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Short note on the vertebral column of the Tapejaridae (Pterosauria, Pterodactyloidea) based on a new specimen from the Crato Formation (late Aptian, Early Cretaceous), northeast Brazil

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Abstract

The Tapejaridae compose a pterodactyloid clade of pterosaurs that is one of the most abundant flying reptiles in the deposits of the Early Cretaceous Crato Formation from the Araripe Basin, northeast Brazil. Until now, only one tapejarid specimen from this locality shows a relatively complete vertebral column. Here we describe a second specimen (LPU 1535) and compare it with more complete tapejarine tapejarids from western Liaoning (China). Among the most striking differences are the absence of a notarium in the Chinese material and the lesser number of dorsal elements in the Brazilian specimens, the latter perhaps being an evolutionary trend in the Tapejarinae. The new material confirms that the number of dorsal elements forming the notarium and taking part in the synsacrum increase during ontogeny. Some member of the Tapejaridae might share the dorsal part of the postacetabular process of ilia extending medially and fusing to the neural spines of the sacral vertebrae, a feature previously observed in the pteranodontid pterodactyloid *Pteranodon*.

Keywords

Flying reptiles, Ontogeny, Axial skeleton, Notarium, Synsacrum, Evolutionary trend

Introduction

The Tapejaridae is a group of edentulous pterosaurs with large nasoantobital fenestrae and developed cranial crests (Wellnhofer, 1991; Kellner, 2006; Wu et al., 2017). This group was first erected on an incomplete skull from the Romualdo Formation (Kellner, 1989), which is part of the Santana Group (see Kellner et al., 2013a for a discussion on the stratigraphy). Later, the Tapejaridae were divided into Thalassodrominae and Tapejarinae (Kellner & Campos, 2007), of which tapejarine pterosaurs are more abundant.

Most tapejarid specimens were discovered in the Araripe Basin (Brazil) and western Liaoning (China) (Kellner, 1989, 2013b; Li et al., 2003; Wang & Zhou, 2003; Lü & Yuan, 2005; Lü et al., 2006; Sayão & Kellner, 2006; Kellner & Campos, 2007; Lü et al., 2007; Eck et al., 2011; Manzig et al., 2014; Lü et al., 2016; Kellner et al., 2019; Zhang et al., 2019). Other specimens include the partial skull with lower jaw of *Europejara olcadesorum* from Spain (Vullo et al., 2012), a partial lower jaw from Morocco (Wellnhofer & Buffetaut, 1999), and the accumulation of hundreds of bones of *Caiuajara dobruskii* from the South of Brazil at Cruzeiro do Oeste city (Manzig et al., 2014; Kellner et al., 2019).

With the exception of the Chinese tapejarid materials, specimens with a relatively complete vertebral column are very rare in the geological record. From the Crato Formation that outcrops in northeast Brazil (Saraiva et al., 2014) only one specimen (MN 6588-V) with a fairly complete vertebral column has been recovered, containing the vertebrae from posterior cervical to anterior caudal (Sayão & Kellner, 2006). Based on the observation of MN 6588-V, the notarium and synsacrum are present in the Tapejaridae (Sayão & Kellner, 2006). Because of the preservation, some aspects of the tapejarid axial column are still uncertain in MN 6588-V. So far there is no news if the MN 6588-V was recovered from the National Museum that was hit by a fire in September 2018 (e.g., Kellner, 2019). This tragedy has happened a few months after our reexamination of this specimen and therefore does not affect our study.

Here we report on a new tapejarid specimen (LPU 1535) that provides supplementary anatomical information for the tapejarid axial column, including the exact number of the dorsal vertebrae. This specimen also provides new evidence for the development of the notarium in the Tapejaridae.

Institutional Abbreviations

LPU-Laboratório de Paleontologia da URCA, Universidade Regional do Cariri, Crato, Ceará, Brazil

MN-Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Systematic Paleontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Tapejaridae Kellner, 1989

genus et species indet.

Specimen: LPU 1535 (Fig. 1), partial axial column and pelvic girdle with several gastralia housed in the Laboratório de Paleontologia da URCA, Universidade Regional do Cariri, Crato, CE, Brazil.

Locality and horizon: Crato Formation, Early Cretaceous (late Aptian, Heimhofer & Hochuli 2010), Araripe Basin, Santana do Cariri, Crato, Northeastern Brazil.

Comments: This new specimen is not complete enough to allow a classification at the generic or specific levels. Based on the shape of the pelvis, where the pubis and ischium form a complete ischiopubic plate (Fig. 2), LPU 1535 is considered as a member of the Tapejaridae (see e.g., Sayão & Kellner, 2006).

Description

LPU 1535 is preserved in a pale-yellow limestone slab and the bones were dorsal-laterally compressed, a typical feature of the fossils discovered in the Crato Formation (Fig. 1; Saraiva et al., 2014). The specimen is composed of a partial postcranial skeleton, including the vertebral column from the last cervical vertebra to the sixth sacral vertebra, some ribs, several gastralia, both prepubes, and pelvic girdle from both sides. During the collection, LPU 1535 was exposed in the dorsal view, and later was prepared from the opposite side, allowing the examination of the ventral surface of the preserved elements (Fig. 2 & 3).

Vertebral Column

Cervical vertebrae - Most researchers argue that the total number of cervical vertebrae in Pterosauria is nine (e.g. Andres et al., 2014; Bennett, 2014; Zhang et al., 2019). In dorsal view of LPU 1535, it is difficult to confirm if the most anterior vertebra is the ninth cervical or the first dorsal element (Fig. 1). After the preparation from the opposite side, it is clear that this vertebra bears both preexapophyses and postexapophyses (Fig. 3), which is the main difference between the last cervical and the first dorsal vertebra (e.g., Bennett, 2001). The most anterior preserved vertebra of LUP 1535 bears two large prezygapophyses (Fig. 1) and can therefore be identified as the ninth cervical element.

The right transverse process is still connecting with the rib, which is broken at the distal end, preventing the comparison with the first dorsal rib except for being thinner than the latter. The postexapophysis is bigger than the preexapophysis. At the anterior ventral margin, on both side of the midline the ninth cervical vertebra has two small projections (Fig. 3).

Dorsal series - The dorsal series consists of twelve vertebrae and has a total length of 172.3 mm.

The first four dorsal vertebrae have their centra fused with the fifth and is in the process of fusing with the preceding element, forming a notarium. Such a structure is present in many derived Cretaceous pterosaurs (Eaton, 1910; Wellnhofer et al., 1983; Wellnhofer, 1991; Kellner, 2003; Unwin, 2003; Sayão & Kellner, 2006; Andres et al., 2014) and varies during the ontogeny in pterodactyloid pterosaurs (e.g., Bennett, 2001; Kellner, 2013a, 2015). The neural spines of the dorsal vertebra 1-3 are fused into the supraneural plate (Fig. 1). Unfortunately, the neural spine of the fourth was broken during the collection, so it is unclear if the supraneural plate in this specimen included the fourth and fifth dorsal vertebrae.

The ribs are not fused with dorsal vertebrae 1- 4. The first rib is very robust and the following get gradually more gracile. Following the notarium, there are five dorsal vertebrae.

The last two form part of the synsacrum, with the neural spines and centrums fused to the sacral vertebrae (Fig. 1 & 4B). The transverse processes of the last two dorsals are a little broader than that of the preceding element. However, the transverse processes are directed laterally, differing from the subsequent sacral vertebrae. During the fossilization, the right transverse process of the eleventh dorsal vertebra was displaced above the preacetabular process of the ilium (Fig. 1).

Synsacrum - The synsacrum consists of two dorsal and six sacral elements (Fig. 1). The first sacral vertebra is distinguished from the last dorsal by the posterolateral-directed transverse processes which is the main difference from the preceding dorsal vertebrae (e.g. Bennett 2001, 2014). The neural spines of the sacral vertebrae are fused into a supraneural plate. In all available sacral vertebrae, the transverse processes are elongated, wide and fused together, and also fused with the ilium (Fig. 4B).

Pelvic Girdle

LPU 1535 preserves the pelvic girdles of both sides (Figs. 1 & 2). The ilium, pubis, and ischium are fused and also fused to the synsacrum. The ilium is an elongated bone with a length of about 100.2 mm from the anterior tip of the preacetabular process to the posterior end of the postacetabular process. The preacetabular process is over twice the length of the postacetabular process. The anterior portion of the preacetabular process is expanded, differing from MN 6588-V (Sayão & Kellner, 2006). The dorsal portion of the postacetabular processes tightly contacts the supraneural plate of the synsacrum, where two depressions are present (Fig. 1). Below the acetabulum, the obturator foramen is located between the pubis and ischium, which is also present in MN 6588-V (Fig. 2). At the ventral portion, the pubis and ischium form an ischiopubic plate, a typical character to distinguish the Tapejaridae from the Anhangueridae (Kellner, 1995; Kellner & Tomida, 2000; Sayão & Kellner, 2006). The opposite ischia are fused at the ventral midline (Fig. 2).

Both prepubes are complete (Fig. 1). It is a fan-shaped bone with a thin “fan leaf” like distal plate and a thick “fan handle” like proximal branch. The proximal branche is comparably shorter than the distal plate. The join at the midline forming a smooth arc. The anterior margin of the distal plate is nearly right-angled. Both prepubes contact each other at the midline and are almost fused leaving an indistinct suture. Fused prepubes have been previously reported in *Pteranodon* (Bennett, 2001) and the non-pterodactyloid Wukongopteridae (Cheng et al., 2016), but for the first time in tapejarids.

Gastralia

One set of V-shaped medial gastralia and two slender lateral elements are preserved close to the anterior margin of the prepubes. They are similar as the ones reported in MN 6588-V (Sayão & Kellner, 2006).

Discussion

There are interesting preliminary comparisons that can be made between regarding the occurrence of tapejarine tapejarids from the Cretaceous deposits from China and Brazil.

Based on the $^{40}Ar/^{39}Ar$ dating data, the age (120.3 ± 0.7 Ma) of the Jiufotang Formation corresponds to the early Aptian (late Early Cretaceous, He et al., 2004). This indicates that the tapejarids from this deposit are older than those from the Crato Formation, whose age are regarded as late Aptian (Heimhofer & Hochuli, 2010). Wang & Zhou (2006) extrapolated that tapejarid pterosaurs might have dispersed to the Araripe Basin (Brazil) from western Liaoning (China) during the Early Cretaceous. But it should be noted that there is very little information about the pterodactyloid fauna from Africa that surely must have more tapejarid pterosaurs, most likely closely related to the Brazilian forms. The limited tapejarid specimens from this continent (Wellnhofer & Buffetaut, 1999; Martill et al, 2020) is too incomplete and does not contribute to this discussion. And there is still some uncertainty about the age of the deposits from the Araripe Basin (e.g., Fabin et al., 2018; Lúcio et al., 2020). Furthermore, the relationship of tapejarids has still to be better resolved (e.g., Kellner et al., 2019).

In all tapejarids reported so far, only specimens from Brazil and China have the axial column completely preserved that can be compared (Wang & Zhou, 2003; Lü & Yuan, 2005; Lü et al., 2006; Sayão & Kellner, 2006; Zhang et al., 2019). The first to be described was MN 6558-V (Sayão & Kellner, 2006) from the Crato Formation, who argued that the dorsal series consisted of eleven elements. However, our reexamination considers that one vertebra was missed during the collecting process and the total number should have been 12.

In contrast, the dorsal series has been reported in many Chinese tapejarine materials (Wang & Zhou, 2003; Lü & Yuan, 2005; Lü et al., 2006; Zhang et al., 2019) but not described in detail. In Chinese specimens, the number of dorsal elements varies between twelve (Lü & Yuan, 2005), thirteen (Lü et al., 2006) to more than fourteen (Zhang et al., 2019). Therefore, *Sinopterus*-like tapejarines apparently have had more dorsal elements than MN 6558-V and LPU 1535. If the Chinese tapejarine pterosaur were more basal than the ones from the Crato Formation as suggested by Wang & Zhou (2006), this would indicate that along the evolutionary path of this group of pterodactyloids a reduction in the number of dorsal vertebrae might have occurred.

The discrepant number of dorsal vertebrae composing the notarium in pterodactyloid taxa is considered an ontogenetic feature (Wellnhofer, 1975; Bennett, 1993, 2001; Frey & Martill, 1994;

Kellner & Tomida, 2000; Sayão & Kellner, 2006; Kellner, 2013a; Kellner, 2015). The Crato taperarids show a similar size suggesting that they might have had the same ontogenetic age at time of death. However, the number of fused elements that compose the notarium differ. In MN 6588-V it is formed by the first four dorsal vertebrae (Sayão & Kellner, 2006), whereas LPU 1535 shows five vertebrae with the fifth element being in the process of fusion. So far, we cannot be sure what kind of information this variation provides since knowledge about pterosaur ontogeny is still at an early stage (e.g., Kellner, 2015). It is also unknown if both specimens represent the same species and the degree of how ontogenetic variation is expressed in closely related pterosaur taxa.

The referred specimen (D2525) of *Sinopterus dongi* is the only purported adult individual of tapejarine tapejarids reported from China (Li et al., 2003; Wang & Zhou, 2003; Lü & Yuan, 2005; Lü et al., 2006; Lü et al., 2007; Lü et al., 2016; Zhang et al., 2019) and based on the fusion of the proximal tarsals to the tibia might have reached the Ontogeny Stage 5 (OS5), or even OS6 (Lü et al., 2006; Kellner, 2015). However, in D2525 the anterior dorsal vertebrae are still unfused and do not form a notarium (Lü et al., 2006). Although more data is needed, there is a strong possibility that the tapejarine pterosaurs from China might not have developed a notarium or that this structure was only developed in the very final ontogenetic stages.

The last dorsal vertebrae taking part in the synsacrum was reported in *Pteranodon* and the Tapejaridae (Bennett, 2001; Sayão & Kellner, 2006; Hyder et al., 2014). In both tapejarid specimens (LPU 1535 and MN 6588-V), the neural spines of 11th and 12th dorsal vertebra were fused with the subsequent sacral vertebrae, forming a supraneural plate. However, a suture is clearly present between 11th and 12th dorsal vertebra in MN 6588-V and absent in LPU 1535, which indicates that the number of dorsal vertebrae participating synsacrum might increase in later ontogenetic stages in this clade.

In the skeletally mature Chinese tapejarid specimen (D2525), the sacral vertebrae were fused, the neural spines formed the supraneural plate, and five sacral vertebrae form a compact unit (Lü et al., 2006). This configuration suggests that the last dorsal vertebra was probably unfused to the sacrum. Although more data is needed, there is a possibility that the incorporation of the last dorsal vertebrae into the synsacrum might have been developed only in derived tapejarine tapejarids.

The dorsal part of the postacetabular process extending medially and fusing to the neural spines of the sacral vertebrae was previously reported only in *Pteranodon*, which was considered an autapomorphic character of this taxon (Bennett, 2001; Hyder et al., 2014). The preservation of the postacetabular processes of both ilia and the depressions in the lateral surface of the supraneural plate of the synsacrum in LPU 1535 indicates that this feature is also present in the Tapejaridae. It is not known if this particular condition, unknow in non-pterodactyloids, might have been more widespread within derived pterodactyloid pterosaurs.

Conclusion

The discovery of LPU 1535, referred to the Tapejaridae, provides new anatomical and ontogenetic information for this clade. Although it is impossible to determine its genus and species, LPU 1535 shows the reduced number of dorsal vertebrae (12 elements), what is lesser than in any tapejarid reported so far. Comparisons with Chinese materials suggest that the notarium probably was absent in tapejarine tapejarids from western Liaoning. Several other ontogenetic indications like the number of vertebrae that compose the notarium or its presence at all are various in the Tapejaridae. More data is needed to establish that if there was an evolutionary trend within tapejarids regarding the total number of dorsal vertebrae and the development of a notarium in more derived species.

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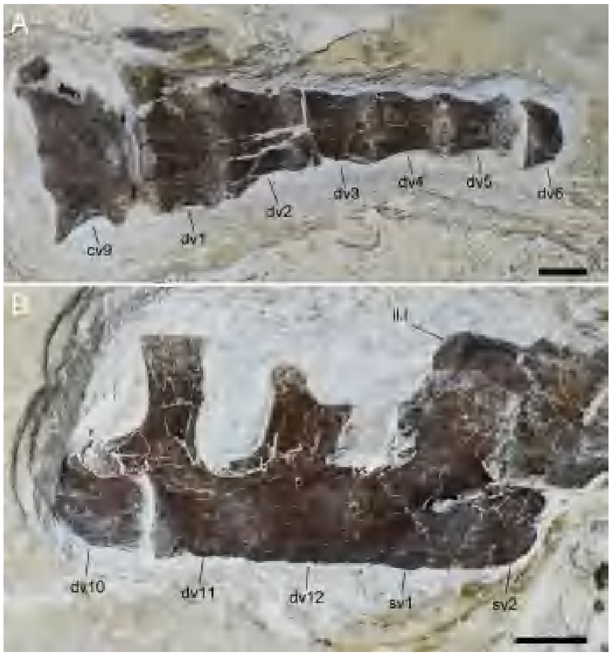
Figure 1 –LPU 1535, Tapejaridae indeterminate from the dorso-lateral view: (A) photo and (B) drawing. Abbreviations: ac, acetabulum; cri, cervical rib; cv, cervical vertebra; dv, dorsal vertebra; gas, gatralia; il, ilium; l, left; ppu, prepubis; prz, prezygapophysis; r, right; ri, rib; snp, supraneural plate; sv, sacral vertebra. Scale bar: 100 mm.

Figure 2. Detail of LPU 1535 pelvis in ventral view: (A) photo and (B) drawing, with the dark grey part showing the broken bones. Abbreviations: ac, acetabulum; il, ilium; is, ischium; l, left; obfo, obturator foramen; pu, pubis; r, right; sv, sacral vertebra. Scale bar: 10 mm.

Figure 3. Detail of the ninth cervical vertebra of LPU 1535 in ventral view: (A) photo and (B) drawing, with the dark grey part showing the broken bones. Abbreviations: con, condyle; pt, protuberance; l, left; poex, postexapophysis; prex, preexapophysis; r, right. Scale bar: 10 mm.

Figure 4. Detail of LPU 1535 axial column in ventral view: (A) anterior dorsal vertebrae and (B) posterior dorsal vertebrae. Abbreviations: cv, cervical vertebra; dv, dorsal vertebra; il, ilium; l, left; sv, sacral vertebra. Scale bar: 10mm.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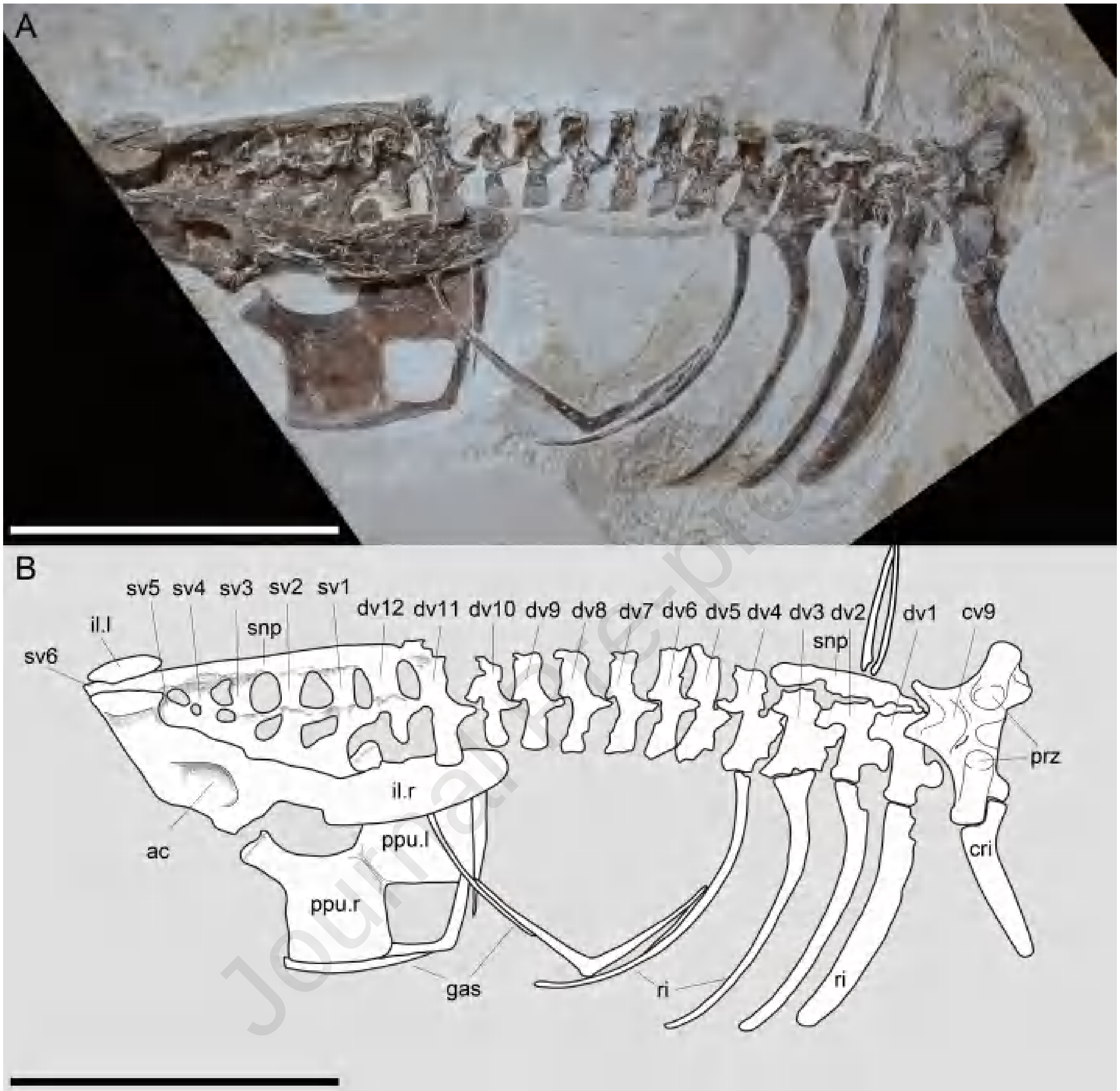
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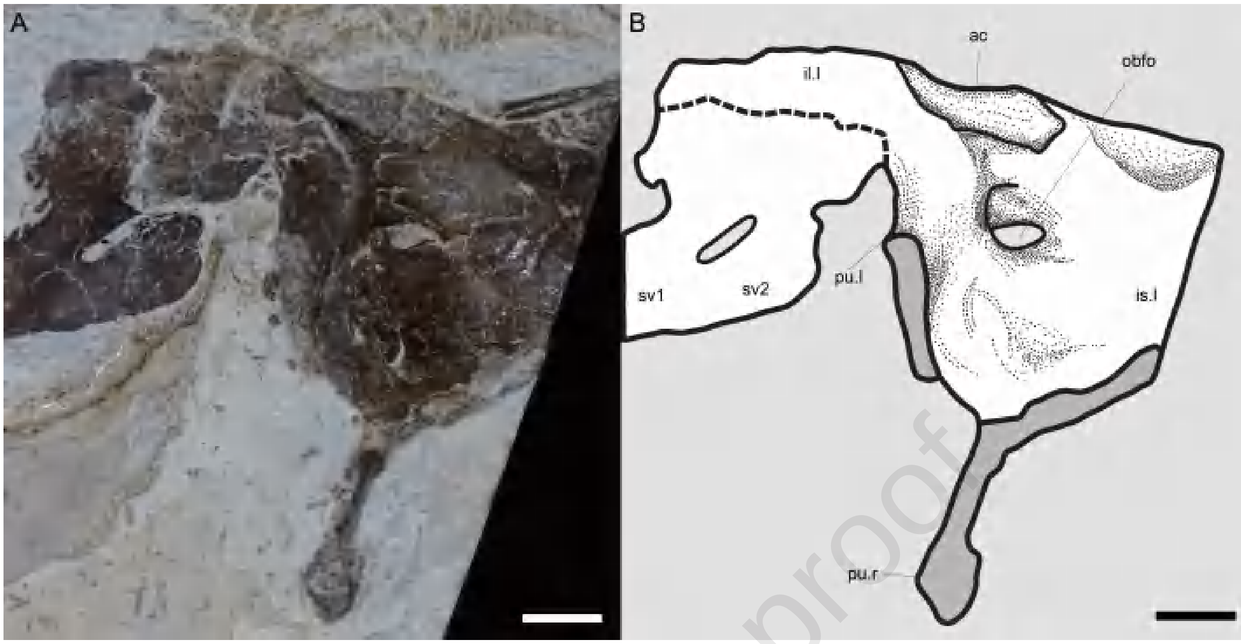
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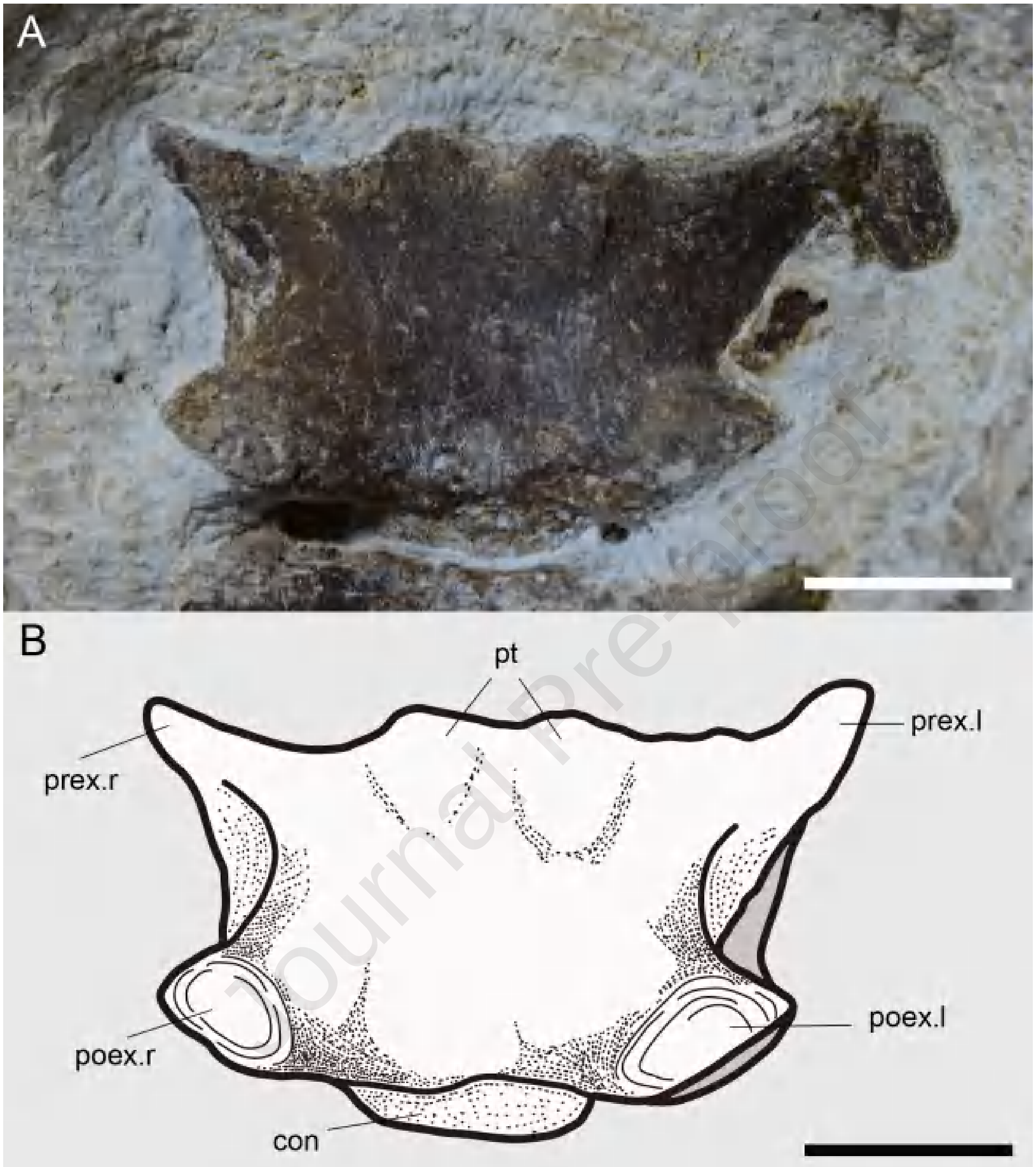
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1. A new tapejarid specimen from the Crato Formation is described here.
2. Determining the number of dorsal vertebrae of tapejarid pterosaurs from the Crato Formation.
3. Proving the number of vertebrae that compose the notarium or its presence at all are various in the Tapejaridae.

Declaration of interests

☒ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: