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A taxonomic note on the tapejarid pterosaurs from the Pterosaur Graveyard site (Caiuá Group, ?Early Cretaceous of Southern Brazil): evidence for the presence of two species

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ABSTRACT

The Caiuá Group (Cretaceous of Southern Brazil) is famous for the Pterosaur Graveyard site, a location that has yielded hundreds of tapejarid specimens, among other taxa. Previous works had already presented various specimens of Pterosaur Graveyard (PG) tapejarids, reporting on several cranial elements showing substantial anatomical variations. These variations have been interpreted as intraspecific in nature, with all tapejarid specimens having been attributed to a single species, *Caiuajara dobruskii*. The present contribution reassesses the morphological diversity found in PG tapejarid specimens. Evidence is provided for the interpretation of several variations as interspecific in nature, particularly regarding rostral, palatal, occipital, and third cervical morphology. The present data indicate a segregation of the PG tapejarid specimens between two consistent morphotypes, which are interpreted here as two distinct, coexisting species: *Caiuajara dobruskii* and *Torukjara bandeirae* gen. et sp. nov.

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Introduction

The Tapejaridae are a clade of Cretaceous toothless pterosaurs easily recognised by their short, downturned rostra and peculiar premaxillary crests (Kellner and Campos 2007; Martill et al. 2020a; Pêgas et al. 2023). Members of the larger clade Azhdarchoidea, tapejarids comprise over 10 species, spanning from the Barremian to the Santonian; with records from Brazil, Morocco, Europe, and China (see Andres et al. 2014; Vullo et al. 2012; Martill et al. 2020a, 2020b; Pêgas et al. 2023).

Manzig et al. (2014) reported on the fantastic discovery of a pterosaur accumulation site filled with hundreds of tapejarid specimens, distributed throughout four bone bed layers of a single locality of the Caiuá Group in Paraná State, Southern Brazil. Even though the skeletal remains are usually incomplete, disarticulated, and often jumbled together, the quality of the preservation is outstanding, with three-dimensional elements and well-preserved bone surfaces (Manzig et al. 2014). All of these tapejarid specimens were considered as members of a single species, thereby named *Caiuajara dobruskii* (Manzig et al. 2014). The Caiuá Group tapejarid assemblage is notorious for including specimens of various sizes and ontogenetic stages. Noticeable variations were found in the size and shape of the premaxillary crests, which were interpreted as ontogenetic in nature (Manzig et al. 2014). Variation concerning the presence/absence of a delicate palatal ridge was also reported, though not further discussed (Manzig et al. 2014). No further variations were reported, and it was noted that no particular ontogenetic variations could be observed in postcranial elements, safe for the relative robustness of the prepubic plate and coracoidal tubercle (see Manzig et al. 2014).

This tapejarid accumulation site became later known as the Pterosaur Graveyard (Kellner et al. 2019). From this site, several

other taxa have been described: the stem-acrodontan lizard *Gueragama sulamericana* (Simões et al. 2015), the azhdarchoid pterosaur *Keresdrakon vilsoni* (Kellner et al. 2019), and the noasaurid dinosaurs *Vespersaurus paranaensis* (Langer et al. 2019) and *Berthasaura leopoldinae* (de Souza et al. 2021).

More recently, Canejo et al. (2022) described several new pterosaur specimens coming from the Pterosaur Graveyard site, which were all attributed to *Caiuajara dobruskii* (Canejo et al. 2022). This work reported on several morphological variations within the Caiuá tapejarid assemblage, including the variable presence/absence of a palatal ridge and of a pair of large foramina posterior to the incisive foramen (Canejo et al. 2022). This conspicuous variation in palatal morphology was interpreted therein as intraspecific in nature, with the Caiuá tapejarid assemblage presumably comprising a single species, *Caiuajara dobruskii* (Canejo et al. 2022).

Concerning azhdarchoid diversity and proposed diagnoses, the patterns of occlusal modifications are of notable importance (e.g. Pêgas et al. 2021; Smith et al. 2023). In azhdarchoid jaws, occlusal surfaces exhibit a plethora of anatomical variations, many of which represent distinctive, diagnostic apomorphies of many taxa (see Pêgas et al. 2021; Smith et al. 2023). In this way, such diversity seems to carry useful taxonomic signals (see Pêgas et al. 2021; Smith et al. 2023 for comments on this subject).

For this reason, the notorious palatal variation previously reported for the Pterosaur Graveyard (PG) tapejarid assemblage can be seen as intriguing, and this subject is deemed here as worthy of further investigation. With this in mind, the present work aims at testing the interpretation that a single tapejarid species exists in the PG assemblage (Manzig et al. 2014; Canejo et al. 2022). For this purpose, this work provides a critical

reassessment of the morphological variation found in the PG tapejarids, revisiting specimens that were already studied and described previously (e.g. Manzig et al. 2014; Canejo et al. 2022).

Material and methods

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; BMNH, Beijing Museum of Natural History, Beijing, China; BPMC, Beipiao Pterosaur Museum of China, Beipiao, China; BPV, Beijing Natural History Museum, Beijing, China; BXGM, Benxi Geological Museum, Benxi, China; CENPALEO, Centro de pesquisa paleontológica da Universidade do Contestado, Mafra, Brazil; CPCA, Centro de Pesquisas Paleontológicas da Chapada do Araripe (Departamento Nacional de Produção Mineral), Crato, Brazil; CP.V, Contestado University Centro de Pesquisa Paleontológica vertebrate collection, Mafra, Brazil; D, Dalian Natural History Museum, Dalian, China; GMN, Geological Museum of Nanjing, Nanjing, China; GP/2E, Laboratório de Paleontologia Sistemática do Instituto de Geociências (Universidade de São Paulo), São Paulo, Brazil; IMNH, Iwaki Museum of Natural History, Iwaki, Japan; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; JPM, Jinzhou Museum of Paleontology, Jinzhou, China; MCT, Museu de Ciências da Terra, Rio de Janeiro, Brazil; MN, Museu Nacional (Universidade Federal do Rio de Janeiro), Rio de Janeiro, Brazil; SAO, Collection of Urs Oberli, St Gallen, Switzerland.; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; XHPM Xinghai Museum of Prehistoric Life of Dalian, Dalian, China; ZMNH Zhejiang Museum of Natural History, Hangzhou, China.

Specimens' provenance

All the specimens discussed here come from the site known as Pterosaur Graveyard, a locality where rocks of the Caiuá Group are exposed and abundant fossils can be found (Manzig et al. 2014; Kellner et al. 2019). No permits were required for this study, which is collection-based. All specimens discussed here are housed in the scientific collection of the CENPALEO (*Paleontological Center of the Contestado University*), and have already been presented before in the literature (Manzig et al. 2014; Wantowsky and Weinschütz 2018; Kellner et al. 2019; Canejo et al. 2022; Araújo et al. 2023).

Geological setting

The Pterosaur Graveyard outcrops were originally attributed to the Goio-Erê Formation on the basis of lithology (Manzig et al. 2014; Kellner et al. 2019), but were then reinterpreted as part of the Rio Paraná Formation on the basis of geographic position (Langer et al. 2019; Alves et al. 2019). The Goio-Erê and Rio Paraná Formations are inter-digitating deposits that (debatably together with the Santo Anastácio Formation as well) form the Caiuá Group (Batezelli and Ladeira 2016; Batezelli, 2017). The Caiuá Group comprises, mainly, a quartz-sandstone aeolian sedimentary unit, deposited under arid conditions (Batezelli and Ladeira 2016; Batezelli 2017). Until a careful geological reassessment of the area is provided, it is regarded here that the Pterosaur Graveyard is best attributed to the Caiuá Group in general terms.

The Caiuá Group, together with the Bauru Group, form the Bauru Supersequence, deposited over the Valanginian-Aptian Serra Geral basalt flows (Bruckmann et al., 2014; Batezelli and

Ladeira 2016; Batezelli 2017). Situated in the south-central region of the South American Platform, its paleolatitudes correspond to the so-called 'Southern Hot Arid Belt' (Chumakov et al. 1995). Some researchers have considered the Caiuá and Bauru Groups to be partially chronocorrelated, representing, respectively, a dryer area and a surrounding alluvial paleoenvironment (Fernandes and Ribeiro 2015). Based on such tentative stratigraphic correlations between the Caiuá Group and part of the Bauru Group (particularly the Adamantina Fm.), the Caiuá Group has been regarded by some researchers as Late Cretaceous in age, ranging from the Turonian to the Campanian (Fernandes and Ribeiro 2015). However, these tentative correlations have been solidly refuted (Basilici et al. 2019), and it can be considered that there are no grounds for a confident assignment of the Caiuá Group to the Late Cretaceous (Batezelli and Ladeira 2016; Batezelli 2017). Importantly, micropalaeontological evidence contradicts the purported correlation between the Caiuá Group and the Adamantina Formation (Dias-Brito et al. 2001).

A more traditional interpretation regards the Caiuá Group as older than the Bauru Group, representing an earlier desertic phase that was eventually succeeded by the more humid conditions documented in the Bauru Group (Dias-Brito et al., 2001). Magnetostratigraphic studies, which have only been preliminary published, have indicated a roughly Barremian-Aptian age for this Group (Ernesto et al. 2006; Batezelli, 2017). Based on facies analysis and palaeoclimatic evidence, other researchers have suggested an Aptian-Albian age for the Caiuá Group (Fulfaro et al., 1999, Dias-Brito et al. 2001; Batezelli and Ladeira 2016; Batezelli 2017). It is clear that further work is needed in order to achieve a confident temporal resolution for the Caiuá Group. Still, based on the available evidence, an Early Cretaceous age seems better supported than a Late Cretaceous one.

Quantitative analyses

Of the anatomical features herein explored and discussed, one pertains to a morphometric character – rostrum deflection angle. Carefully assessing whether this character is influenced by allometry or not is therefore important. Hence, a bivariate allometric analysis has been performed between log-transformed values of rostrum deflection angle and log-transformed values of prenarial rostral length (as a proxy for body size), in order to test for potential allometric relationships. For this purpose, the standardised major axis (SMA) line-fitting method has been employed, and the p-value was calculated to determine if the correlation is significant ($p < 0.05$) or not (Warton et al. 2006; Yang et al. 2021; Pégas et al. 2023). Isometry is considered as the null hypothesis. The analyses were performed using the software PAST (Hammer et al., 2001). The measurements utilised for the analysis are presented further below (see Results).

Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The ZooBank Life Science Identifiers (LSIDs) can be resolved and the associated information viewed by appending the LSIDs to the prefix <http://zoobank.org/>. The LSID for this publication is urn:lsid:zoobank.org:pub:70DCFD01-9207-44DD-8FE8-08504DCE3E13.

LSID for the new subtribe Caiuajarina: urn:lsid:zoobank.org:act:1F7FECEF-58 DB-4DF4-8C07-B7B7674DA995. LSID for the new genus *Torukjara*: urn:lsid:zoobank.org:act:00505A32-B98D-49AA-A28E-E63D018C63CF. LSID for the new species

Torukjara bandeirae: urn:lsid:zoobank.org:act:9B005D28-D609-4079-AB25-F151F1AF1335.

Phylogenetic analysis

In order to investigate the phylogenetic relationships of the species herein analysed, this paper is accompanied by a new pterosaur phylogenetic matrix. For this new matrix, effort was made in order to assemble taxon and character lists as comprehensive as possible. Morphological characters have been mostly gathered from the literature (Howse 1986; Bennett 1994; Kellner 2003, 2004; Unwin 2003; Dalla Vecchia 2009, 2019; Lü et al. 2010; Wang et al. 2012; Naish et al. 2013; Andres et al. 2014; Pêgas et al. 2016, 2018, 2019, 2021, 2023; Vidovic and Martill 2018; Longrich et al. 2018; Holgado et al. 2019; Kellner et al. 2019; Zhou et al. 2019, 2021; Andres 2021), resulting in a total of 520 discrete characters. Concerning taxon list, the new matrix includes 4 outgroup taxa (*Euparkeria capensis*, *Ornithosuchus woodwardi*, *Herrerasaurus ischigualastensis*, *Lagerpeton chanarensis*) and 188 pterosaur species-level Operational Taxonomic Units (OTUs; 185 nominal species plus 3 unnamed species). As a result, this is the most comprehensive pterosaur phylogenetic matrix so far.

All character statements have been formulated following Sereno (2007). All characters and states were constructed with the effort of representing primary homology hypotheses (de Pinna 1991). Some characters available in the literature do not reflect hypotheses of shared evolutionary traits (e.g. Vidovic and Martill 2018; character 101: 'occlusal surface process: present (0), absent (1)', which mixes structures with different origins, i.e. from the upper and lower jaws), or do not reflect biological features (e.g. Andres 2021; character 0: 'skull, aspect ratio, length to maximum height preserved exclusive of crests', which is unexpectedly coded as a preservational feature), and were thus not included here. All characters have been treated as unordered and unweighted. Following previous works, we have avoided composite coding (Colless 1985), as well as treatment of continuous data as such (for discussions on the subject, see Goloboff et al. 2008; Bardin et al., 2014; Mongiardino Koch et al., 2015; Vidovic, 2018). In order to minimise the effect of overweighting in biologically dependent characters, conditional clauses and inapplicable states were employed when necessary. Characters known to vary only within advanced ontogenetic stages were coded only for species known from osteologically mature specimens (e.g. when present, the notarium is known to develop only late in ontogeny; thus, the presence of a notarium was accordingly coded as '?' for species known solely from immature specimens such as *Anhanguera piscator*, as the coding should reflect the species, and not the specimen).

The analysis was conducted under maximum parsimony, using the software TNT 1.5 (Goloboff et al. 2008). The analysis was divided in two steps, following the same protocol as previously described by Wei et al. (2021). New Technology Search was used for the first step (using Sectorial Search, Ratchet, Drift and Tree fusing, default parameters), with random seed = 0. Subsequently, with tree memory space set to maximum, a Traditional Search was performed using trees from RAM (using TBR, collapsing trees after search).

Supplementary data associated with this work contain (1) the data matrix written in Nexus format (for Mesquite); (2) the data matrix written in TNT format; and (3) a text file with further

details concerning utilised OTUs and coding sources. For better illustration of palatal morphology (and its relevant characters) in the analysed sample, the Supplementary Data further includes additional photographs (Supplementary Data 4) and a 3D PDF (Supplementary Data 5; produced using *AgiSoft PhotoScan Professional 1.2.6*). All Supplementary Data, including the data matrix in both Nexus (ready for editing in Mesquite) and TNT formats (ready for analysis execution in TNT), are also available at the MorphoBank online repository, under project number 5237.

Phylogenetic nomenclature

The present work follows the PhyloCode (de Queiroz et al. 2020) as a means of standardising and stabilising phylogenetic nomenclature. The phylogenetic definitions put forward by Andres (2021) concerning azhdarchoids are followed here, with further incrementations (Table 1). The informal emendation of Tapejaridae previously proposed by Pêgas et al. (2023) produces a clade conceptualisation distinct (broader) from that originally registered under the PhyloCode's database RegNum (Andres 2021), thus failing the requirements for a formal unrestricted emendation (de Queiroz et al. 2020). Therefore, for this broader concept, a new clade name (Tapejariformes) is herein proposed (Table 1), and the informal emendation of Tapejaridae by Pêgas et al. (2023) is left aside. The nomenclatural scheme adopted here, following recommendations of the PhyloCode, is presented in Table 1.

Results

Survey of anatomical variations

The generalised osteological pattern of the PG tapejarids has already been described elsewhere (Manzig et al. 2014; Canejo et al. 2022). The present contribution does not intend to provide a monographical account of the morphology of the assemblage, nor of any specimen; but to report the most striking variable features, according to the present survey of the known specimens (Manzig et al. 2014; Wantowsky and Weinschütz 2018; Kellner et al. 2019; Canejo et al. 2022; Araújo et al. 2023). Following the original observations by Manzig et al. (2014), very small specimens (with prenarial rostra of ~20 mm in length) with underdeveloped cranial crests are interpreted as juveniles (e.g. CP.V 1450, CP.V 8171; see Manzig et al. 2014; Canejo et al. 2022). Larger specimens (with prenarial rostra of ~30–50 mm in length) are interpreted as sub-adults (such as CP.V 1001, CP.V 1005, CP.V 1448, CP.V 1449, CP.V 8175; see Manzig et al. 2014; Canejo et al. 2022), while the largest specimens (prenarial rostra of ~70 mm in length) may be regarded as close to maturity. The results of the allometric correlation analysis, performed for the rostrum deflection angle as explained above (see Materials and Methods – Quantitative analyses), are presented within the subsection relative to this same feature (see below; Results – Rostrum deflection angle).

Palatal ridge

As already briefly expressed before in the literature (Manzig et al. 2014; Canejo et al. 2022), some PG tapejarid specimens exhibit a delicate palatal ridge, while other specimens lack such feature. When present, this delicate palatal ridge is restricted to the posterior region of the prenarial palate, and located within a depression. Such structure thus differs in shape and location from any other

Table 1. Phylogenetic nomenclature. Reference phylogeny: this work. Definitional authors and Regnum codes are given between brackets.

Clade	Nominal author	Definition	Composition and remarks	ICPN conversion and Regnum code
Tapejaromorpha	Andres et al. (2014)	The most inclusive clade containing <i>Tapejara wellnhoferi</i> Kellner 1989 but not <i>Azhdarcho lancicollis</i> Nessov 1984.	Includes the sister-taxa Tapejariformes and Thalassodromidae. Equivalent to Tapejaridae sensu Kellner and Campos (2007).	[Andres 2021], [356].
Thalassodromidae	Witton (2008)	The least inclusive clade containing <i>Thalassodromeus sethi</i> Kellner & Campos 2002 and <i>Tupuxuara longicristatus</i> Kellner & Campos 1988.	Includes <i>Thalassodromeus</i> , <i>Tupuxuara</i> , and <i>Kariridraco</i> .	[Andres 2021], [770].
Tapejariformes	This work	The clade characterised by a downturned rostrum synapomorphic with that of <i>Tapejara wellnhoferi</i> Kellner 1989 (apomorphy-based).	Includes Caupedactylia and Tapejaridae. Equivalent to Tapejaridae sensu Pêgas et al. (2023).	[Pêgas, 2024], [1042].
Caupedactylia	Pêgas et al. (2023)	The most inclusive clade containing <i>Caupedactylus ybaka</i> Kellner 2013 but not <i>Tapejara wellnhoferi</i> Kellner 1989.	Includes <i>Caupedactylus</i> and <i>Aymberedactylus</i> .	[Pêgas et al. 2023], [821].
Tapejaridae	Kellner (1989)	The least inclusive clade containing <i>Tapejara wellnhoferi</i> Kellner 1989 and <i>Sinopterus dongi</i> Wang & Zhou 2003.	Includes Tapejarinae and Sinopterinae. Equivalent to Tapejarinae sensu Kellner and Campos (2007).	[Andres 2021], [357].
Sinopterinae	Lü et al. (2016)	The most inclusive clade containing <i>Sinopterus dongi</i> Wang & Zhou 2003 but not <i>Tapejara wellnhoferi</i> Kellner 1989.	Under the present reference phylogeny, this clade includes <i>Sinopterus</i> , <i>Eopteranodon</i> , <i>Huaxiadraco</i> , <i>Wightia</i> , <i>Afrotapejara</i> , and <i>Bakonydraco</i> .	[Andres 2021], [360].
Tapejarinae	Kellner and Campos (2007)	The most inclusive clade containing <i>Tapejara wellnhoferi</i> Kellner 1989 but not <i>Sinopterus dongi</i> Wang & Zhou 2003.	Under the present reference phylogeny, this clade includes <i>Europejara</i> , <i>Tupandactylus</i> , <i>Tapejara</i> , <i>Caiuajara</i> , and <i>Torukjara</i> .	[Andres 2021], [358].
Tapejarini	Andres et al. (2014)	The least inclusive clade containing <i>Tapejara wellnhoferi</i> Kellner 1989 and <i>Tupandactylus imperator</i> (Campos & Kellner 1997).	<i>Tupandactylus</i> , <i>Tapejara</i> , <i>Caiuajara</i> , and <i>Torukjara</i> .	[Andres 2021], [359].
Caiuajarina	This work	The most inclusive clade containing <i>Caiuajara dobruskii</i> Manzig et al. 2014 but not <i>Tapejara wellnhoferi</i> Kellner 1989.	Includes the Caiuá Group tapejarids <i>Caiuajara dobruskii</i> and <i>Torukjara bandeirae</i> .	[Pêgas, 2024], [976].

palatal ridges seen in other pterosaurs, such as thalassodromids (see Kellner and Campos 2007; Pêgas et al. 2018) or alanquids (see Smith et al. 2023).

After revisiting previously figured specimens (from Manzig et al. 2014; Canejo et al. 2022), it is noted here that this feature is absent in the holotype specimen of *Caiuajara dobruskii* (CP.V 1449), as well as in paratype specimens CP.V 1001, CP.V 1003, CP.V 1005, CP.V 1447/I and CP.V 1449, and the referred specimen CP.V 5703/I (Figure 1). Similarly, the palatal ridge is absent in all 5 visible palates preserved within block CP.V 1450 (Figure 1). In turn, a palatal ridge can be found in specimen CP.V 8175 (Canejo et al. 2022), as well as specimens CP.V 867, CP.V 1023, CP.V 1448, CP.V 2446, and CP.V 5703/II (Figure 2). For a better visualisation of this delicate feature, the Supplementary Data includes further photographs (Supplementary Data 4), as well as photogrammetric images (in 3D PDF format; Supplementary Data 5) of the palates of the palatal-ridged specimens CP.V 8175 and CP.V 5703/II, and of the ridge-less specimen CP.V 1447/I (see Supplementary Data).

This delicate palatal ridge, restricted to the posterior region of the prenasal palate and located within a depression, as seen in the aforementioned specimens, represents a unique feature that cannot be found in any other pterosaur. This variation is not correlated to body size, with ridge-less palates being found in the diminutive juvenile specimens of block CP.V 1450, as well as in the medium-sized specimen CP.V 1449 and the large specimen CP.V 1005. Similarly, ridged palates can be found in the diminutive juvenile CP.V 867, the small specimen CP.V 1023, the medium-sized specimens CP.V 2446 and CP.V 8175, and the large specimen CP.V 1448 (Table 2).

Incisive foramen

As already demonstrated by previous works (Canejo et al. 2022), some PG tapejarid specimens exhibit a single incisive foramen

(Figure 1), while others exhibit a pair of large foramina posterolateral to the incisive foramen (hereby termed the accessory incisive foramina), constituting what is termed here as a triple incisive foramen (Figure 2). As noted here, this variation regarding incisive foramina is correlated to variation in the palatal ridge, with single foramina occurring in ridge-less palates (CP.V 1003, CP.V 1447/I, CP.V 1449, CP.V 1450, CP.V 5703/I; Figure 1) and triple foramina occurring in ridged palates (CP.V 1023, CP.V 2446, CP.V 8175; Figure 2). The condition of CP.V 1448 is unclear due to the fragmentary preservation of its palatal surface (only a strip of the right side of the bone surface is preserved), although it is likely that a foramen visible there represents the right accessory incisive foramen, as it is not located on what would be the midline of the incompletely preserved palate (Figure 2).

Like the delicate ridge discussed above, the condition of a triple incisive foramen is another unique feature that cannot be found in other pterosaurs. As the presence of a triple incisive foramen is correlated to the presence of a palatal ridge, it is similarly uncorrelated to body size (see above – Palatal ridge).

Rostrum deflection angle

Martill et al. 2020b reported on an impressively large variation in the deflection angle of PG tapejarids, ranging from 31° to 41°. This impressive range was questioned by Pêgas et al. (2023), who expressed wariness due to the difficulty of accurately assessing the point of deflection in fragmentary specimens and the lack of first-hand measurements. Here, upon first-hand analysis of the material, the present work corroborates the large variation found by Martill et al. (2020b), recording a range of 29°–41° ($n = 16$ skulls; Figure 3; Table 2).

This large range of 12° contrasts starkly with the variation seen in other tapejarid species. The range of intraspecific variation is of 3° for *Sinopterus dongi* ($n = 8$ skulls), 3° for *Huaxiadraco corollatus* ($n = 5$), 3° for *Tapejara wellnhoferi* ($n = 5$), 2° for *Tupandactylus*

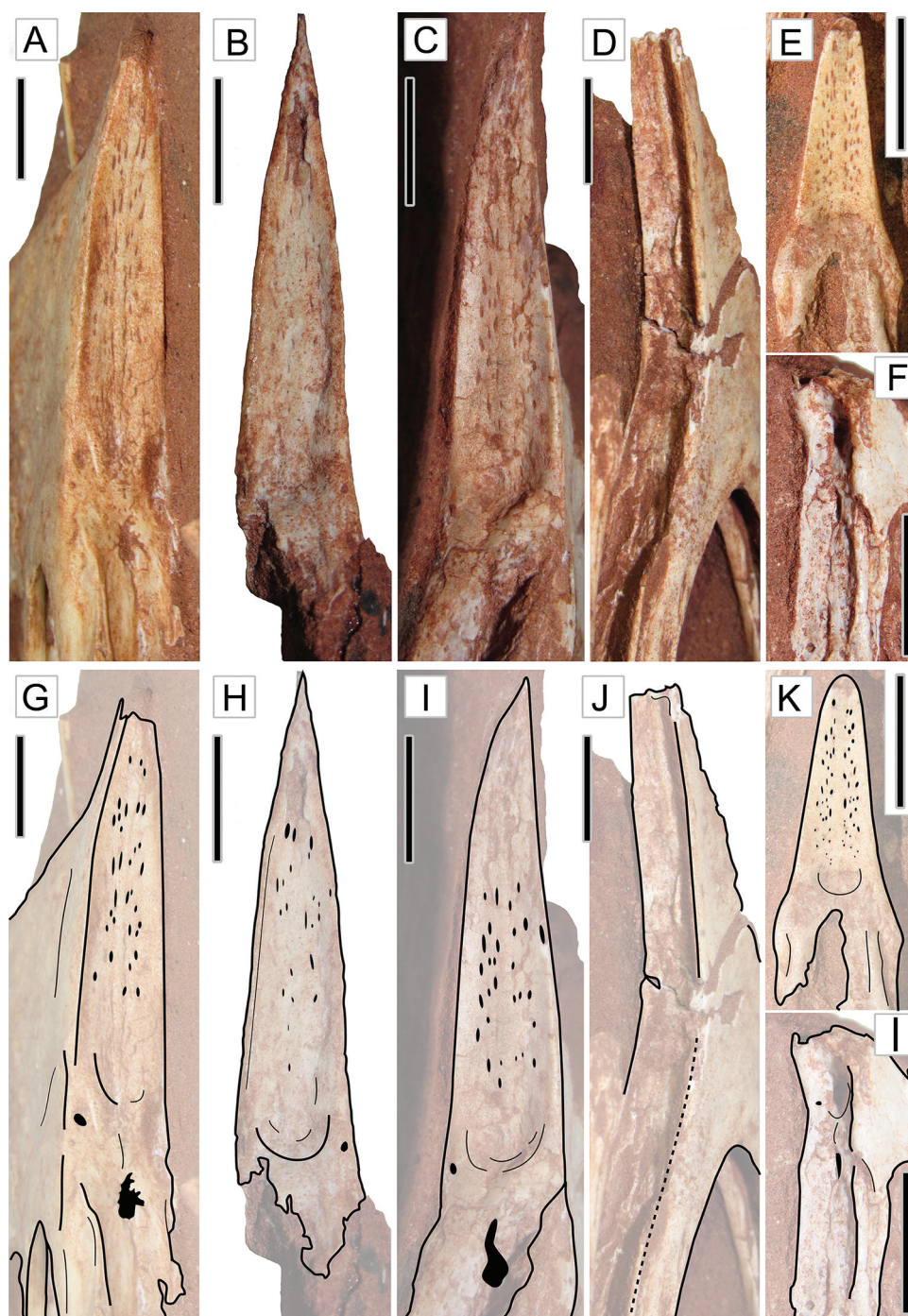


Figure 1. Palatal region of Pterosaur Graveyard tapejarid specimens showing palate morphotype I. Photos of specimens (a) CP.V 1449; (b) CP.V 1001; (c) CP.V 1447/l; (d) CP.V 5703/l; (e) CP.V 1450; (f) CP.V 865; and respective schematic drawings g – i. Scale bars = 10 mm.

imperator ($n = 3$), and 2° for *Tupandactylus navigans* ($n = 3$; see Pinheiro et al. 2011; Elgin and Campos 2012; Beccari et al. 2021; Pêgas et al. 2023). Notwithstanding sampling limitations, this pattern suggests that such an expressive range of 12° could be too extensive to represent variation within a monospecific sample, and could thus be an indication of a multi-taxic assemblage. This range is even larger than the one seen in the multi-taxic Jiufotang tapejarid assemblage, which is of 9° in total (Pêgas et al. 2023).

It is worth pointing out that such variation seems uncorrelated to body size. Low values of $\sim 30^\circ$ can be found in both small (e.g. CP.V 1450) and large specimens (e.g. CP.V 1001 and

CP.V 1449). Similarly, high values of $\sim 40^\circ$ can be found in the small specimen CP.V 1023 as well as the medium specimen CP.V 8175 and the large specimen CP.V 1448 (Table 2). In order to better explore whether this variation is correlated, or not, to body size, a bivariate correlation analysis has been performed here, using the specimens and values listed in Table 2 and employing the SMA approach, as explained above (see Materials and Methods – Quantitative analysis). The analysis provides a high p-value (0.58769), confirming there is no correlation between the two analysed variables (Figure 4). The lower and upper slope confidence intervals, being both very close to

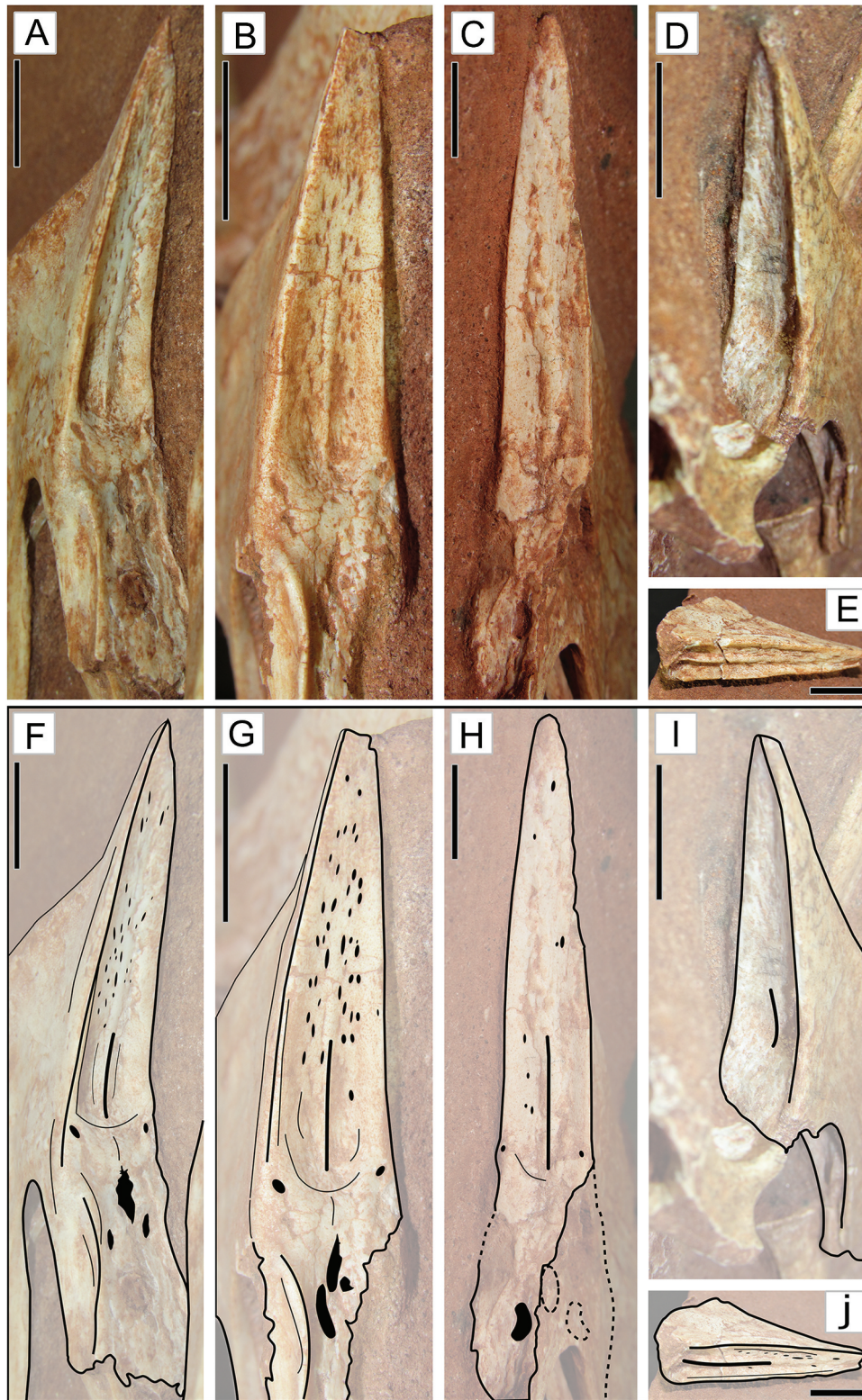


Figure 2. Palatal region of Pterosaur Graveyard tapejarid specimens showing palate morphotype II. Photos of specimens (a) CP.V 8175; (b) CP.V 2446; (c) CP.V 1448; (d) CP.V 1023; (e) CP.V 5703/II; and respective schematic drawings f – j. Scale bars = 10 mm.

zero, indicate that the analysed feature is nearly isometric (Figure 4). Accordingly, it is interpreted here that the great variation in rostrum deflection in PG tapejarids is not correlated to body size, and therefore likely not ontogenetic in nature.

Rostrum deflection steepness seems correlated to the palatal variations already explored above. The rostra that lack palatal

ridges and bear a single incisive foramen tend to exhibit smoother deflection angles, ranging from 29° to 33° , with an average value of 30.8° (Table 2). The rostra that bear palatal ridges and a triple incisive foramen tend to exhibit steeper deflection angles, ranging from 35° to 41° , with an average value of 39.6° (Table 2). While it is true that the two observed ranges are

Table 2. Anatomical variation in the prenarial palate of tapejarid specimens from the Pterosaur Graveyard site (Caiuá Group). Organised by morphotype assignment and prenarial length. The asterisk indicates damaged structure.

Specimen	Palatal ridge	Incisive foramen	Rostrum deflection	Prenarial length
(Morphotype I)				
CP.V 1450 (1050/1)	?	?	30°	~22 mm
CP.V 1450 (1050/2)	Absent	Single	33°	~23 mm
CP.V 1450 (n/n)	Absent	?	33°	~24 mm
CP.V 1450 (n/n)	Absent	?	30°	~27 mm
CP.V 1001	Absent	?	33°	~47 mm
CP.V 1447/I	Absent	Single	31°	50 mm
CP.V 5703/I	Absent	Single	29°	~50 mm
CP.V 1449	Absent	Single	29°	~59 mm
CP.V 1005	Absent	?	30°	~67 mm
(Morphotype II)				
CP.V 867	Present	?	40°	~19,5 mm
CP.V 8171	?	?	41°	25 mm
CP.V 1023	Present	?	41°	~33 mm
CP.V 1004	Present*	?	41°	41 mm
CP.V 2446	Present	Triple	35°	~45 mm
CP.V 8175	Present	Triple	39°	51 mm
CP.V 1448	Present	Triple	40°	~70 mm



Figure 3. Rostrum diversity in Pterosaur Graveyard tapejarid specimens. Specimens (a) CP.V 1005; (b) CP.V 1447/I; (c) CP.V 5703/I; (d) CP.V 1450 (mirrored); (e) CP.V 1449; (f) CP.V 1023 (mirrored); (g) CP.V 8175; (h) CP.V 8171; (i), CP.V 2246; (j) CP.V 1148 (mirrored). Scale bars = 10 mm.

quasi-overlapping (instead of distinctively bimodal), it is also true that these ranges are fairly distinct (with a large difference of $\sim 9^\circ$ between their average values, and of $\sim 12^\circ$ between their extremes), and that the observed quasi-overlap is due to a single outlier in morphotype II (specimen CP.V 2446, with a value of 35° ; see Table 2; Figure 4), as should be expected from individual variation.

Therefore, such variation seen in PG tapejarids, being substantially larger than is usual for tapejarid species (and therefore unlikely to represent individual variation), uncorrelated to body size (and therefore unlikely to represent ontogenetic variation), and consistently correlated to the palatal variations described above,

represents further indication that more than one species could be present in the PG tapejarid assemblage.

Occipital region

It is noted here that the PG tapejarid assemblage also exhibits some variation concerning the anatomy of the occipital region (Figure 5), most notably regarding the shape of the opisthotic, as already illustrated before though not discussed (Canejo et al. 2022). In the holotype of *Caiuajara dobruskii* (CP.V 1449), the opisthotic is a relatively slender bone, roughly as tall as wide in posterior view (Figure 5), differing from the wider condition seen in *Tapejara*

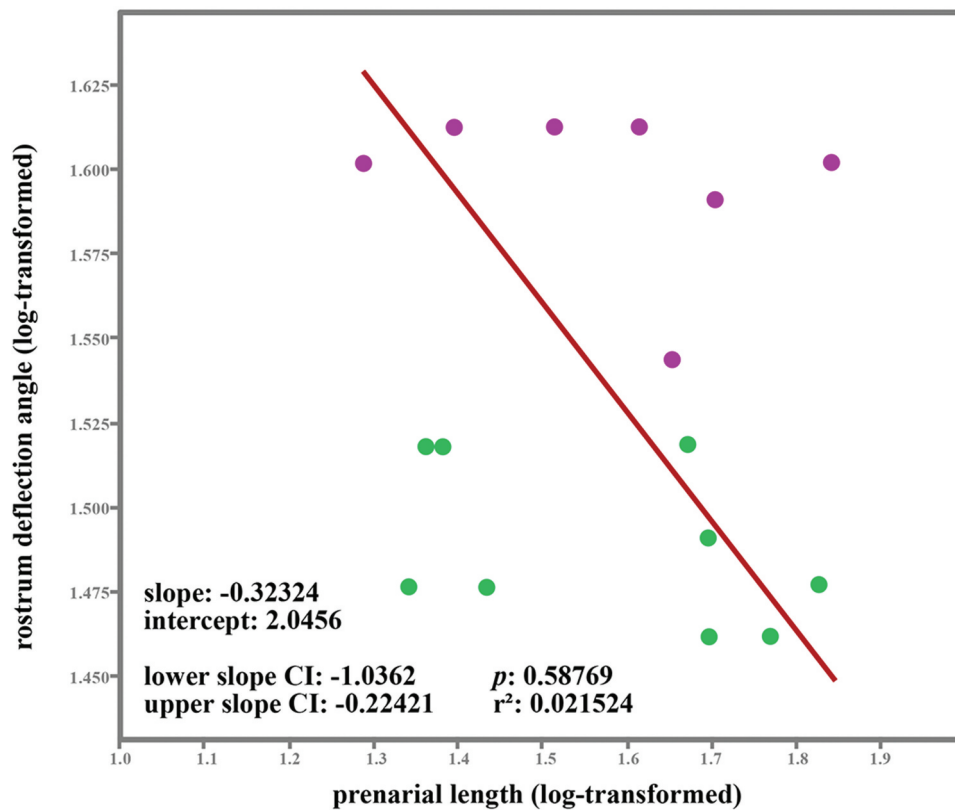


Figure 4. Results of the SMA analysis between rostrum deflection angle and prenarial length. CI: confidence interval. Green: morphotype I. Violet: morphotype II.

wellnhoferi (Kellner 1996). In contrast, specimen CP.V 8175 exhibits a broader opisthotic which is wider than tall (Figure 5), similar to the condition seen in *Tapejara wellnhoferi* (Kellner 1996). Furthermore, block CP.V 1447 (containing at least two individuals) exhibits a fragmentary occipital region that matches the morphology seen in CP.V 8175.

It is also noted here that CP.V 1449 exhibits a pair of occipital tuberosities, located between the occipital condyle and the opening for cranial nerves IX – XII (Figure 5). These paired occipital tuberosities represent a unique feature, distinguishing CP.V 1449 from CP.V 8175, as well as from *Tapejara wellnhoferi* (Wellnhofer and Kellner 1991; Kellner 1996), *Tupandactylus navigans* (Figure 5), and thalassodromids (Pégas et al. 2018).

Another variation concerns the shape of a tuberosity present on the basisphenoid, ventral to the occipital condyle (Figure 5). This basisphenoid tuberosity can be seen in CP.V 1449 and CP.V 8175, as well as in *Tapejara wellnhoferi* (Kellner 1996). It is however absent in *Tupandactylus navigans* (Figure 5) and in thalassodromids (Pégas et al. 2018). In CP.V 1449, this basisphenoid tuberosity is slender, much dorsoventrally taller than laterolaterally wide. This is similar to the condition seen in *Tapejara wellnhoferi* (Kellner 1996). In contrast, in CP.V 8175 this basisphenoid tuberosity is roughly globular in shape.

In summary, two types of occipital region can be seen in the PG tapejarid assemblage: type I, with a narrow opisthotic, presence of a pair of occipital tuberosities, and a slender basisphenoid tuberosity; and type II, with a broad opisthotic, paired occipital tuberosities absent, and a globular basisphenoid tuberosity. Specimen CP.V 1449 combines type I rostrum and palate with a type I occipital region, while specimen CP.V 8175 combines type II rostrum and palate with a type II occipital region.

Cervical III

Variation concerning three aspects of cervical III morphology was observed within the PG tapejarid assemblage (Figure 6). At present, cervical III can be found in three specimens: in the holotype of *Caiuajara dobruskii* (CP.V 1449), and in blocks CP.V 1001 and CP.V 1447, both of which are multi-individual blocks. Both third cervicals found in these two blocks are superficially identical to the third cervical found in CP.V 1449, sharing the same general outline and proportions, differing only in three aspects: presence/absence of the accessory foramen, shape of the prezygapophyseal facet, and presence/absence of a pit-like foramen in the postzygapophyseal pedicle (Figure 6).

The accessory foramen is a pneumatic opening lying dorsal to the neural canal (see Hone et al. 2019). In the holotype of *Caiuajara dobruskii* (CP.V 1449), this accessory foramen is absent (Figure 6), despite being typically present in mid-cervicals of azhdarchoids overall, as seen in *Tapejara wellnhoferi* (Vila Nova et al. 2014), thalassodromids (Cerqueira et al. 2021), *Keresdrakon vilsoni* (Kellner et al. 2019), and most azhdarchids except for some quetzalcoatlins (see Hone et al. 2019; Pégas et al. 2021). In contrast to CP.V 1449, this foramen is present, and well-developed, on the anterior face of the third cervicals found in blocks CP.V 1001 and CP.V 1447 (Figure 6).

Another variation in cervical III concerns the shape of the prezygapophyseal facet. This facet is ovoid in shape in the holotype of *Caiuajara dobruskii* (CP.V 1449), while it is slender and elongate in the specimens from blocks CP.V 1001 and CP.V 1447 (Figure 6).

Finally, the third cervicals present in blocks CP.V 1001 and CP.V 1447 exhibit a pit-like foramen on the posterior face of

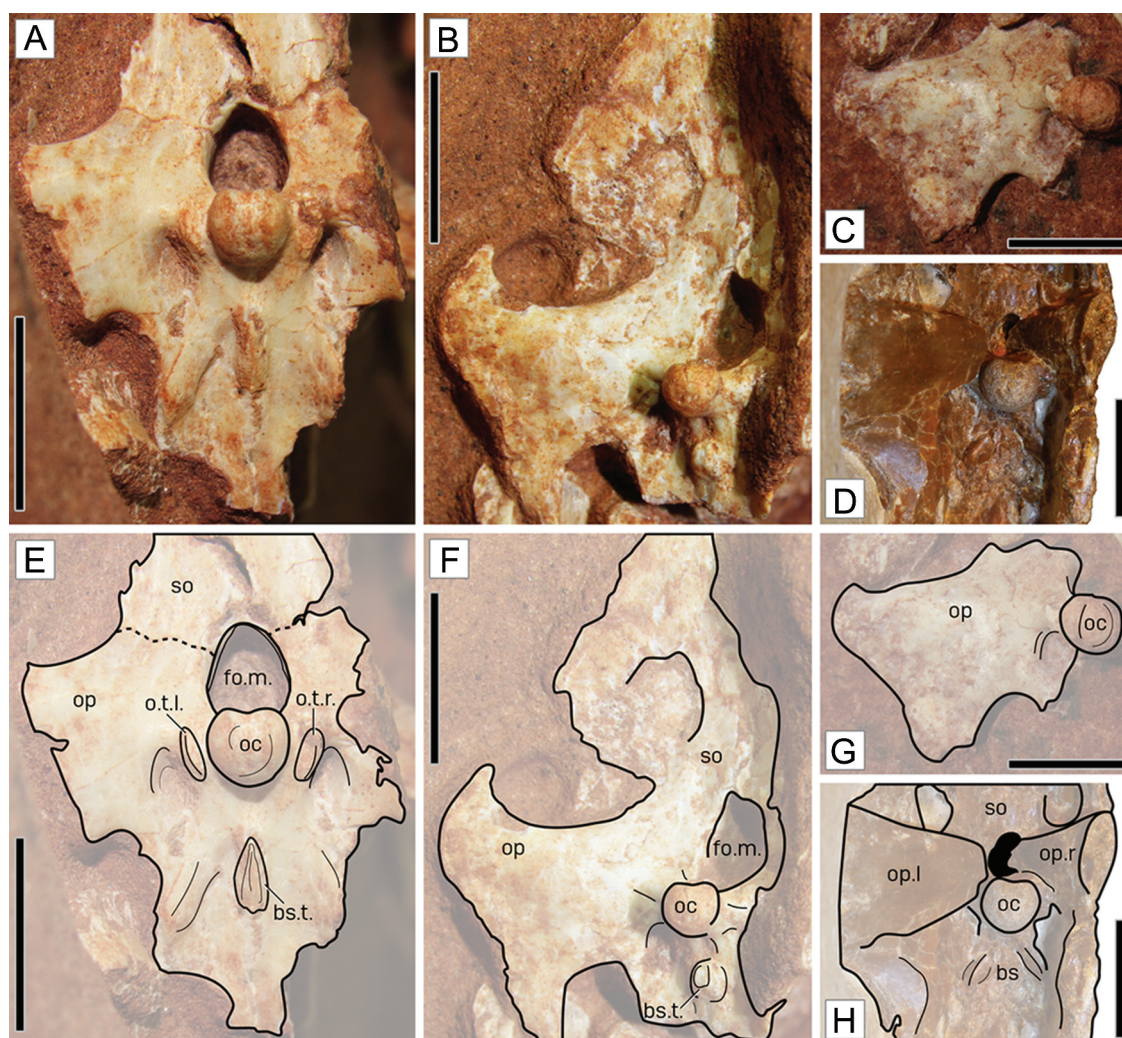


Figure 5. Occipital region of tapejarid specimens. Pterosaur Graveyard specimens (a) CP.V 1449 (holotype of *Caiuajara dobruskii*); (b) CP.V 8175; (c) CP.V 1447/II; and (d) *Tupandactylus navigans* specimen SMNK PAL 2344 (holotype). Abbreviations: bs, basisphenoid; bst, basisphenoid tuberosity; fo.m., foramen magnum; l, left; oc, occipital condyle; op, opisthotic; o.t., occipital tuberosity; r, right; so, supraoccipital. Scale bars = 10 mm.

each postzygapophyseal peduncle (Figure 6). This interesting feature is so far unknown for any other pterosaur, including the holotype of *Caiuajara dobruskii* (CP.V 1449) as well as *Tapejara wellnhoferi* (Wellnhofer and Kellner 1991).

In summary, the third cervical of the holotype of *Caiuajara dobruskii* (CP.V 1449) exhibits the following combination of features: accessory foramen absent, prezygapophyseal facets ovoid in shape, and postzygapophyseal pedicle pit-like foramen absent (type I). In contrast, the third cervicals of blocks CP.V 1001 and CP.V 1447 exhibit the following combination of features: accessory foramen present, prezygapophyseal facets elongate in shape, and postzygapophyseal pedicle pit-like foramen present (type II). It is noteworthy that the type II third cervical of block CP.V 1447 is closely associated to the fragmentary type II occipital region mentioned above. In contrast, the holotype of *Caiuajara dobruskii* (CP.V 1449) combines type I rostrum, palate and occipital region with a type I third cervical.

It is important to note that both of these morphotypes of cervical III differ from *Keresdrakon vilsoni*, as follows. The known mid-cervicals of *Keresdrakon vilsoni* are characterised by a very large neural spine (twice as high as the centrum), as

well as a single and large pneumatic foramen on the lateral surface (Kellner et al., 2019). In contrast, PG tapejarid specimens (both morphotypes) exhibit lower neural spines and 2–3 lateral pneumatic foramina, similar to *Tapejara wellnhoferi* (Wellnhofer and Kellner 1991; Eck et al. 2011; Vila Nova et al. 2014).

Discussion

Evidence for interspecific variation within Pterosaur Graveyard tapejarids

The present survey reveals a considerable amount of morphological variation within the Pterosaur Graveyard tapejarid assemblage. Before discussing the biological significance of such variation (as either intra, or interspecific, in nature), it is important to exclude the effect of taphonomy. It is worth highlighting here the exceptional three-dimensional preservation of Caiuá fossils, which typically show negligible signs of distortion and/or compression (e.g. Langer et al. 2019; Kellner et al. 2019), as is indeed common in aeolian sandstone deposits (e.g. Britt et al., 2018). In the Caiuá tapejarid assemblage, bone surface is usually well-preserved, despite

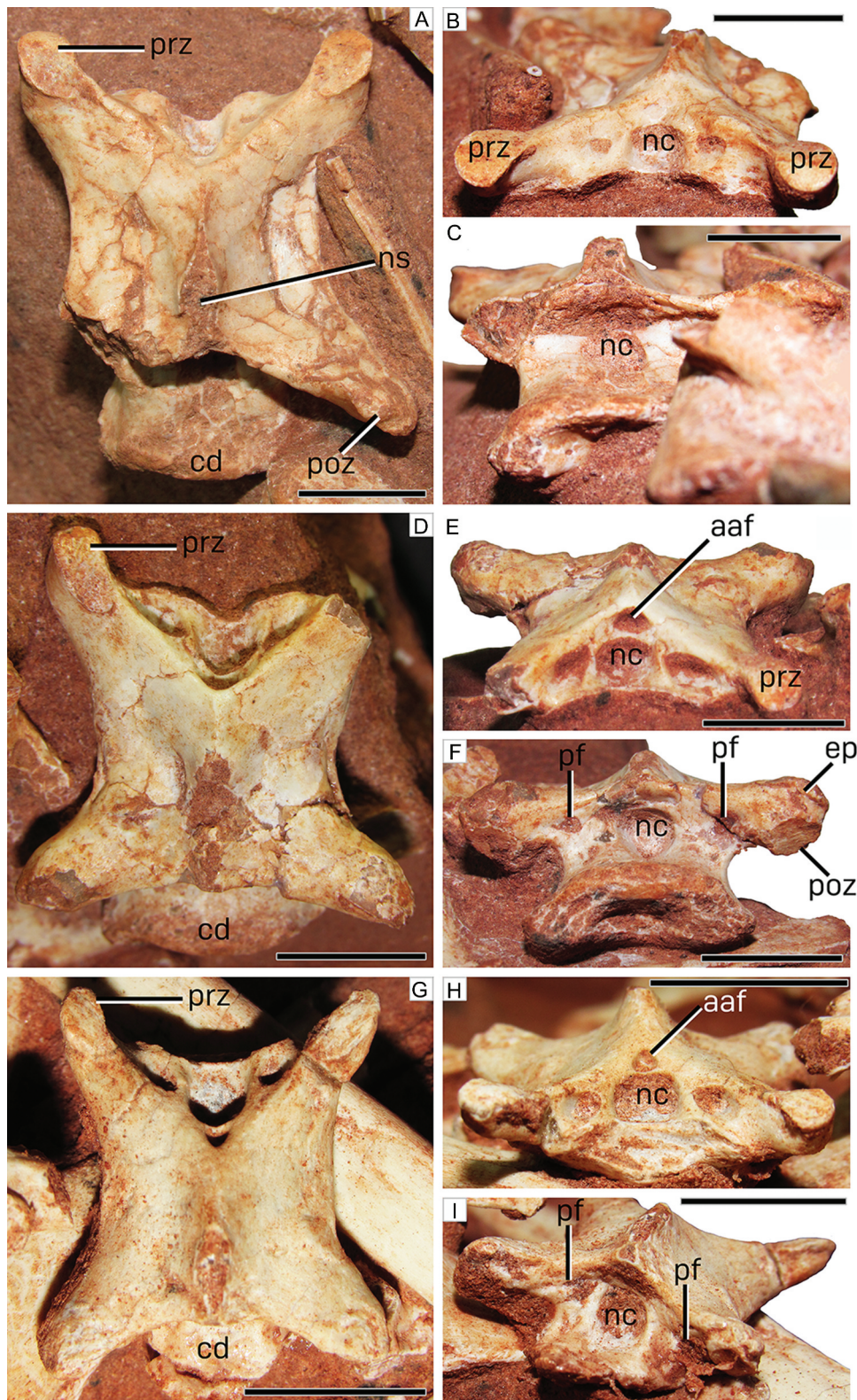


Figure 6. Cervical III diversity in Pterosaur Graveyard tapejarid specimens. Specimens a – c, CP.V 1449 (holotype of *Caiuajara dobruskii*); d – f, CP.V 1447/II; g – i, CP.V 1001; and j – r, respective schematic drawings. Abbreviations: aaf, anterior accessory foramen; cd, condyle; ep, epiphysis; nc, neural canal; ns, neural spine; pf, pneumatic foramen; poz, postzygapophysis; prz, prezygapophysis. Scale bars = 10 mm.

the fragmentary nature of the elements. Bone three-dimensionality is mostly undeformed, with rare instances of taphonomically distorted elements (e.g. the slight lateral curving of the rostral tip in a single specimen, CP.V 1447/I; whilst all other specimens show

undistorted rostra; [Figure 1](#)). With this in mind, it is clear that the anatomical structures herein observed (e.g. palatal ridge, palatal foramination, occipital tuberosities, vertebral foramination) are biologically real, and that morphometric features (e.g. rostrum

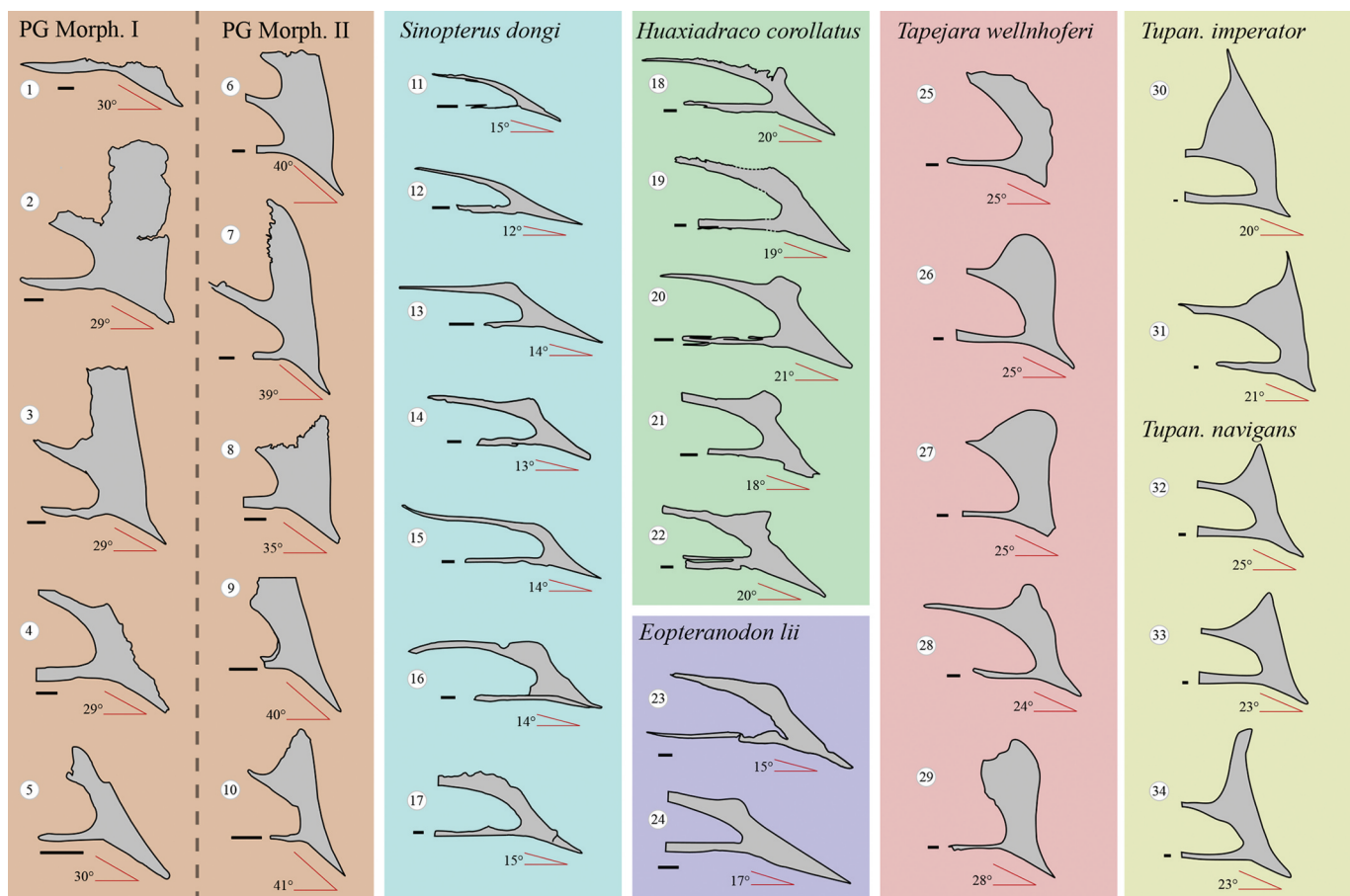


Figure 7. Comparative, schematic drawings of tapejarid rostra in right lateral view, showing variation in rostrum deflection angle. Pterosaur Graveyard (PG) tapejarids, morphotype I: 1, CP.V 1005; 2, CP.V 1449 (holotype of *Caiuajara dobruskii*); 3, CP.V 1447 (mirrored); 4, CP.V 5073/I (mirrored); 5, CP.V 1450 (mirrored). PG morphotype II: 6, CP.V 1448 (mirrored); 7, CP.V 8175; 8, CP.V 2446; 9, CP.V 1023 (mirrored); 10, CP.V 8171 (mirrored). *Sinopterus dongi*: 11, BPV-077 (holotype of '*S. gui*'); 12, JPM-2014-005 (holotype of '*S. lingyuanensis*'); 13, XHPM 1009 (holotype of '*S. atavismus*'); 14, D4019; 15, IVPP V 13363 (holotype of *S. dongi*); 16, GMN-03-11-001 (holotype of '*Huaxiapterus jii*'); 17, BPMC 107. *Huaxiadraco corollatus*: 18, BPMC 103; 19, BPMC 104; 20, ZMNH M813 (holotype of *Huaxiadraco corollatus*); 21, BPMC 105; 22, BXGM V0011 (holotype of '*Huaxiapterus benxiensis*'). *Eopteranodon*: 23, BPC 078 (holotype of *Eopteranodon lii*); 24, IVPP V 14190. *Tapejara wellnhoferi*: 25, AMNH 24440; 26, IMNH 1053; 27, MN 6595-V (holotype); 28, SMNK PAL 1137; 29, SAO 12891. *Tupandactylus imperator*: 30, MCT 1622-R (holotype); 31, CPCA 3590. *Tupandactylus navigans*: 32, SMNK PAL 2344 (holotype); 33, SMNK PAL 2343; 34, GP/ZE 9266. Schematic drawings of *Sinopterus dongi* specimens, *Huaxiadraco corollatus* specimens, and *Eopteranodon lii* holotype: modified from Pégas et al. (2023). IVPP V 14190: modified from Zhang et al. (2023). Schematic drawings of *Tapejara wellnhoferi*: modified from Elgin and Campos (2012). Schematic drawings of *Tupandactylus*: modified from Beccari et al. (2021). Scale bars = 10 mm.

deflection, rostrum length) must be only marginally affected by taphonomy. Furthermore, regarding the anatomical variations found in the rostrum (deflection angle, palatal ridge presence/absence, and foramination configuration), the consistent, non-random association between the variable features also precludes taphonomical explanations, or else a more random or fluid pattern would be expected.

The variable presence/absence of a palatal ridge in the PG tapejarid assemblage had already been noted by Manzig et al. (2014) as well as Canejo et al. (2022). These works consistently regarded the PG tapejarid assemblage as monospecific, with this variation interpreted as intraspecific in nature. However, it is noted here that the variable presence of a palatal ridge is not consistent with intraspecific variation in pterosaurs, as can be concluded from several species known from multiple specimens, as follows. The tapejarid *Tapejara wellnhoferi*, from the Romualdo Formation, is known from five well-preserved skulls, all of which lack any palatal ridge (Kellner 1989; Wellnhofer and Kellner 1991; Eck et al. 2011; Witton 2013). The azhdarchid *Quetzalcoatlus lawsoni*, known from seven skulls coming from a single bone bed, also does not show any

variation regarding this feature, with all known skulls lacking any palatal ridge (Kellner 1996; Andres and Langston 2021).

The anhanguerian *Hamipterus tianshanensis*, known from tens of skulls coming from a multi-aged bone bed, is reported to be diagnosed on the basis of palatal ridge extension (among other features), without any variation regarding the presence/absence of this diagnostic structure (Wang et al. 2014). Similarly, the *Anhanguera* complex is known from about 11 well-preserved rostra, all of which exhibit palatal ridges (see Pinheiro and Rodrigues 2017; Duque et al., 2022).

It has been proposed that variation regarding palatal ridge presence/absence could occur in *Azhdarcho lancicollis* (Martill and Naish 2006), although this has been later questioned (Kellner and Campos 2007). While it is true that some jaw fragments from the Bissekty Fm. exhibit palatal ridges and others do not (Averianov 2010), these isolated fragments cannot be collectively referred to a single species (see Vremir et al. 2015).

Besides the importance of variation regarding palatal ridge presence/absence, it is also worth pointing out that variation in palatal

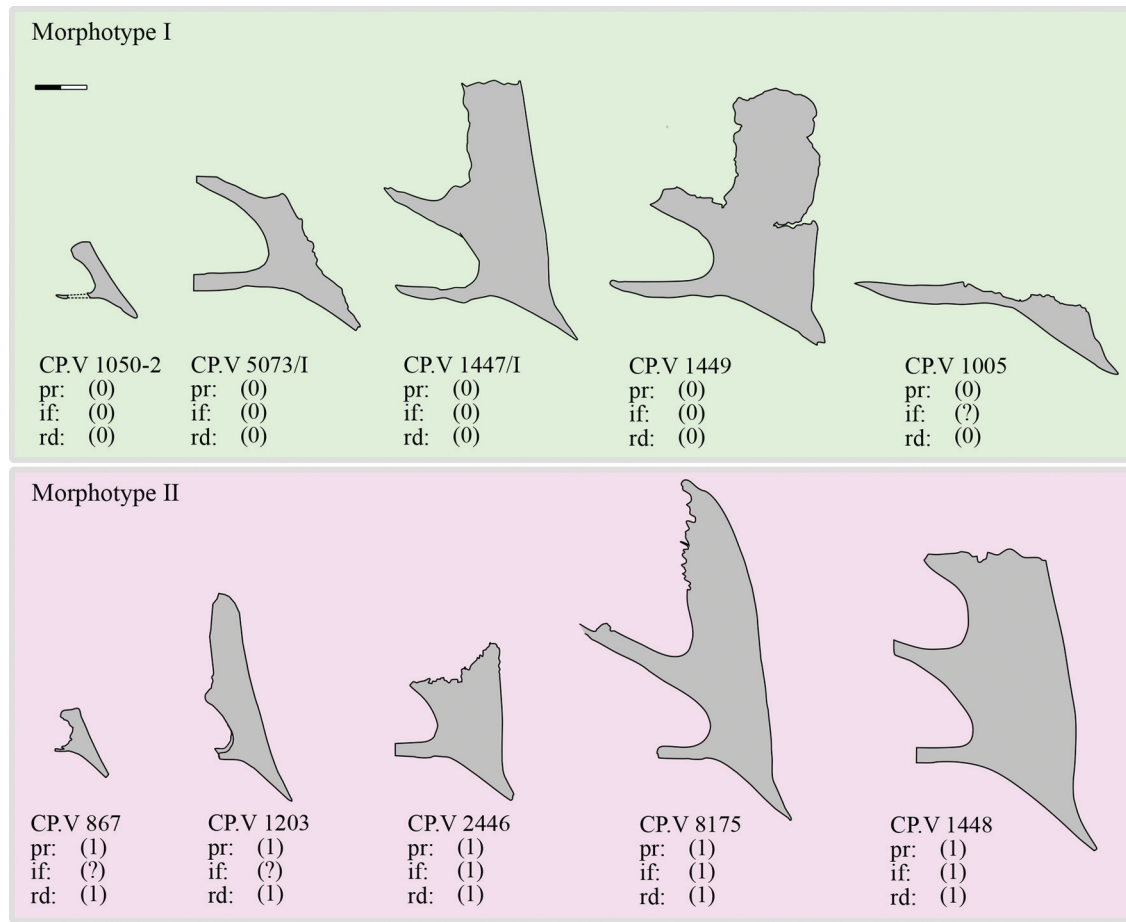


Figure 8. Comparative, schematic drawings of the Caiuá tapejarid morphotypes, summarising variation in body size and character coding. Abbreviations: if: (0), incisive foramen: single; if: (1), incisive foramen: triple; pr: (0), palatal ridge: absent; pr: (1), palatal ridge: present; rd: (0), rostrum deflection: $\sim 30^\circ$; rd: (1), rostrum deflection: $\sim 40^\circ$. All specimens are to scale. Scale bar = 20 mm.

ridge expression (in shape and size) also seems to carry taxonomic signals, as demonstrated by thalassodromids (Kellner and Campos 2007; Pêgas et al. 2018) and alanqids (Smith et al. 2023). Therefore, it is concluded here that such morphological disparity (regarding the presence/absence of a palatal ridge) is more consistent with interspecific, rather than intraspecific, variation in pterosaurs, providing evidence for the potential presence of two tapejarid species in the Pterosaur Graveyard assemblage.

The occurrence of accessory incisive foramina in some specimens is also intriguing, given that it represents a unique feature that cannot be found in any other pterosaur. The fact that this highly distinguished feature co-occurs exclusively with ridged palates, and not with ridge-less palates, further suggests that the palatal-ridged and ridge-less specimens represent two distinct species, with the accessory incisive foramina representing a further autapomorphy of the palatal-ridged species.

In addition, the fact that the two palatal morphotypes are further correlated to distinct ranges of rostrum deflection is further suggestive of taxonomic distinction, with a range of 29° – 33° (mean: $\sim 31^\circ$) for the ridge-less palates and a range of 35° – 41° (mean: $\sim 40^\circ$) for the ridged ones. Importantly, this large range of variation (of 12° in total; and of $\sim 9^\circ$ between mean values) in deflection angle in the total assemblage is far superior to what is known for tapejarid intraspecific variation (Figure 7), as discussed above (see also Pêgas et al. 2023). In summary, two rostrum morphotypes can be clearly observed within the PG tapejarid assemblage: morphotype I, with a gentler rostrum deflection of $\sim 31^\circ$ (29° – 33°), a ridge-less

palate, and a single incisive foramen; and morphotype II, with a steeper rostrum deflection of $\sim 40^\circ$ (35° – 41°), a ridged palate, and a triple incisive foramen (Figure 8). As explored above, these features are consistently associated to each other within each morphotype, irrespective of body size. This pattern suggests that these variations are not due to either taphonomy or individual variation, or else more variable combinations would be expected.

These rostrum morphotypes are also correlated to variations in the occipital region, even though only two PG tapejarid specimens comprise both rostral and occipital regions preserved: the holotype of *Caiuajara dobruskii* (CP.V 1449) and CP.V 8175. The holotype of *Caiuajara dobruskii*, which presents a morphotype I rostrum, exhibits an occipital region with a slender opisthotic (about as wide as tall), a pair of tuberosities lateral to the occipital condyle, and an elongate basisphenoid tuberosity. In contrast, specimen CP.V 8175, which presents a morphotype II rostrum, exhibits an occipital region with a broad opisthotic (wider than tall), lacking a pair of tuberosities lateral to the occipital condyle, and with a roughly rounded basisphenoid tuberosity.

In addition to occipital region variation, rostrum morphology also seems correlated to some cervical variations as well. As discussed above, two cervical III morphotypes can be found in the PG tapejarid assemblage. Morphotype I is characterised by the following combination of features: accessory foramen absent, prezygapophyseal facets ovoid in shape, and postzygapophyseal pedicle pit-like foramen absent. In contrast, cervical III morphotype II exhibits the following combination of

features: anterior accessory foramen present, prezygapophyseal facets elongate in shape, and postzygapophyseal pedicle pit-like foramen present. The anatomical discrepancy between these two cervical morphotypes is further suggestive of the presence of two tapejarid species in the PG assemblage. Cervical III morphotype I is unambiguously correlated to the skull morphotype I, as indicated by the holotype of *Caiuajara dobruskii*, specimen CP.V 1449. This specimen includes a morphotype I skull along with a closely associated morphotype I cervical III. Cervical III morphotype II can be tentatively associated to skull morphotype II, due to a close association between a cervical III and a type II opisthotic in block CP.V 1447.

Considering all of the variations discussed above, it seems that these features effectively separate the PG tapejarid assemblage into two consistent morphotypes, each with their own combination of variations; thus, indicating the occurrence of heterobaty. Morphotype I, which includes the holotype of *Caiuajara dobruskii*, can be characterised by: a rostrum deflection angle of $\sim 31^\circ$ (29° – 33°); palatal ridge absent; a single incisive foramen; opisthotic relatively slender (about as tall as wide in posterior view); paired occipital tuberosities present; basisphenoid median tuberosity elongate in shape; cervical III prezygapophyseal facets ovoid in shape; cervical III accessory foramen absent; and cervical III postzygapophyseal pedicles lacking a small, pit-like foramen. In turn, morphotype II can be characterised by the following combination of features: a high rostrum deflection angle of $\sim 40^\circ$ (35° – 41°); palatal ridge present; paired accessory foramina posterolateral to the incisive foramen; opisthotic wider than tall in posterior view; paired occipital tuberosities absent; basisphenoid median tuberosity globular in shape; cervical III prezygapophyseal facets slender and elongate in shape; cervical III accessory foramen present; and cervical III postzygapophyseal pedicles bearing a small, pit-like foramen.

It is worth pointing out that these anatomical variations do not conform to what would be expected from sexual dimorphism in ornithodirans (e.g. Bennett 1992; Chapman et al. 1997; Wang et al. 2014; Angst et al. 2020; Tereshchenko 2020), suggesting these two morphotypes do not represent two sexes of a single species. As demonstrated by previous works, ornithodiran sexual dimorphism is usually expressed in terms of body size, bone robustness, abdominal and pelvic dimensions, and presence/expression of ornaments/armaments (Bennett 1992; Chapman et al. 1997; Wang et al. 2014; Angst et al. 2020; Tereshchenko 2020); and difficult to be statistically detected with confidence (see Mallon 2017; Hone et al. 2017; Saitta et al. 2020). In addition, considering what is presently known concerning individual variation in pterosaurs as discussed above (see also Wang et al. 2014; Andres and Langston 2021; Pêgas et al. 2023), along with the lack of correlation between the observed variations and body size, the herein observed variations seem to be incompatible with either sexual, individual, or ontogenetic variations. Further considering the consistent distinction between the two morphotypes (with a consistent association between the variable features) and the occurrence of heterobaty between them, it is considered here that the best explanation for this pattern is the existence of two distinct tapejarid species in the Pterosaur Graveyard assemblage. While the first morphotype corresponds to *Caiuajara dobruskii*, the second morphotype represents a newly recognised species (Figure 9), for which the name *Torukjara bandeirae* gen. et sp. nov. is proposed (see further below – Systematic Paleontology).

Comments on the co-occurrence of closely-related pterosaur species

Some Pterosaur Graveyard blocks exhibit close associations between different species, such as tapejarids and *Keresdrakon*; tapejarids and noasaurids; and even tapejarids, *Keresdrakon*, and noasaurids (see Kellner et al. 2019). Therefore, given the recognition of two tapejarid species in the Pterosaur Graveyard assemblage, it should be no surprise to find blocks showing a close association between multiple individuals of these two species. At least two such cases are identified here, exemplified by blocks CP.V 1447 and CP.V 5703 (Figure 10). These findings suggest that *Caiuajara dobruskii* and *Torukjara bandeirae* coexisted, along with the azhdarcho-morph pterosaur *Keresdrakon wilsoni* as well (see Kellner et al. 2019).

Taking into consideration recent developments in pterosaur research (e.g. Vremir et al. 2015; Longrich et al. 2018; Pêgas et al. 2023), the coexistence of multiple, closely related pterosaur species seems to have been more common than usually thought (e.g. Averianov 2010, 2014; Bennett 2017). Multiple tapejarid species had already been reported for the Jiufotang Formation, represented by the *Sinopterus* complex – previously thought to comprise up to seven species (Lü et al. 2016; Zhang et al. 2019), but now restricted to two, *Sinopterus dongi* and *Huaxiadraco corollatus* (Pêgas et al. 2023). The coexistence between these two species can be inferred from the identification of a few specimens that come from the same localities and horizons (Pêgas et al. 2023).

Coexistence of the Crato Fm. tapejariforms (*Tupandactylus imperator*, *Tupandactylus navigans*, and *Aymberedactylus cearensis*), as well as between the Romualdo Fm. tapejariforms (*Tapejara wellnhoferi* and *Caupedactylus ybaka*), is hard to confirm due to the lack of stratigraphic control concerning Santana Group fossils (Pinheiro and Rodrigues 2017). The same is true for the multiple species of: Cambridge Greensand anhanguerids (Holgado and Pêgas 2020); Kem Kem Group alanquids (Smith et al. 2023); Jiufotang Fm. chaoyangopterids (Ji et al. 2023); Romualdo Fm. anhanguerids (Pinheiro and Rodrigues 2017); and Romualdo Fm. thalassodromids (Pêgas et al. 2018; Cerqueira et al. 2021).

The occurrence of more than one tapejarid species has also been recently suggested for the Yixian Fm., after the proposal of the nominal species *Eopteranodon yixianensis* (Zhang et al. 2023). This potential new species has been tentatively set apart from *Eopteranodon lii* on the basis of rostrum deflection angle; proportions of the rostrum and cranial crests; and proportions between the humerus and fourth wing phalanx (Zhang et al. 2023). However, there is no significant difference between the rostrum deflection angle between these species (15° in *E. lii*; see Pêgas et al. 2023; and 17° in '*E. yixianensis*'; see Zhang et al. 2023). Furthermore, differences in proportions of the rostrum and cranial crests should be seen as ontogenetic in nature (Pinheiro and Rodrigues 2017; Zhang et al. 2019; Pêgas et al. 2023); and the purportedly shorter fourth wing phalanx of '*E. yixianensis*' apparently cannot be measured with confidence due to breakage on the slab (see Zhang et al. 2023). Therefore, it is considered here that, at present, there is no sufficient evidence for the distinction between *Eopteranodon lii* and '*Eopteranodon yixianensis*', which may represent synonyms – even though future discoveries may still uncover further Yixian tapejarid species.

Further notable cases of diverse assemblages of closely related pterosaurs can be found within azhdarchoids, with three species in the latest Maastrichtian of the Transylvanian Basin (Buffetaut et al. 2002; Vremir et al. 2015; Solomon et al., 2019); three

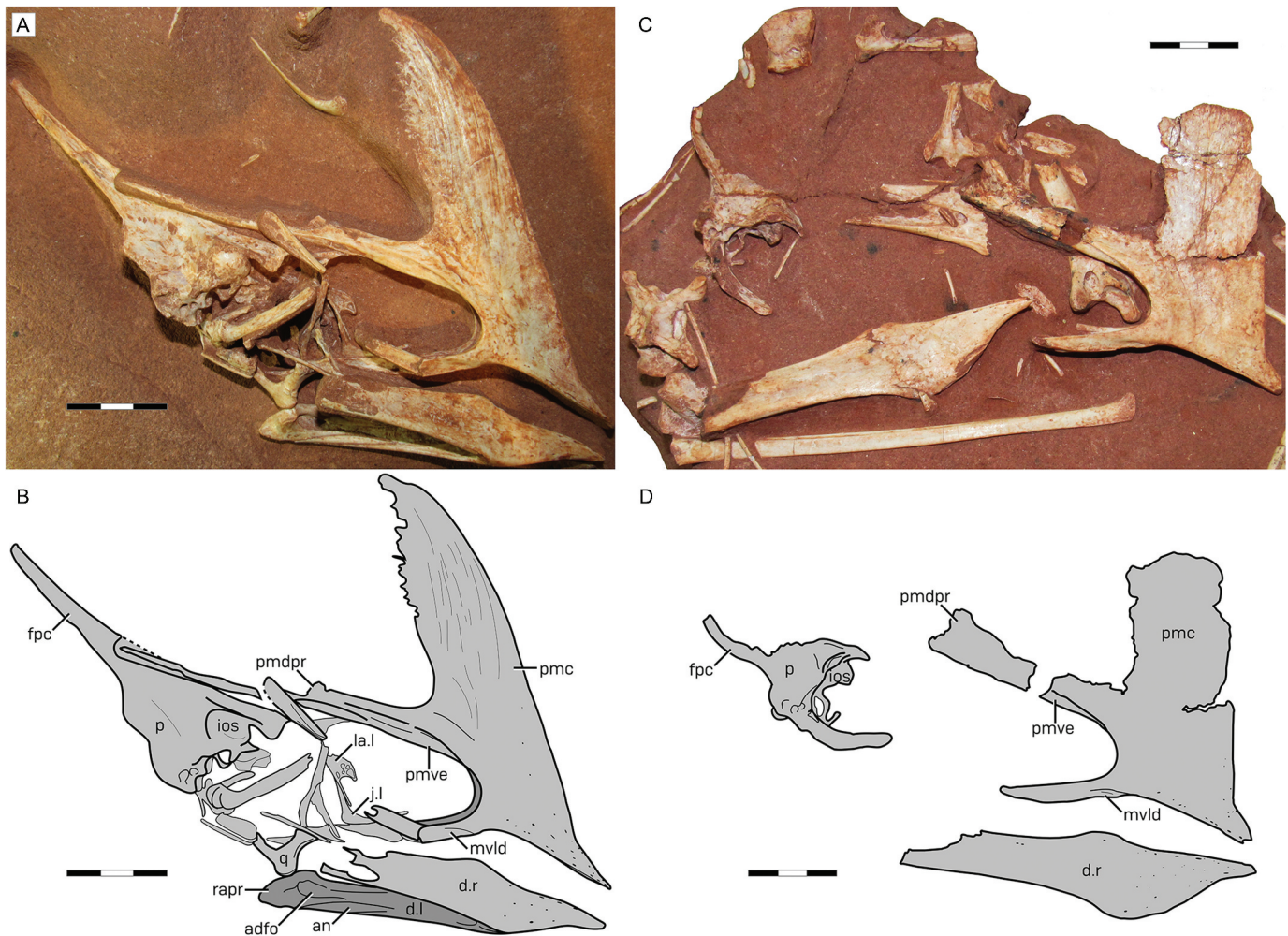


Figure 9. The Pterosaur Graveyard tapejarids: (a) *Torukjara bandeirae* gen. et sp. nov. CP.V 8175 (holotype); and (b) *Caiuajara dobruskii* CP.V 1449 (holotype). Abbreviations: adfo, adductor fossa; an, angular; (d) dentary; ios, interorbital septum; j, jugal; l, left; la, lacrimal; mvlid, maxillary lateroventral depression; p, parietal; pmc, premaxillary crest; pmdpr, premaxillary dorsal process; pmve, premaxillary ventral expansion; q, quadrate; rapr, retroarticular process. Scale bars = 30 mm.

species in the Javelina Fm. (Andres and Langston 2021); and three species in the Ouled Abdoun Basin (Longrich et al. 2018). The same is true for the Ouled Abdoun Basin nyctosaurids, with three or four species occurring at the same levels (Longrich et al. 2018); and the Linglongta beds wukongopterids, with at least four species coming from the same strata (Wang et al. 2010; Cheng et al. 2017; Zhou et al. 2021). Even though pterosaur diversity in past ecosystems does not seem to have reached high ‘passerine-like’ levels, the idea that it was restricted to low ‘crocodilian-like’ levels (Bennett 2017) may be slightly exaggerated, and it may as well have been intermediate between these two extremes.

The largest specimens of *Caiuajara dobruskii* and *Torukjara bandeirae* are of similar size, with prenarial rostrum lengths of ~70 mm (Table 2). This value equals ~74% of the prenarial length in the *Tupandactylus navigans* specimen GP/2E 9266, which exhibits a wingspan of 2.7 m (see Beccari et al. 2021), indicating a wingspan of ~2 m for the Caiuá tapejarids. This is close to the estimate of 2.35 m provided by Manzig et al. (2014) for *Caiuajara dobruskii*, which was based on the largest appendicular elements available in the PG tapejarid assemblage. It seems likely that both species were of roughly similar sizes, despite their coexistence – as with the similar-sized Jiufotang tapejarids *Sinopterus dongi* and *Huaxiadraco corollatus* (Pêgas et al. 2023).

Considerations regarding premaxillary crest morphology

The role of cranial crest morphology in pterosaur species identification has been the subject of great debate, especially due to the great plasticity of this structure and uncertainties over the influence of ontogenetic and sexual variations (e.g. Bennett 1992, 1993; Martill and Naish 2006; Kellner and Campos 2007; Hone et al. 2012; Knell et al. 2013; Wang et al. 2014; Pinheiro and Rodrigues 2017; Cheng et al. 2017; Pêgas et al. 2023). At present, it seems clear that pterosaur cranial crest shape can be greatly influenced by ontogeny and sexual dimorphism, mainly in terms of development and size (Bennett 1992, 1993; Wang et al. 2014; Pinheiro and Rodrigues 2017; Pêgas et al. 2023). The influence of ontogeny and sexual dimorphism may thus confound the use of cranial crest variation in pterosaur taxonomy (e.g. Pinheiro and Rodrigues 2017).

On the other hand, at times, closely-related pterosaur species may exhibit distinct cranial crest expressions (mainly in terms of shape), which may then carry taxonomic signals (Cheng et al. 2017). This seems to be the case for *Pteranodon longiceps* and *Pteranodon sternbergi* (Bennett 1994), the Tiaojishan Fm. wukongopterids (Cheng et al. 2017), the Crato Fm. tapejarids *Tupandactylus imperator* and *Tupandactylus navigans* (Pinheiro et al. 2011; Beccari et al. 2021), and the Jiufotang Fm. tapejarids *Sinopterus dongi* and *Huaxiadraco corollatus* (Pêgas et al. 2023). However, in other

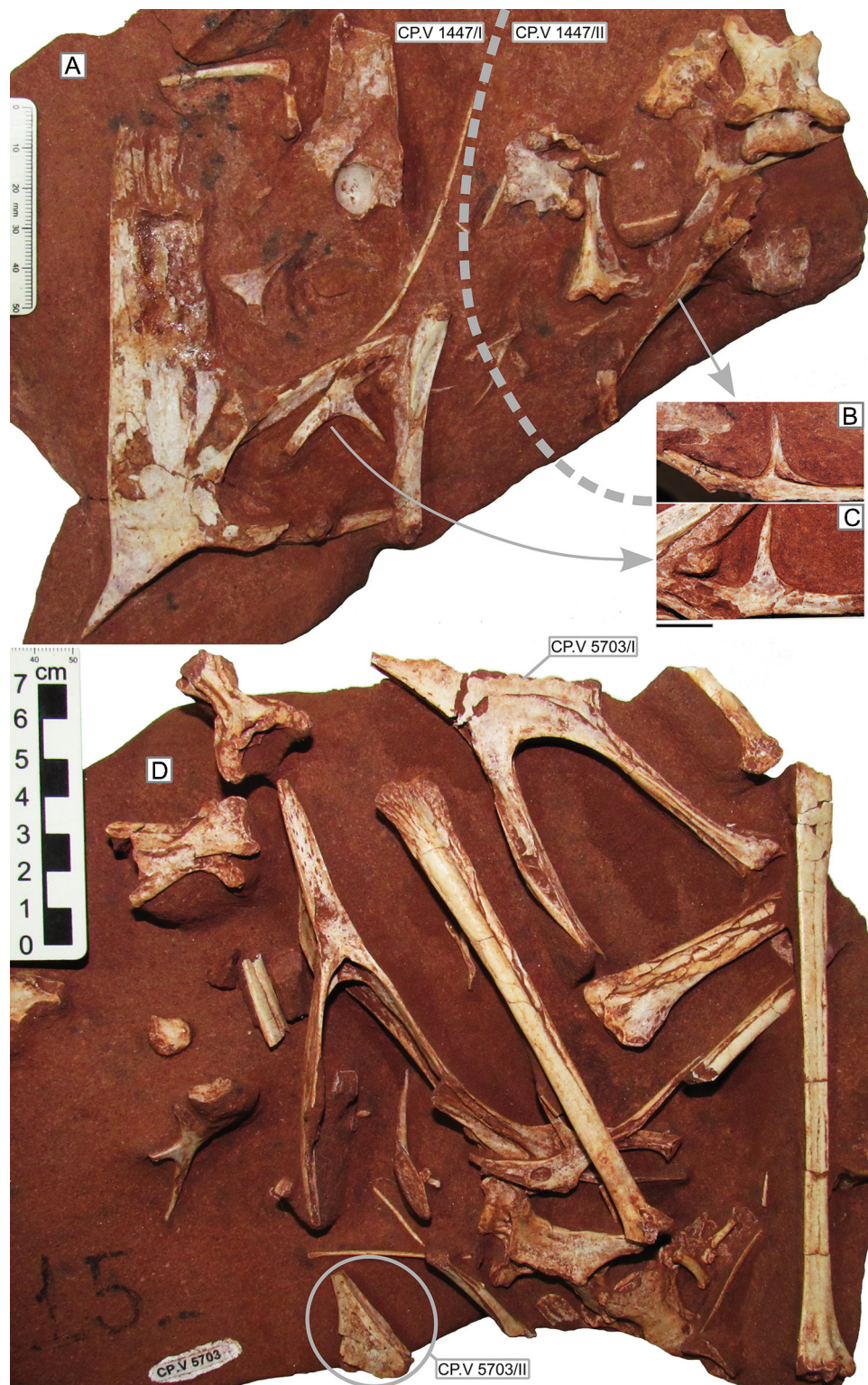


Figure 10. Multi-individual blocks showing association between specimens attributed to *Caiuajara dobruskii* and *Torukjara bandeirae*: a, block CP.V 1447; b, the smaller, slender jugal of CP.V 1447/II; c, the larger, more robust jugal of CP.V 1447/I; and d, block CP.V 5703. Note CP.V 1447/I and CP.V 5703/I (herein referred to *C. dobruskii*), and CP.V 1447/II and CP.V 5703/II (herein referred to *T. bandeirae*). Scale bar for c, d = 10 mm.

cases, closely related species may be indistinguishable in terms of cranial crest morphology alone, exhibiting substantial overlaps and similarities in their ranges of crest shape variation. This seems to be the case between *Anhanguera* species (Pinheiro and Rodrigues

2017), as well as between *Sinopteris* and *Eopteranonodon* (Pêgas et al. 2023).

It is unclear at this point if *Caiuajara dobruskii* and *Torukjara bandeirae* differed, or not, relative to premaxillary crest

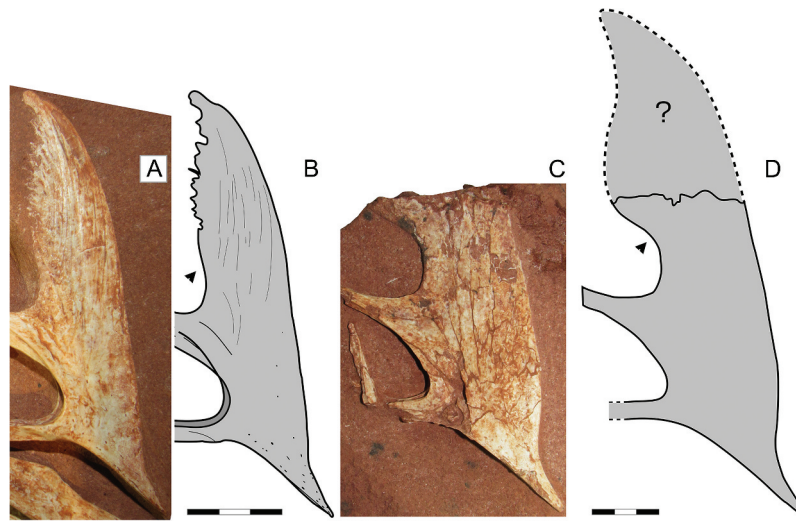


Figure 11. Crest variation in Pterosaur Graveyard tapejarids: a and b, *Torukjara bandeirae* gen. et sp. nov. CP.V 8175 (holotype); c and d, *Torukjara bandeirae* specimen CP.V 1148 (mirrored). Scale bars = 30 mm.

morphology. It is interesting to note that non-juvenile specimens herein attributed to *Torukjara bandeirae* seem to exhibit a notched or ‘flipper-shaped’ premaxillary crest, as seen in CP.V 8175. This ‘flipper-shape’ exhibits a notched base, whose posterior limit is roughly level with the anterior margin of the nasoantorbital fenestra (as seen in CP.V 8175, CP.V 1023, and CP.V 1448). This base is marked by a slight notch (a ‘neck-like’ constriction), followed dorsally by an expansion of the posterior margin (Figure 11). This shape is clearly seen in the completely preserved premaxillary crest of CP.V 8175, and a similar configuration is suggested by the incompletely preserved crest of CP.V 1448. The posterior expansion in CP.V 1448 is much more exacerbated than in CP.V 8175, but, at present, there seems to be no reason to conclusively infer the presence of a *Nyctosaurus*-like bifurcation as previously hypothesised (Canejo et al. 2022). This unique morphology is so far restricted to *Torukjara bandeirae*, being absent in other tapejarids such as *Tapejara wellnhoferi* (Kellner 1989; Wellnhofer and Kellner 1991; Witton, 2013) and *Tupandactylus* (Frey et al. 2003; Pinheiro et al. 2011; Beccari et al. 2021). Unfortunately, non-juvenile specimens herein attributed to *Caiuajara dobruskii* are too incomplete to allow for a precise reconstruction of the mature premaxillary crest morphology in *Torukjara bandeirae* and *Caiuajara dobruskii*.

Phylogenetic analysis

The present search produced 15 minimum-length trees, with 2128 steps, ensemble consistency index of 0.351, and ensemble retention index of 0.783. In the strict consensus tree (Figures 12, 13), a clade joining the PG tapejarids *Caiuajara dobruskii* and *Torukjara bandeirae* is recovered. For this group, the new subtribe/clade name Caiuajarina is proposed (see further below – Systematic Paleontology). This Caiuá clade is supported by four synapomorphies: character 71(1): premaxillae with a ventral sagittal expansion projected within the nasoantorbital fenestra; character 74(1): posterior premaxillary process with a dorsal triangular process; character 97(1): maxillae exhibiting paired ventrolateral depressions; and character 205(1): paired pit-like foramina on the occlusal surface of the dentary step-like process. These features are absent in the closely related taxa *Tapejara wellnhoferi* (see Kellner 1989; Wellnhofer and Kellner 1991; Eck et al. 2011) and *Tupandactylus*

navigans (Frey et al. 2003; Beccari et al. 2021), as well as in sinopterines (Pêgas et al. 2023) and *Caupedactylus ybaka* (Kellner 2013).

Caiuajarina was recovered as the sister-group of *Tapejara wellnhoferi*. The node joining Caiuajarina and *Tapejara wellnhoferi* was supported by five synapomorphies: character 121(0), jugal ventral margin straight; character 148(1): presence of a median basisphenoid tuberosity ventral to the occipital condyle; character 154(1): numerous rows of palatal neurovascular foramina; character 190(1): relatively deep mandibular rami (mandibular length/height ratio < 9); and character 311(1): mid-cervical prezygapophyseal pedicles with a convex medial margin in dorsal view. These features set *Tapejara wellnhoferi* plus caiuajarinans apart from other tapejarids, being absent in other taxa such as *Tupandactylus navigans* (see Beccari et al. 2021) and sinopterines (see Pêgas et al. 2023). Still regarding tapejarids, the remaining of the strict consensus tree is equivalent to the results of Pêgas et al. (2023) concerning topology and synapomorphies.

Systematic paleontology

Pterosauria Owen, 1842 [Andres & Padian, 2020]
 Pterodactyloidea Plieninger, 1901 [Andres & Padian, 2020]
 Azhdarchoidea Unwin, 1995 [Andres 2021]
 Tapejaridae Kellner 1989 [Andres 2021]
 Tapejarinae Kellner and Campos 2007 [Andres 2021]
 Tapejarini Andres et al. 2014 [Andres 2021]

Caiuajarina new clade, new subtribe

RegNum registration number
 976.

Definition

The most inclusive clade containing *Caiuajara dobruskii* Manzig et al. (2014) but not *Tapejara wellnhoferi* Kellner (1989). Qualifying clause: provided it is included in Tapejarini Andres et al. 2014 [Andres 2021].

Composition

Caiuajara dobruskii and *Torukjara bandeirae*.



Figure 12. Time-calibrated strict consensus phylogenetic tree, part 1 (non-ornithocheiroid pterosaurs). Circles indicate apomorphy/node-base clades, and brackets indicate branch-based clades. Clades: 1, Macronychoptera; 2, Novialoidea; 3, Breviquartossa; 4, Rhamphorhynchidae; 5, Scaphognathinae; 6, Rhamphorhynchinae; 7, Anurognathidae; 8, Monofenestrata; 9, Darwinoptera; 10, Pterodactyloidea; 11, Archaeopteroactyloidea; 12, Ctenochasmatoidea.

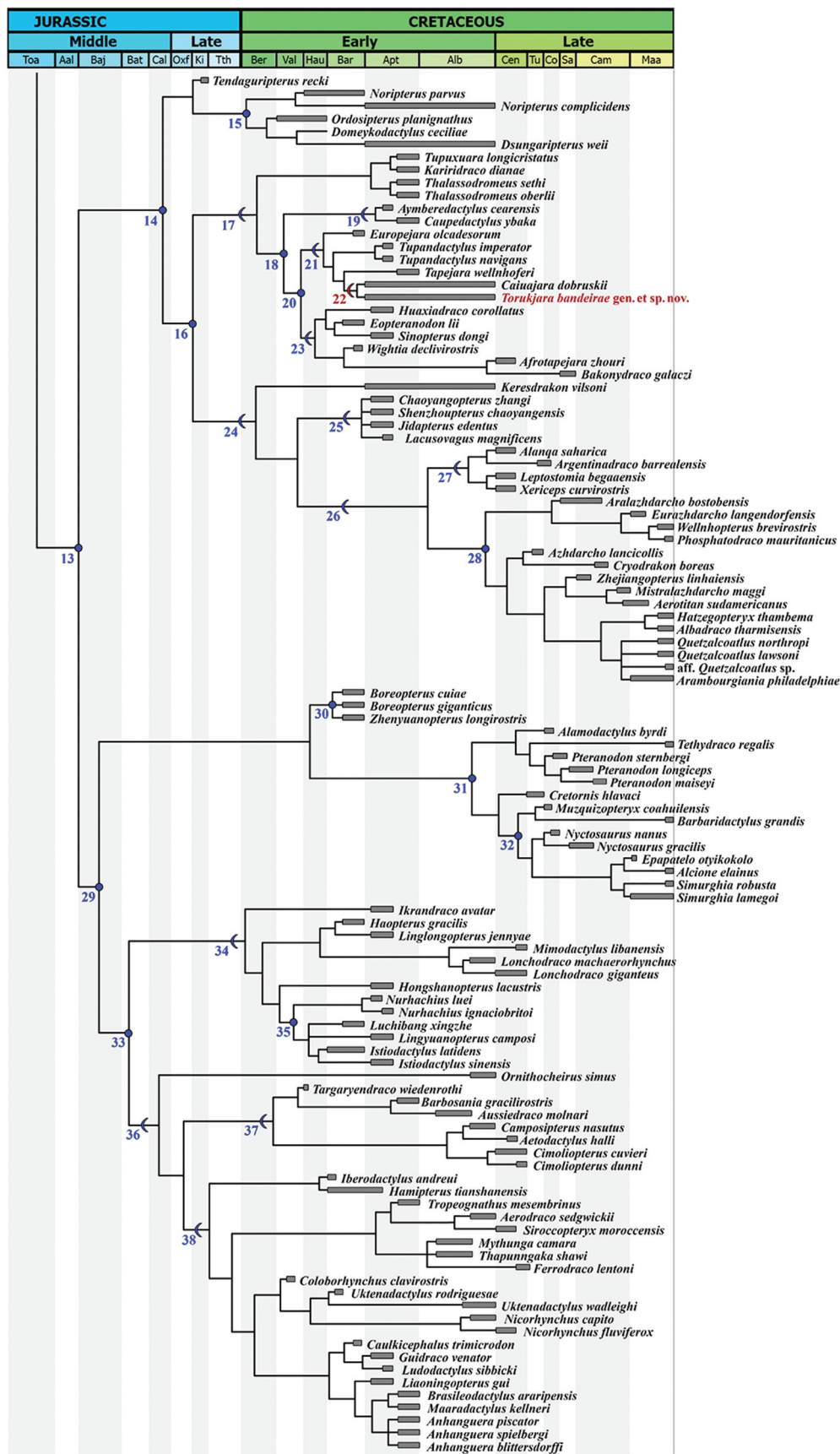


Figure 13. Time-calibrated strict consensus phylogenetic tree, part 2 (ornithocheiroid pterosaurs). Circles indicate apomorphy/node-based clades, and brackets indicate branch-based clades. Clades: 13, Ornithocheiroidea; 14, Tapejaroidea; 15, Dsungaripteridae; 16, Azhdarchoidea; 17, Tapejaromorpha; 18, Tapejariformes; 19, Caupedactylia; 20, Tapejaridae; 21, Tapejarinae; 22, Caiuajarina; 23, Sinopterinae; 24, Azhdarchoomorpha; 25, Chaoyangopteridae; 26, Azhdarchiformes; 27, Alanqidae; 28, Azhdarchidae; 29, Pteranodontoidea; 30, Boreopteridae; 31, Pteranodontia; 32, Nyctosauridae; 33, Lanceodontia; 34, Istiodactyliformes; 35, Istiodactylidae; 36, Ornithocheiriformes; 37, Targaryendraconia; 38, Anhangueria.

Diagnostic apomorphies

Premaxillae with a ventral sagittal expansion projected within the nasoantorbital fenestra; posterior premaxillary process with a dorsal triangular process; maxillae exhibiting paired ventrolateral depressions; paired pit-like foramina on the occlusal surface of the dentary step-like process.

Caiuajara dobruskii Manzig et al. (2014)**Holotype**

CP.V 1449.

Paratypes

For the complete list of designated paratypes, see Manzig et al. (2014). Some of the paratypes are reinterpreted here as specimens of *Torukjara bandeirae* (as listed below). Other paratypes are retained here as specimens of *Caiuajara dobruskii*: CP.V 865, CP.V 1001 (skull), CP.V 1003, CP.V 1005, CP.V 1447/I, CP.V 1450. The remaining specimens are regarded as *Caiuajarina* indet.

Referred specimens

CP.V 5703/I.

Type locality and horizon

Pterosaur Graveyard site, Cruzeiro do Oeste Municipality, Paraná State, Brazil. Caiuá Group.

Diagnostic apomorphies (revised)

Opisthotic relatively slender (about as tall as wide in posterior view); presence of paired occipital tuberosities lateral to the occipital condyle; cervical III lacking an anterior accessory foramen.

Differential diagnosis (autapomorphies marked with an asterisk)

Tapejarinin pterosaur with a rostrum deflection angle of $\sim 31^\circ$ (29° – 33°); a delicate ridge on the posterior region of the prenarial palate absent (= *Tapejara*, \neq *Torukjara*); single incisive foramen (= *Tapejara*, \neq *Torukjara*); opisthotic relatively slender (about as tall as wide in posterior view)*; paired occipital tuberosities lateral to the occipital condyle*; basisphenoid median tuberosity elongate in shape (= *Tapejara*, \neq *Torukjara*); cervical III prezygapophyseal facets ovoid in shape (= *Tapejara*, \neq *Torukjara*); cervical III anterior accessory foramen absent*; cervical III postzygapophyseal pedicles lacking a small, pit-like foramen (= *Tapejara*, \neq *Torukjara*).

Remarks

The following diagnosis has been previously provided for *Caiuajara dobruskii*: (1) strong rostrum deflection (31° – 38°); (2) premaxillae with a ventral sagittal expansion projected within the nasoantorbital fenestra; (3) dentary occlusal surface with a rounded depression; (4) anterolateral quadrate groove; (5) maxillae exhibiting paired ventrolateral depressions; and (6) double dentary fossa (Canejo et al. 2022). Of these features, character (1) is revised here as explored above (see Results and Discussion sections). Characters (2) and (5) are reinterpreted as diagnostic for *Caiuajarina* rather than *Caiuajara*. Character (3) is actually similar to the condition seen in *Tapejara wellnhoferi* (e.g. Wellnhofer and Kellner 1991; Eck et al. 2011). Character (4) is seen in the holotype of *Caiuajara dobruskii* and is still unclear for *Torukjara bandeirae*, and could thus be diagnostic for either *Caiuajara* or *Caiuajarina*, pending further discoveries. Similarly, character (6) is present in specimens herein referred

to *Torukjara bandeirae* and is still unclear in *Caiuajara dobruskii*, and could thus be diagnostic for either *Torukjara* or *Caiuajarina*, pending further discoveries.

Torukjara gen. nov.**Etymology**

The generic epithet *Torukjara* combines the words *toruk*, the Na'vi name of a fictional creature from the *Avatar* cinematographic saga (also known as *great leonopteryx*), and *jara* (Tupi for *lord*), a common suffix for tapejarid genera. The name refers to the superficial resemblance between the *toruk* and tapejarids, both of which are winged creatures that bear large sagittal crests on the rostrum and mandible.

Type species

Torukjara bandeirae gen. et sp. nov., type by monotypy.

Diagnosis

As for type and only species.

Torukjara bandeirae gen. et sp. nov.**Holotype**

CP.V 8175 (Figure 9a).

Referred specimens

CP.V 867; CP.V 1004; CP.V 1023, CP.V 1447/II, CP.V 1448, CP.V 2446, CP.V 5703/II.

Etymology

The specific epithet *bandeirae* honours Brazilian palaeontologist Kamila Bandeira, in recognition of her many contributions to Brazilian palaeontology. In addition, Bandeira is responsible for first noticing the potential taxonomic diversity of Caiuá tapejarids, and for subsequently stimulating the present author to further explore this topic.

Type locality and horizon

Pterosaur Graveyard site, Cruzeiro do Oeste Municipality, Paraná State, Brazil. Caiuá Group.

Diagnostic apomorphies

High rostrum deflection angle of $\sim 40^\circ$ (35° – 41°); delicate palatal ridge present on the posterior region of the prenarial rostrum; paired accessory foramina posterolateral to the incisive foramen; basisphenoid median tuberosity rounded in shape; cervical III prezygapophyseal facets slender and elongate in shape; cervical III postzygapophyseal pedicles bearing a small, pit-like foramen.

Differential diagnosis (autapomorphies marked with an asterisk)

Tapejarinin pterosaur with a high rostrum deflection angle of $\sim 40^\circ$ (35° – 41°)*; a delicate ridge present on the posterior region of the prenarial palate*; paired accessory foramina posterolateral to the incisive foramen*; opisthotic wider than tall in posterior view (= *Tapejara*, \neq *Tupandactylus*, \neq *Caiuajara*); paired occipital tuberosities absent (= *Tapejara*, \neq *Tupandactylus*, \neq *Caiuajara*); basisphenoid median tuberosity rounded in shape*; cervical III prezygapophyseal facets slender and elongate in shape*; cervical III anterior accessory foramen present (= *Tapejara*, \neq *Caiuajara*); cervical III postzygapophyseal pedicles bearing a small, pit-like foramen*.



Figure 14. Life restoration of the coexistence between *Torukjara bandeirae* (front; a couple engaging in courtship ritual) and *Caiuajara dobruskii* (back; a single individual interacting with a juvenile *Berthasaura leopoldinae*) in the Caiuá Desert. Artwork by Matheus Gadelha.

Conclusions

The Pterosaur Graveyard tapejarid assemblage exhibits a large amount of anatomical variation. The present work highlights noticeable variations in rostral, palatal, occipital, and cervical anatomy which are not related to body size and allow for the identification of two consistent morphotypes, herein interpreted as two closely-related, coexisting species: *Caiuajara dobruskii* and the newly recognised *Torukjara bandeirae* (Figure 14). The coexistence of two tapejarid species at the Pterosaur Graveyard site has several implications for the study of the site's fossil assemblage. A comprehensive, detailed account of the osteology of Pterosaur Graveyard tapejarid remains is necessary. This should provide a solid framework for the osteological characterisation of the Caiuajarina, which could provide further insights into the diagnosis of the group and its members *Caiuajara dobruskii* and *Torukjara bandeirae*. It is also important to note that, under the present taxonomic proposal, results from palaeobiological studies on collective PG tapejarid specimens (such as works focusing on the histology and ontogenetic characterisation of collective caiujarinan specimens) cannot be presumed to apply specifically to *Caiuajara dobruskii* alone; but could still presumably apply to the Caiuajarina as a group.

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