observed in BSP 1987 I 47, MZSP-PV 368, SAO 200602, and SMNK PAL 2302. However, since this feature pertains to the mandibular crest, its condition in MN 4805-V is also unknown.

To assess the impact of SMNK PAL 2302 on the phylogenetic relationships within *Anhanguera*, we performed exploratory analyses by either treating the coding for the new character 520 as unknown or excluding SMNK PAL 2302 from the dataset (reducing the matrix to 195 terminal taxa). In both cases, the results remained unchanged, except that within *Anhanguera*, all specimens and species formed a completely unresolved polytomy (see Supplementary Material).

7. Discussion

7.1. Teeth and diet in *Anhanguera* and other anhanguerids

The number and morphology of the teeth have long been considered diagnostic features in pterosaurs, including anhanguerids such as *Maaradactylus kellneri* Bantim et al. (2014), and *Anhanguera blittersdorffi* (Bantim et al. 2014). However, dentition in archosaurs exhibits high degree of plasticity and variation, both in morphology and tooth count, with multiple instances of homoplasies (D'Emic et al. 2013; Ősi, 2014; Hendrickx et al. 2019). Bantim et al. (2014) further demonstrated that *Anhanguera* shows intraspecific variation in tooth count (Table 5).

Nonetheless, *Anhanguera* as a genus can be characterized by a specific range of alveolar pairs, typically between 18 and 26 in the upper jaw. In contrast, other anhanguerid genera exhibit counts outside of this range, with *Tropeognathus* possessing fewer teeth (14 pairs), whereas *Maaradactylus* presents a notably higher count of 35 pairs.

A comparable pattern is observed in the lower jaw. MZSP-PV 368 possesses 18 alveolar pairs, a number consistent with NSM-PV 19892, the holotype of *A. piscator* (Table 5). The spectrum for *Anhanguera* mandibles seems to range from 16 to 21 alveolar pairs, distinguishing it from other genera, such as *Tropeognathus*, which has only 11 pairs. However, the holotype of *A. robustus* (BSP, 1987 I 47) presents a particular challenge, because tooth counts reported in the literature vary: Wellnhofer (1987) and Veldmeijer et al. (2006) noted 17 pairs, whereas Kellner and Tomida (2000) recorded a total of 35–36 alveoli, which means 18 on one side of the jaw and 17–18 on the other, and Veldmeijer (2003) later documented 18 pairs. A recounting in this study (Figs. 5 and 6A) identified 20 alveolar pairs, with possibly 21 on the

right dentary. Although this falls within the *Anhanguera* spectrum, it exceeds the number observed in MZSP-PV 368 and previous reports for BSP 1987 I 47. Notably, this specimen exhibits an anomaly in which the right fifth alveolus is absent, leaving a diastema in its place.

Given this variability, it seems unlikely that an exact tooth count could serve as an autapomorphy for any *Anhanguera* species, at least in the lower jaw. Variability in the number of teeth primarily affects the posterior half of the jaw, particularly the cheek teeth in the rami, whereas the anterior half of the jaw, mostly the mesial teeth at the symphysis, tend to remain stable in position, shape, size, and number — aside from individual anomalies such as the missing alveolus in BSP 1987 I 47. This pattern suggests that natural selection may have exerted stronger pressure on the anterior teeth, while the distal teeth were subject to weaker selective forces or even genetic drift. However, testing this hypothesis and assessing its impact on both the upper and lower jaws is beyond the scope of this study.

Pinheiro and Rodrigues (2017) established a large number (26 pairs)

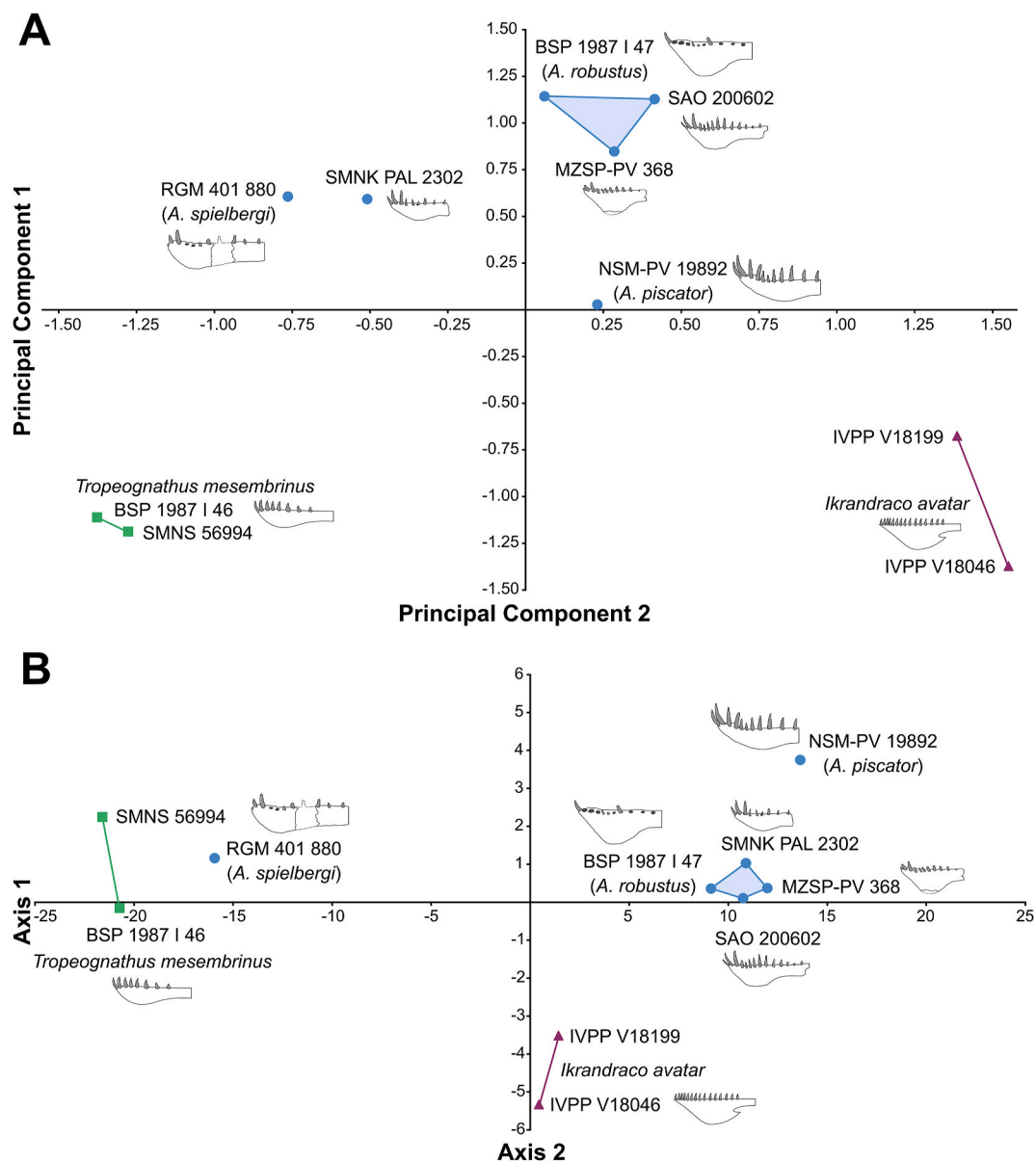


Fig. 12. Geometric morphometric analysis of the six lower jaws with mandibular crests referable to *Anhanguera* (blue dots) and four jaws of closely related taxa (*Tropeognathus* as green squares, *Ikrandraco* as purple triangles): (A) Principal Component Analysis; (B) Linear Discriminant Analysis. The “robustus-like” morphotype is indicated as the blue area connected by the dots of the specimens composing this morphotype. Linearts of the lower jaws are the same as in Fig. 8, except the representative linearts of the closely related taxa, redrawn from Veldmeijer (2003) for *Tropeognathus* and Wang et al. (2014b) for *Ikrandraco*.

of alveoli on the upper jaw as the sole valid autapomorphy of *A. blittersdorffi*. However, this creates taxonomic uncertainty for specimens attributed to *A. blittersdorffi* such as Pz-DBAV-URJ 40, which lacks a fully preserved upper jaw, leaving its total tooth count unknown. Until a complete description is provided, its precise identification within *Anhanguera* remains unresolved. A similar issue arises with MN 7019-V, the holotype of *Cearadactylus atrox* Leonardi and Borgomanero (1985), which preserves 16 alveolar pairs but likely had additional pairs in its damaged and missing regions (Vila Nova et al. 2014). This suggests that MN 7019-V may fall within the tooth count range established for *Anhanguera*. The same challenge observed in the skull extends to the lower jaw, as both Pz-DBAV-URJ 40 and MN 7019-V exhibit missing regions where additional alveoli were likely present. These specimens may ultimately fall within the established *Anhanguera* spectrum, but their classification remains uncertain until more complete material is analyzed.

As noted by Pinheiro and Rodrigues (2017), *Anhanguera* can be diagnosed — among other characters — by a main autapomorphy: the fifth and sixth teeth are subequal in size and smaller than both the fourth and seventh teeth. While Pinheiro and Rodrigues (2017) originally specified this trait for the skull and upper dentition, this distinctive morphology is also applicable to the lower jaw and lower dentition (Kellner and Campos, 1988), as observed in *A. piscator* (NSM-PV, 19892), *A. robustus* (BSP, 1987 I 47), and the new specimen (MZSP-PV 368). This morphology is likely associated with an extreme specialization for piscivory among ornithocheiromorphs. Vullo et al. (2016) demonstrated that certain fish-eating predators inhabiting marine environments — such as spinosaurids and the Pike Conger Eel — exhibit similar morphological adaptations for piscivory. *Anhanguera* possesses a mediolaterally compressed and elongated rostrum with a spoon-shaped tip, forming a terminal “rosette” bearing enlarged teeth in both the upper and lower jaws (e.g. Kellner and Tomida, 2000; Veldmeijer, 2003; Pinheiro and Rodrigues, 2017). A distinctive notch is present posterior to this “rosette”, characterized by reduced teeth, a feature also observed in the taxa analyzed by Vullo et al. (2016). However, in *Anhanguera* this notch occurs in both upper and lower jaws, and is not defined by the jaw bones themselves but rather by a unique pattern of strong heterodonty in tooth size. This morphological convergence likely results from similar feeding behaviors, suggesting an efficient biomechanical adaptation for capturing and holding onto slippery prey such as fish. This heterodonty pattern is not unique to *Anhanguera* in pterosaurs: large mesial teeth, followed by smaller teeth, and then followed by distally large teeth is shared among ornithocheiromorphs, with variation regarding number and the position of the reduced teeth (e.g. Veldmeijer et al. 2006; Pégas, 2025).

This interpretation aligns with the findings of Bestwick et al. (2020) on dental microwear texture and Pégas et al. (2021b) on predicted bite force. Bestwick et al. (2020) identified *Anhanguera* as a strict piscivore, while Pégas et al. (2021b) found that it has a very weak absolute bite force and bite force quotients, comparable to other obligate fish-eating taxa such as *Nyctosaurus gracilis* Marsh (1876), and *Pteranodon longiceps* Marsh (1876). In contrast, larger ornithocheiromorphs, such as the species referred as *Coloborhynchus* by Bestwick et al. (2020), were interpreted with a more generalist carnivory. Similarly, Pégas et al. (2021b) found that *Tropeognathus mesembrinus* exhibited a relatively stronger bite force than *Anhanguera*, suggesting differences in feeding mechanics and prey selection among these closely related taxa.

Vullo et al. (2016) also noted that spinosaurids and eels possess integumentary mechanoreceptors associated with specialized jaw morphology, which aid in prey detection. Whether a similar sensory system was present in *Anhanguera* and other anhanguerids is still subject to investigation. MZSP-PV 368 displays numerous tiny foramina anteriorly, at the tip of the rostrum (Fig. 7A), which could be indicative of such a system. However, since these foramina are located within the symphyseal region, they could alternatively represent suture scars, thus their identification is tentative.

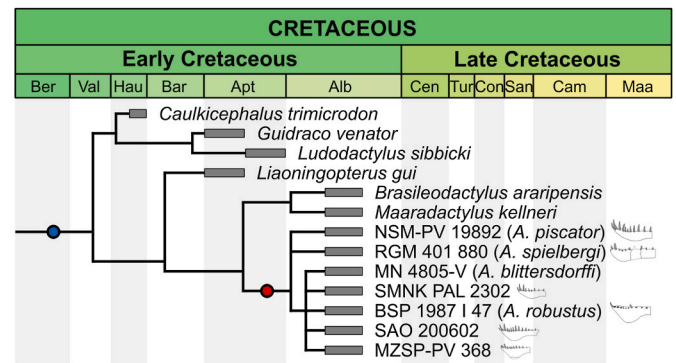


Fig. 13. Time-scaled strict consensus phylogenetic tree, reduced to display only *Anhanguera* and closely related taxa. The remainder of the tree has the same topology as Pégas (2024). Circles indicate the clades Anhanguerinae (Blue) and *Anhanguera* (Red). Linearts of the lower jaws are the same presented in Fig. 8.

7.2. Morphometric remarks on the mandibular crest of *Anhanguera*

Both PCA and LDA analyses recovered a distinct “robustus-like” morphotype, with the shape of the mandibular crest differentiating at least *A. robustus* (BSP, 1987 I 47), MZSP-PV 368, and SAO 200602 from other *Anhanguera* specimens — regardless of ontogenetic stage. While BSP 1987 I 47 appears to represent a mature, adult specimen, and MZSP-PV 368 an immature, subadult one, the holotypes of *A. spielbergi* (RGM 401 880) and *A. piscator* (NSM-PV, 19892) could similarly be classified as an adult and a subadult, respectively. This suggests that the “robustus-like” mandibular crest morphotype is not solely influenced by ontogenetic variation, at least among subadult and adult individuals, and may hold taxonomic significance. This aligns with previously stated conclusions by Kellner and Tomida (2000), but contradicts more recent studies that focused on premaxillary crests (Pinheiro and Rodrigues, 2017; Duque et al. 2022). The potential for independent modularity between different cranial crests is intriguing; however, further investigating into this hypothesis falls beyond the scope of this study.

The inclusion of SMNK PAL 2302 within the “robustus-like” morphotype remains ambiguous due to the conflicting results between the PCA and LDA analyses. Morphologically, its lower jaw exhibits notable similarities to all specimens of the “robustus-like” morphotype (i.e., BSP, 1987 I 47, MZSP-PV 368, and SAO, 200602) — particularly in possessing a straight anteroventral margin of the mandibular crest — yet it also differs from these specimens in having a relatively smaller crest and a shallower anteroventral angle. While PCA place SMNK PAL 2302 closer to a presumed “spielbergi-like” morphotype, the LDA analysis clusters it within the “robustus-like” morphotype, indicating that the shape of the anteroventral margin may drive its classification despite differences in crest size.

Cranial crests in anhanguerids are known to develop further with ontogeny (Pinheiro and Rodrigues, 2017; Duque et al. 2022), though the extent of this influence in SMNK PAL 2302 remains uncertain. Notably, all specimens clustered within the “robustus-like” morphotype appear to be subadults or adults, and SMNK PAL 2302 is substantially larger than MZSP-PV 368, being comparable in size to BSP 1987 I 47 (Fig. 8). The distinct crest of SMNK PAL 2302 could reflect interspecific variation or sexual dimorphism. Sexual selection influencing cranial ornaments in pterosaurs is well-documented (see Bennett, 1992; Manzig et al. 2014; Wang et al. 2014a), and the possibility that SMNK PAL 2302 represents a sexually dimorphic variant rather than a specimen belonging to the “robustus-like” morphotype cannot be ruled out — particularly given its closer resemblance to RGM 401 880.

Ultimately, the affinities between SMNK PAL 2302 and *A. robustus* remain inconclusive. A more comprehensive dataset will be necessary to clarify its taxonomic position and determine whether its morphology represents intraspecific variation, sexual dimorphism, or a distinct

Table 5

Comparisons between teeth count, in pairs of alveoli, and dentary crest position, relative to the toothrow, among anhanguerid specimens.

Specimen	Species Reference	Upper Jaw	Lower Jaw	Crest Limit	Count Reference
MN 4805-V	<i>Anhanguera blittersdorffi</i> H	26	?	?	Bantim et al. (2014) Veldmeijer (2003) Kellner and Tomida (2000)
Pz-DBAV-UERJ 40	<i>Anhanguera blittersdorffi</i> (?)	22* ¹	21* ²	?	¹ Bantim et al. (2014) ² Veldmeijer (2003)
SMNK PAL 2302	<i>Anhanguera blittersdorffi</i> (!)	10 ^A	9 ^A	9–10	Veldmeijer et al. (2006)
NHMK R11978	<i>Anhanguera blittersdorffi</i> (!)	25–28	?	?	This work
NSM-PV 19892	<i>Anhanguera piscator</i> H	20 ¹³ 25 ^{R4} 25 ²	18 ^R /19 ^{L4} 18 ² 19 ³	10–11	¹ Bantim et al. (2014) ² Veldmeijer et al. (2006) ³ Veldmeijer (2003) ⁴ Kellner and Tomida (2000)
RGM 401 880	<i>Anhanguera spielbergi</i> H	18 ¹³ 19 ²	16 ²³	9–10	¹ Bantim et al. (2014) ² Veldmeijer et al. (2006) ³ Veldmeijer (2003)
BSP 1987 I 47	<i>Anhanguera robustus</i> H	?	17 ¹ 17–18 ² 18 ³ 20 ^L /21 ^{R4}	10–11	¹ Veldmeijer et al. (2006) ¹ Wellnhofer (1987) ² Kellner and Tomida (2000) ³ Veldmeijer (2003) ⁴ This work
MZSP-PV 368	<i>Anhanguera robustus</i> (!)	?	18	10–11	This work
SAO 200602	<i>Anhanguera robustus</i> (!)	?	18 ^{R*}	10–11	Veldmeijer et al. (2005)
BSP 1982 I 89	<i>"Anhanguera araripensis"</i> H	12 ^P	6 ^{LP}	?	Wellnhofer (1985)
SAO 16494	<i>"Anhanguera araripensis"</i>	18*	?	?	Veldmeijer et al. (2006) Veldmeijer (2003)
MN 4735-V	<i>"Anhanguera araripensis"</i>	13 ¹ 18 ² 23–25 ³	?	?	¹ Veldmeijer et al. (2006) ² Bantim et al. (2014) ³ Kellner and Tomida (2000)
BSP 1982 I 90	<i>"Anhanguera santanae"</i> H	13 ^P	7 ^P	?	Wellnhofer (1985)
AMNH 22555	<i>"Anhanguera santanae"</i>	12–15*	?	?	Pinheiro and Rodrigues (2017) Wellnhofer (1991)
SMNK PAL 1136	<i>Anhanguera</i> sp. <i>indet</i>	?	17*	10–11*	Elgin (2014)
DGEO-CTG-UFPE 8283	<i>Anhanguera</i> sp. <i>indet</i>	12 ^A	?	?	Duque et al. (2022)
BSP 1987 I 46	<i>Tropeognathus mesembrinus</i> H	13 ¹ 14 ²	11	7	¹ Wellnhofer (1987) ² Bantim et al. (2014) ² Veldmeijer (2003)
SMNS 56994	<i>Tropeognathus mesembrinus</i>	?	12 ⁶	7	Veldmeijer (2002)
MPSC R 2357	<i>Maaradactylus kellneri</i> H	35	?	?	Bantim et al. (2014)
MN 7019-V	<i>Cearadactylus atrox</i> H	15–16*	14*	Crestless	Veldmeijer (2003) Kellner and Tomida (2000)

Abbreviations: H Holotype; (?) Referral uncertain; (!) Referral on this work; *Incomplete, preserved value; ^AIncomplete, only rostral (anterior); ^PIncomplete, only cheek (posterior); ^RRight; ^LLeft.

taxonomic character.

7.3. Phylogenetic affinities of MZSP-PV 368

The new character incorporated on our phylogenetic analysis (character 520) reflects the distinct morphology of the mandibular crest observed in specimens belonging to the “robustus-like” morphotype, including SMNK PAL 2302, as identified by our morphometric analysis. This character groups *A. robustus* (BSP, 1987 I 47), MZSP-PV 368, SAO 200602, and SMNK PAL 2302 into a subclade within *Anhanguera*. Additionally, this subclade further includes *A. blittersdorffi* (MN 4805-V), supported by a posteriorly restricted palatal keel (character 156, state 1), a feature shared by MN 4805-V and SMNK PAL 2302. While the close affinities among these specimens appear well supported, the question remains whether they represent a single species, two distinct taxa, or a greater degree of species-level diversity within this subgroup. The relationship between SMNK PAL 2302 and *A. robustus* remains unresolved, pending the discovery of additional specimens and a larger comparative dataset. However, the phylogenetic analysis strongly supports the close relationship between MZSP-PV 368 and *A. robustus*. Additionally, the analysis suggests a closer affinity between SMNK PAL 2302 and *A. blittersdorffi*, highlighting the potential taxonomic complexities within *Anhanguera*.

7.4. Cranial crests and its implications on the taxonomy of *Anhanguera*

Pinheiro and Rodrigues (2017) recognized three valid species within

the genus *Anhanguera*: *A. blittersdorffi* (Campos and Kellner, 1985), *A. piscator* (Kellner and Tomida, 2000), and *A. spielbergi* (Veldmeijer, 2003). Other previously described species, such as ‘*A. santanae*’ (Wellnhofer, 1985), ‘*A. araripensis*’ (Wellnhofer, 1985), and *A. robustus* (Wellnhofer, 1987), were deemed invalid due to the absence of reliable autapomorphies.

In their revised diagnosis of *Anhanguera*, Pinheiro and Rodrigues (2017) defined the genus as a member of the Anhangueridae, characterized by the following combination of cranial characters: the presence of premaxillary and dentary sagittal crests in advanced ontogenetic stages; a thin, highly asymmetric premaxillary crest, that originates near — but not exactly at — the tip of the skull, extends beyond the anterior-most portion of the skull, and exhibits allometric growth in both height and length during ontogeny; fifth and sixth upper teeth being subequal in size and smaller than both fourth and seventh teeth; a thin, blade-like parietal crest; and a shallow palatal ridge. Notably, all diagnostic features of *Anhanguera* are cranial in nature, including the variation in tooth size, with the sole exception being the presence of a dentary crest.

Kellner and Campos (1988) argued that the morphology of the teeth and the general aspect of the crest could also be applied to the lower jaw, supporting the reassignment of *A. robustus* as a species of *Anhanguera*. Specimen MZSP-PV 368, similar to the holotype of *A. robustus* (BSP, 1987 I 47), exhibits a distinct dental pattern in which the third pair of teeth is the largest in the mandible, the fourth and seventh teeth are of similar size but smaller than the third and, most importantly, the fifth and sixth teeth are subequal in size yet smaller than both the fourth and

seventh. This pattern is consistent on both sides of the dentition, and is unique to *Anhanguera*, at least among anhanguerians from the Romualdo Formation (see Pinheiro and Rodrigues, 2017; Pêgas, 2025). As examples, in *Liaoningopterus gui* Wang and Zhou (2003), the fourth upper teeth are the largest of the skull (Wang and Zhou, 2003), and in *Ferrodraco lentoni* Pentland et al. (2019), the third lower teeth are the largest in the mandible, whereas the fourth and fifth teeth have a similar size and are smaller than the sixth and seventh, which in turn are subequal in size yet smaller than both the third and eighth (Pentland et al. 2021, tbl. 1). Given this dental morphology, the shape and size of the crest, and the results of our phylogenetic analysis, MZSP-PV 368 can be confidently assigned to *Anhanguera*.

Wellnhofer (1987) originally proposed four characters for the diagnosis of *A. robustus*, though Kellner and Tomida (2000) suggested that two of these — the spoon-shaped rostrum and the dental morphology — were more widespread among anhanguerids. Both studies, however, considered the deep mandibular crest with a straight anterior margin, forming an angle of approximately 50° relative to the dorsal margin of the jaw, as a valid autapomorphy. Pinheiro and Rodrigues (2017) contested this, arguing that crest shape could not be regarded as diagnostic due to its probable association with advanced ontogenetic stages, leading them to invalidate *A. robustus* as a distinct species. However, observations of MZSP-PV 368, the holotype (BSP, 1987 I 47), and SAO 200602, suggest that the deep dentary crest with a straight anterior margin remains a unique feature among anhanguerids. Within ornithocheiromorphs a comparable crest morphology is only found in *Ikrandraco avatar* (Wang et al. 2014b). While crest shape and size are known by ontogeny (Pinheiro and Rodrigues, 2017; Duque et al. 2022), the distinctiveness of these specimens within *Anhanguera* cannot be solely attributed to ontogenetic variation — especially considering that MZSP-PV 368 is significantly smaller than BSP 1987 I 47 (Fig. 8).

Furthermore, *A. spielbergi* (RGM 401 880) is represented by a fully mature individual (Veldmeijer, 2003), yet its dentary crest is rounded and shallow, almost confluent with the anterior margin of the lower jaw, and lacking the straight anterior margin seen in *A. robustus*, instead resembling the crest of *A. piscator* (NSM-PV, 19892). This contrast suggests that variations in mandibular crest morphology among mature individuals of *Anhanguera* from the Romualdo Formation may reflect interspecific differences, rather than purely ontogenetic variation. Similar patterns of interspecific variation in cranial crests have been documented in most groups of pterosaurs bearing crests (Bennett, 1994; Cheng et al. 2017; Pêgas et al. 2018, 2023), further suggesting that there is a taxonomic relevance on the morphology of dentary crest in *Anhanguera*.

Our morphometric analysis strongly suggests the presence of a distinct mandibular morphotype within *Anhanguera*, clustering around *A. robustus* — referred here as the “*robustus*-like” morphotype. This pattern was consistently recovered in both the PCA and LDA results, grouping at least the holotype (BSP, 1987 I 47), MZSP-PV 368, and SAO 200602. The distinct shape of the mandibular crest in this “*robustus*-like” assemblage appears unique among anhanguerids, and cannot be satisfactorily explained by ontogenetic variation alone. As previously suggested (Kellner and Tomida, 2000), this indicates that the crest morphology observed in specimens assigned to *A. robustus* could be considered diagnostic, supporting the revalidation of the species.

While our results support the validity of *A. robustus*, a direct comparison between *A. robustus* and *A. blittersdorffi* — the type species of the genus — remains problematic due to the lack of overlapping material between the holotypes. The holotype of *A. blittersdorffi* (MN 4805-V) consists of a skull without a mandible, whereas the holotype of *A. robustus* (BSP, 1987 I 47) represents a lower jaw without a skull. As a result, resolving their taxonomic distinction requires the discovery of more complete specimens confidently referable to both species. To date, purported referred specimens have offered limited comparative potential. SAO 200602 and MZSP-PV 368, which our morphometric analysis recovered within the “*robustus*-like” morphotype and are

referred here to *A. robustus*, also consist of lower jaws without associated skulls.

SMNK PAL 2302, originally referred to *A. robustus* by Fastnacht (2001), occupies an ambiguous position in our morphometric analysis, failing to clearly distinguish between *A. robustus* and *A. blittersdorffi*. However, its morphology offers valuable insights, as it represents the only specimen with some overlap between known materials of both species. Notably, SMNK PAL 2302 exhibits a posteriorly restricted palatal keel, a condition identified as unique to *A. blittersdorffi* (Bantim et al. 2014) and observed in the holotype MN 4805-V. Here, we note that this posterior palatal keel is located behind the eighth teeth on both specimens. Given that this trait is also present in SMNK PAL 2302, we consider it sufficient evidence to reassign the specimen to *A. blittersdorffi*, rather than *A. robustus*.

Further supporting this conclusion, a posteriorly restricted palatal keel is also observed on NHMUK R11978. This specimen comprises a complete skull, and it was initially labelled *A. blittersdorffi* before being relabeled ‘*A. santanae*’. Pinheiro and Rodrigues (2017), acknowledging this specimen on their review, assigned it to *Anhanguera* sp. With at least three specimens now recognized as *A. blittersdorffi* exhibiting this distinctive palatal morphology, a character that is not found in other specimens referred to *Anhanguera*, we consider it a valid autapomorphy for the species. This feature is also less ambiguous than the sole diagnostic character proposed by Pinheiro and Rodrigues (2017): “Large number (52) of alveoli on the upper jaw” (see Table 5 for examples). The poor preservation of Pz-DBAV-UERJ 40 makes its referral to *A. blittersdorffi* uncertain at best, leaving its true position within *Anhanguera* unresolved until a more complete description is available.

An alternative interpretation of our findings is that *A. robustus* may not represent a distinct species, but instead corresponds to the lower jaw of *A. blittersdorffi*. One line of evidence supporting this hypothesis is the horizontal straight occlusal line in the upper jaw of *A. blittersdorffi* (MN 4805-V), which closely matches the straight occlusal margins observed in the lower jaws of *A. robustus* (holotype BSP, 1987 I 47, MZSP-PV 368, and SAO, 200602). Moreover, as far as comparisons allow, both the upper and lower jaws of SMNK PAL 2302 appear to share this feature. This shared occlusal trait is in stark contrast to other anhanguerids, which typically exhibit anteriorly curved occlusal lines in both upper and lower jaws (see Kellner and Tomida, 2000; Veldmeijer et al. 2006 for illustrated examples). If true, this feature could serve as a potential autapomorphy for *A. blittersdorffi*, encompassing what has traditionally been considered *A. robustus*. Additionally, sexual dimorphism remains a possible explanation for the observed morphological differences between SMNK PAL 2302 (here reassigned to *A. blittersdorffi*) and the “*robustus*-like” specimens. If this is the case, all of these individuals may represent a single species, exhibiting sexual variation in crest morphology.

However, the presence of a horizontally straight occlusal line in *A. robustus* and *A. blittersdorffi* could also be interpreted as a synapomorphy uniting these two species into a distinct internal group within *Anhanguera*, separate from the species *A. piscator* and *A. spielbergi*. This interpretation aligns with the results of our phylogenetic analysis. Under this scenario, the differences in mandibular crest morphology between *A. robustus* and SMNK PAL 2302 may reflect interspecific variation rather than ontogenetic or sexual dimorphism. However, our PCA analysis suggests a more complex relationship among the species, as SMNK PAL 2302 clusters more closely with *A. spielbergi*, adding another layer of ambiguity to its taxonomic placement. Despite this, *A. robustus* remains somewhat comparable to *A. blittersdorffi* through SMNK PAL 2302, which, based on our analyses, is most likely distinct from *A. robustus*.

Comparative assessments among *Anhanguera* specimens remain limited, and sexual dimorphism in the genus has yet to be clearly defined. In other pterosaurs, such as *Pteranodon* and *Hamipterus* Wang, Kellner, Jiang, Wang, Ma, Paidoula, Cheng, Rodrigues, Meng, Zhang, Li & Zhou (2014a), presumed females have been reported to exhibit

smaller cranial crests than their adult male counterparts (Bennett, 1992; Wang et al. 2014a). Consequently, sexual dimorphism cannot be entirely dismissed as a possible explanation for the observed differences between SMNK PAL 2302 (here referred to *A. blittersdorffi*) and the “robustus-like” specimens.

MZSP-PV 368 (Fig. 8A), recognized here as *A. robustus*, is interpreted here as a subadult, exhibiting a largely developed crest but being significantly smaller in overall size compared to RGM 401 880, the holotype of *A. spielbergi* (Fig. 8E) and BSP 1987 I 47, the holotype of *A. robustus* (Fig. 8B), both classified as fully mature individuals (Wellnhofer, 1987; Veldmeijer, 2003). It is also notably smaller than NSM-PV 19892, the holotype of *A. piscator* (Fig. 8F), which is also considered a subadult (Kellner and Tomida, 2000). If *A. robustus* were to be synonymized with *A. blittersdorffi*, and the pattern observed on *Pteranodon* and *Hamipterus* (Bennett, 1992; Wang et al. 2014a) is applied to *Anhanguera*, then MZSP-PV 368 could potentially represent a young male entering sexual maturity.

However, the similarities between the mandibular crests of SMNK PAL 2302 and that of *A. spielbergi* (RGM 401 880) — which has been proposed as a presumed adult, mature male (Veldmeijer, 2003) — suggest that the smaller crest of SMNK PAL 2302 is unlikely to represent a sexual morph of “robustus-like” specimens. Therefore, we conclude that the most probable scenario remains an interspecific distinction between SMNK PAL 2302 and *A. robustus*, reinforcing the validity of *A. robustus* as a distinct species. Thus, the present work provides new anatomical and comparative data which we interpret as compelling evidence for supporting the existence of four *Anhanguera* species within the Romualdo Formation. However, given the lack of precise provenance and stratigraphic control for most specimens recovered from the Romualdo Formation, we recognize that it remains challenging to determine whether these anatomical differences reflect true distinct coexisting species, population-level variations distributed across different temporal intervals, or even anagenetic variation.

8. Systematic paleontology

PTEROSAURIA Kaup (1834).

PTERODACTYLOIDEA Plieninger (1901).

ORNITHOCHEIROIDEA Seeley (1870) (*sensu* Bennett, 1994).

PTERANODONTOIDEA Marsh (1876) (*sensu* Kellner, 2003).

ORNITHOCHEIRIFORMES Andres (2021).

ANHANGUEROIDEA Pêgas (2025).

ANHANGUERIA Rodrigues and Kellner (2013).

ANHANGUERIDAE Campos and Kellner (1985) (*sensu* Pêgas, 2025).

ANHANGUERINAE Holgado et al. (2019).

***Anhanguera* Campos and Kellner, 1985**

Type species. *Anhanguera blittersdorffi* Campos and Kellner (1985).

Locality. Almost all specimens assigned to *Anhanguera* were discovered at unknown provenances, originating from the Romualdo Formation, Araripe Basin, northeast Brazil.

Age range. Early Cretaceous, Late Aptian–Early Albian (Bom et al. 2023).

Revised diagnosis. Members of the Anhangueridae characterized by the presence of premaxillary and dentary sagittal crests starting at immature, juvenile stages; premaxillary crest thin, highly asymmetric, initiating near the skull's tip but not at the tip, extending beyond the anterior-most portion of the skull, and exhibiting allometric growth in height and length during ontogeny; fifth and sixth teeth smaller than the fourth and seventh, being subequal in size; parietal crest thin and blade-like; palatal ridge shallow (revised from Kellner and Campos, 1988; Pinheiro and Rodrigues, 2017).

Remarks. The dental formula of *Anhanguera*, where the fifth and sixth teeth are smaller than the fourth and seventh, can still be considered the main autapomorphy that defines *Anhanguera* aside from any anhanguerid pterosaur (Duque et al. 2022). A putative character that could define *Anhanguera* is 18–26 pairs of maxillary teeth, and 16–21 pairs of

mandibular teeth, but teeth counting in anhanguerids requires a careful re-evaluation (see Table 5 for examples).

***Anhanguera blittersdorffi* Campos and Kellner (1985)**

Holotype. MN 4805-V, a complete skull (Campos and Kellner, 1985) (Fig. 14A).

Referred specimens. Here, we identify SMNK PAL 2302 and NHMUK R11978 as referred specimens. SMNK PAL 2302 comprises the anterior portion of the rostrum and lower jaw (Fastnacht, 2001), while NHMUK R11978 represents a complete skull.

Revised diagnosis. Medium-sized *Anhanguera*, with a palatal keel posteriorly restricted, located posterior to the eighth teeth (revised from Bantim et al. 2014).

Remarks. The character defined by Pinheiro and Rodrigues (2017), which is the large number of alveoli (52) on the upper jaw, is too ambiguous to be used as an autapomorphy (see Table 5 for examples), and until a careful re-evaluation is performed, teeth counting in anhanguerids as an autapomorphic trait should be discouraged, aside from extreme cases such as *Maaradactylus* (Bantim et al. 2014). The poor preservation of Pz-DBAV-UERJ 40 makes its referral to *A. blittersdorffi* ambiguous, thus here we consider it an indeterminate specimen.

***Anhanguera piscator* Kellner and Tomida (2000)**

Holotype. NSM-PV 19892, an almost complete skeleton including the skull, lower jaw and most elements of the postcranium (Kellner and Tomida, 2000) (Fig. 14B).

Diagnosis. Large-sized *Anhanguera*, with a constriction at the middle part of the basisphenoid; neural spine of the axis forms a 45° angle; caudal vertebrae relatively elongated; neural spines of the middle caudal vertebrae reach the preceding vertebra, with a well-developed ventral process; shaft of the scapula constricted; coracoid with a small anterior process; distal articulation of the ulna bears a sharp ventral crest (Kellner and Tomida, 2000; Pinheiro and Rodrigues, 2017).

Remarks. *A. piscator* remains as the sole species of *Anhanguera* with autapomorphies identified at the appendicular skeleton.

***Anhanguera spielbergi* (Veldmeijer, 2003)**

Holotype. RGM 401 880, an almost complete skeleton including the skull, lower jaw and most elements of the postcranium (Veldmeijer, 2003) (Fig. 14C).

Diagnosis. Large-sized *Anhanguera*, with the mandibular groove not extending until the anterior lateral expansion of the mandible; sternal plate triangular and as long as wide (Veldmeijer, 2003; Pinheiro and Rodrigues, 2017).

Remarks. *A. spielbergi* is the only species of *Anhanguera* with autapomorphies identified at the lower jaw that are not related to the dentary crest. Thus, it can be directly compared to *A. robustus*. While the mandibular groove in both species does not reach the tip of the lower jaw, in *A. robustus* (BSP, 1987 I 47 and MZSP-PV 368) it reaches the anterior spoon-shaped expansion of the mandible, whereas in *A. spielbergi* it does not. The condition in *A. piscator* is unknown, and the mandibular groove in *A. blittersdorffi* (SMNK PAL 2302) reaches the tip of the lower jaw.

***Anhanguera robustus* (Wellnhofer, 1987)**

Holotype. BSP 1987 I 47, a mandibular symphysis and the right mandibular ramus (Wellnhofer, 1987) (Figs. 5 and 6).

Referred specimens. Here, we identify MZSP-PV 368 and SAO 200602 (Veldmeijer et al. 2005) as referred specimens. Both specimens are complete lower jaws.

Revised diagnosis. Medium-sized *Anhanguera*, with a dentary crest at least as high as the height of the mandibular rami, at least in advanced ontogenetic stages, and the anterior margin of the crest straight, forming an angle between 45° and 50° relative to the dorsal margin of the jaw (revised from Wellnhofer, 1987; Kellner and Tomida, 2000).

Remarks. As concluded here, the shape and size of cranial crests (exemplified here with the mandibular crest) can bear autapomorphies for anhanguerid pterosaur species. Fastnacht (2001) originally described SMNK PAL 2302 as the paratype of *A. robustus*, but here we identify this specimen as a referred specimen of *A. blittersdorffi*.



Fig. 14. Cranial material of the holotypes of *Anhanguera*: (A) MN 4805-V, the holotype of *Anhanguera blittersdorffi* Campos and Kellner (1985); (B) Skull and lower jaw of NSM-PV 19892, the holotype of *Anhanguera piscator* Kellner and Tomida (2000); (C) Skull of RGM 401 880, the holotype of *Anhanguera spielbergi* (Veldmeijer, 2003). Scale bars equal 10 cm.

Moreover, as per the ICZN Recommendation 73D (ICZN IC on ZN-, 1999), a paratype can only be designated as part of the type series on the original description, thus Fastnacht (2001) identification of SMNK PAL 2302 as the paratype of any species described previously is equivocal.

Anhanguera sp. indet

Referred specimens. Other unidentified specimens of *Anhanguera* are as follows.

- BSP 1982 I 89, the holotype of '*Anhanguera araripensis*', comprising a fragmentary middle portion of the skull and lower jaw, and elements of the right wing (Wellnhofer, 1985);
- BSP 1982 I 90, the holotype of '*Anhanguera santanae*', comprising the posterior half of the skull, a fragmentary middle portion of the lower jaw, and various elements of the wings (Wellnhofer, 1985);
- AMNH 22555, A putative referred specimen of '*Anhanguera santanae*', which is a rather complete specimen, with a complete skull, posterior pieces of the lower jaw, an almost complete cervical and dorsal series, complete and associated scapular and pelvic girdles, and various fragments of a right wing (Wellnhofer, 1991; Pinheiro and Rodrigues, 2017);

- SMNK PAL 1136, a fragmentary but almost complete skeleton including a skull, a lower jaw, girdles and elements of the wings (Frey and Martill, 1994);
- MN 4735-V, A putative referred specimen of '*Anhanguera araripensis*', which is a complete skull (Kellner and Tomida, 2000);
- Pz-DBAV-UERJ 40, which includes a fragmentary skull and lower jaw (Kellner and Tomida, 2000);
- SAO 16494, A putative referred specimen of '*Anhanguera araripensis*', which is a complete skull (Veldmeijer et al. 2006);
- DGEO-CTG-UFPE 8283, the anterior fragment of a pterosaur rostrum (Duque et al. 2022).

Remarks. As of Pinheiro and Rodrigues (2017), '*Anhanguera araripensis*' and '*Anhanguera santanae*' have no diagnostic characters, thus the holotypes and all putative referred specimens of both species are classified as *nomina dubia*. Pz-DBAV-UERJ 40 and SMNK PAL 1136 lacks a complete description, and the preservation of Pz-DBAV-UERJ 40 makes its identification ambiguous. Both specimens are identified here as indeterminate until a complete description is published. As for DGEO-CTG-UFPE 8283, it is too fragmentary to be assigned to a species

of *Anhanguera*, although it can be recognized as a juvenile specimen of *Anhanguera* (Duque et al. 2022). Finally, as Dalla Vecchia et al. (2015) concluded, MCFO 0595 is a composite of reconstructions and possibly many pterosaur specimens, making its identification unreliable. At least the cranial remains can be referred to Anhangueridae.

9. Conclusions

MZSP-PV 368 is identified as a new specimen of *Anhanguera* based on the morphology of its medial crest at the dentary symphysis, the configuration of its mandibular teeth, and its position in our phylogenetic analysis. This specimen represents an additional example of the “robustus-like” mandibular morphology in *Anhanguera*, alongside the holotype of *A. robustus* (BSP, 1987 I 47) and SAO 200602. All three specimens share a distinctive straight anterior margin of the dentary crest, forming an angle between 45° and 50° relative to the dorsal margin of the jaw. MZSP-PV 368 is regarded here as a subadult, and the presence of scars consistent with blood vessel channels is suggestive of a keratinous sheath.

Our morphometric analysis reinforces that the “robustus-like” mandibular crest morphology is a distinct and consistent trait within *Anhanguera*, forming a well-defined cluster separate from other specimens of similar ontogenetic stages. Since this trait cannot be solely attributed to ontogenetic variation, contrary to previous assumptions, we revalidate *A. robustus* as a distinct species within *Anhanguera*. This species includes BSP 1987 I 47 (the holotype), MZSP-PV 368 and SAO 200602 — all recovered with a “robustus-like” morphology.

Comparisons between the new specimen and all previously described *Anhanguera* specimens indicate that the taxonomy of the genus is more complex than previously thought, requiring careful re-evaluation, based on more complete specimens. Based on the available evidence, we assign MZSP-PV 368 and other “robustus-like” specimens, such as SAO 200602, to *A. robustus*, recognizing that further discoveries may refine this classification. Additionally, we reassign SMNK PAL 2302 to *A. blittersdorffi*, along with NHMUK R11978, based on the position of the palatal ridge, which we consider an autapomorphy of this species.

Ultimately, this study underscores the **diagnostic value of mandibular crest morphology** in anhanguerid systematics, highlighting its importance in refining species distinctions within *Anhanguera*. Future discoveries of more complete specimens will be crucial to further clarify the taxonomy and evolutionary relationships within this group.

CRediT authorship contribution statement

Lucas C. Piazzentin: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bruno A. Navarro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **R.V. Pêgas:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alberto B. Carvalho:** Writing – review & editing, Validation, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Hussam Zaher:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jsames.2025.105684>.

Data availability

Data will be made available on request.

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