Comments on the cervical vertebrae of the Tapejaridae (Pterosauria, Pterodactyloidea) with description of new specimens

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The cervical series is poorly known in several pterosaur clades despite the fact that distinct morphotypes of individual elements have been recognised. Among the least known is the neck of the Tapejaridae that until recently has received little attention. In order to provide further data on the tapejarid cervical anatomy, we describe three specimens from the Romualdo Formation (Lower Cretaceous, Brazil): AMNH 22568 comprises the last five cervical elements of a large individual, AMNH 24445 and MN 4728-V, both including three meso-cervical elements of small individuals. Despite size differences, AMNH 22568 and MN 4728-V are anatomically more similar to each another, showing a pattern of high, laterally flattened (blade-like) neural spines, short centra pierced by two lateral pneumatic foramina. AMNH 24445 presents a distinct anatomy, with low (but still evident) neural spines, more elongated centra with concave ventral surface, and only one lateral pneumatic foramen. Based on comparative studies we refer AMNH 22568 and MN 4728-V to the Thalassodrominae and AMNH 24445 to the Tapejarinae, helping to differentiate the cervical elements of these clades. Thalassodromine cervical vertebrae can be distinguished by the presence of two lateral pneumatic foramina, a broad centrum (length/width ratio lower than two), and a flat ventral surface. Tapejarinae cervical vertebrae show only one lateral pneumatic foramen, the length/width ratio higher than two, and a concave ventral surface. Thalassodromine and tapejarine cervical vertebrae differ from those of azhdarchids in the presence of lateral pneumatic foramens, developed neural spine, and length/width ratio lower than three, and by being comparatively shorter.

Keywords: Pterosauria; Tapejaridae; cervical vertebrae; Araripe Basin; Romualdo Formation; Cretaceous

Introduction

Pterosaur cervical vertebrae have been debated since the beginning of last century, when Williston (1903) and Eaton (1904) disagreed on the number of elements present in the neck of the pterodactyloid *Pteranodon*. Since then, despite the fact that several distinct morphologies have been acknowledged (e.g. Wellnhofer 1978; Wild 1984; Howse 1986), there is still limited information regarding the pterosaur neck and only few characters have been employed in cladistic studies (e.g. Kellner 2003; Unwin 2003; Andres and Ji 2008). The pioneer work of Howse (1986) recognised two different categories of pterodactyloid cervical vertebrae, and hinted that they could represent natural units. Latter, Bennett (1994) on his extensive systematic review of *Pteranodon*, used the following cervical characters to diagnose his newly named infraorder Eupterodactyloidea: presence of exapophyses, tall neural spines, pneumatic foramina lateral to the neural canal (Bennett 1994). The studies by Kellner (2003) and Unwin (2003) on pterosaur phylogeny employed similar characters regarding the cervical anatomy, which were

also used in later works (e.g. Wang et al. 2009; Lü et al. 2010; Vila Nova et al. 2014).

From those studies it is presently agreed that some of the different morphotypes of cervical vertebrae observed so far in pterosaurs are clade-specifics while others are more wide spread (e.g. Bennett 2001; Kellner 2003; Andres and Ji 2008). For example, tall neural spines and short centra are present in *Pteranodon* (e.g. Bennett 2001) and in the Anhangueridae (e.g. Kellner and Tomida 2000). Likewise, the vertebra elongation of the centrum and reduction of the neural spine, although commonly observed in the more derived pterodactyloids (e.g. Andres and Ji 2008; Wang et al. 2009; Lü et al. 2010), were used to identify the azhdarchids (Nessov 1984; Padian 1986; Kellner 2003; Andres and Ji 2008; Averianov 2010), and also seen to some extent (although not to the same degree) in ctenochasmatid pterodactyloids (Andres and Ji 2008) and in *Pterodactylus*. The presence and distribution of postexapophyses among pterosaurs is also complex, with authors suggesting independent origin in some taxa (Andres and Ji 2008). In fact, the evolution of the neck

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structure of pterosaurs is still poorly understood, with only a few studies published so far [see Witton (2009) and Averianov (2013) for further comments on neck reconstruction and biomechanics].

Detailed descriptions of cervical elements, such as these provided for *Anhanguera* (Wellnhofer 1991b; Kellner and Tomida 2000; Kellner et al. 2013), *Pteranodon* (Bennett 2001) and *Azhdarcho lancicollis* (Averianov 2010) are limited for the Tapejaridae, a clade of pterodactyloid pterosaurs reported in several Cretaceous deposits (e.g. Wang and Zhou 2003; Sayão and Kellner 2006; Kellner and Campos 2007; Vullo et al. 2012). First recovered from the Romualdo Formation (Albian) of the Araripe Basin, northeastern Brazil (Kellner 1989), tapejarids have been subsequently recorded in other deposits of Brazil, Morocco, China and Spain (Sayão et al. 2012; Vullo et al. 2012; Costa et al. 2014; Manzig et al. 2014). The fact that most of these descriptions are based on cranial elements is another problem for the study of tapejarid necks.

Two distinct lineages within the Tapejaridae have been recognised (Kellner and Campos 2007). The Thalasso-drominae, presently composed only by *Thalassodromeus* and *Tupuxuara*, consists of comparatively large taxa (wingspan around 4 m) with elongated skulls, whereas the Tapejarinae show a higher diversity, are comparatively small (wingspan: < 3 m), with a shorter rostrum (Kellner and Campos 2007; Pinheiro et al. 2011). Few tapejarids with complete necks have been described, most of which are small individuals of the Jehol Biota of China (e.g. Wang and Zhou 2003, Liu et al. 2014). As for isolated neck elements of that clade, there is one specimen tentatively referred to the Thalassodominae (Aires et al. 2014), and two Tapejarinae mesocervical vertebrae from the Romualdo Formation (Eck et al. 2011). Most recently, Liu et al. (2014) described an almost complete neck attributed to the Tapejarinae from the Jiufotang Formation (China). In order to bring more information on the cervical series of the Tapejaridae, we describe three new incomplete series of tapejarid cervical vertebrae from the Romualdo Formation (AMNH 22568, AMNH 24445 and MN 4728-V), preserved three-dimensionaly and provide new information of the morphological variation in the neck of this derived pterodactyloid group of flying reptiles.

See Supplementary Material for table of measurements.

Anatomical abbreviations: co, cotyle; con, condyle; hyp, hypapophysis; nc, neural canal; ns, neural spine; pf, pneumatic foramen; poex, postexapophysis; poz, post-zygapophysis; prz, prezygapophysis.

Institutional abbreviations: AMNH, American Museum of Natural History – New York, USA; MN, Museu Nacional/Universidade Federal do Rio de Janeiro – Rio de Janeiro, Brazil; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology – Beijing, China; SMNK, Staatliches Museum für Naturkunde Karlsruhe – Karlsruhe, Germany.

Institutional abbreviations

AMNH: American Museum of Natural History – New York, USA, BSP: Bayerische Staatssammlung für Paläontologie und Geologie – Munich, Germany, MN: Museu Nacional/Universidade Federal do Rio de Janeiro – Rio de Janeiro, Brazil, IVPP: Institute of Vertebrate Paleontology and Paleoanthropology – Beijing, China, SMNK: Staatliches Museum für Naturkunde Karlsruhe – Karlsruhe, Germany, SMNS: Staatliches Museum für Naturkunde Stuttgart – Stuttgart, Germany.

Geological setting

Located in northeastern Brazil, within the states of Pernambuco, Ceará and Piauí (Figure 1), the Araripe Basin went through different tectonic phases, with the basal layers having been formed during the Palaeozoic and the youngest deposits regarded as Cenomanian (Assine 2007). The most fossiliferous layers belong to two *lagerstätten*

Figure 1.   The Araripe Basin, located on the Brazilian northeast. Despite all three individuals being preserved on typical concretions from the Romualdo Formation, there is no further reference from local of origin. After Vila Nova et al. (2011).
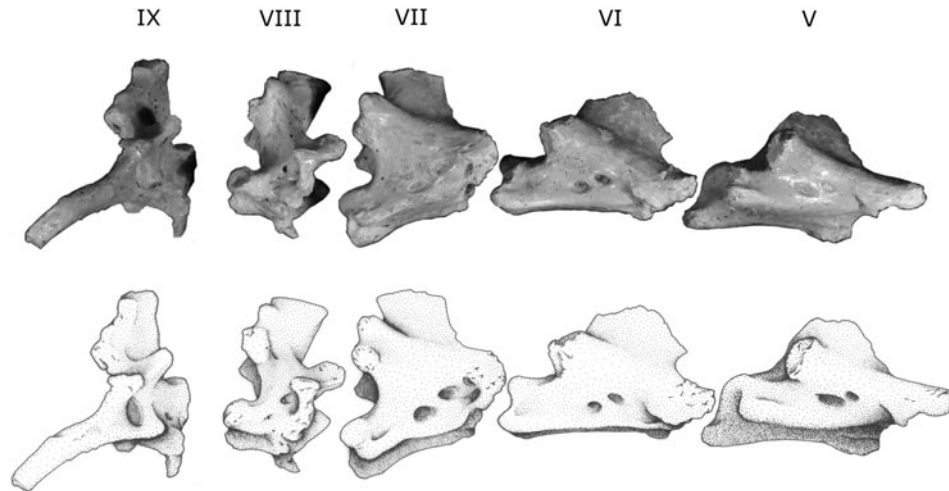
Figure 2. AMNH 22568 cervical series in right lateral view. Scale bar 50 mm.

known as the Crato and Romualdo Formations (Neumann and Cabrera 1999), which were deposited during the Aptian–Albian (Valença et al. 2003; for comments on nomenclatural issues, see Kellner et al. 2013). Known since the nineteenth century (e.g. Maisey 1991), most specimens have been collected by local farmers and controlled excavations are very limited (e.g. Fara et al. 2005; Vila Nova et al. 2011).

All three specimens described here are preserved in calcareous concretions typical of the Romualdo Formation. Since they were collected by local farmers the precise locality is unknown.

Systematic palaeontology

PTEROSAURIA Kaup, 1834
PTERODACTYLOIDEA Plieninger, 1901
AZHDARCHOIDEA Nessov, 1984
TAPEJARIDAE Kellner, 1989

THALASSODROMINAE Kellner and Campos, 2007
Genus and species indet 1 – AMNH 22568

Description and comparison

AMNH 22568 consists of five articulated cervical vertebrae. As common in specimens from the Romualdo Formation, all show no perceptible compression (Figure 2). They are interpreted as cervical vertebrae V–IX based on comparisons with other cervical series (e.g. Wellnhofer 1991b; Kellner and Tomida 2000; Bennett 2001; Aires et al. 2014). They can be referred to Thalassodrominae due to their large size, the presence of a developed hatchet-like neural spine that, according to Aires et al. (2014) are typical of this clade. They also show very pronounced postexapophyses, and reduced hypapophyses. The preserved mesocervical vertebrae (V, VI and VII) are elongated, more than two times longer than wide at their narrowest point (Figure 3). As usual for derived azhdarchoids, there are well-developed exapophyseal articulations, indicating a limited movement range for the neck (Averianov 2010). Cervical vertebrae VIII and IX
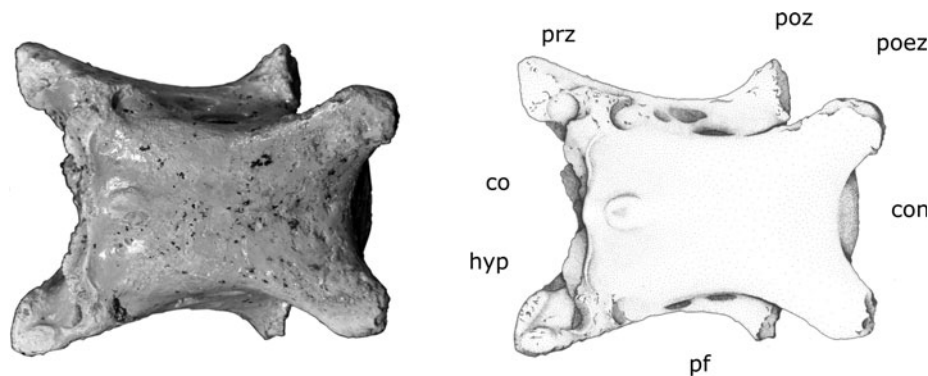

Figure 3. AMNH 22568 cervical vertebra V in ventral view. See text for anatomical abbreviations. Scale bar 30 mm.
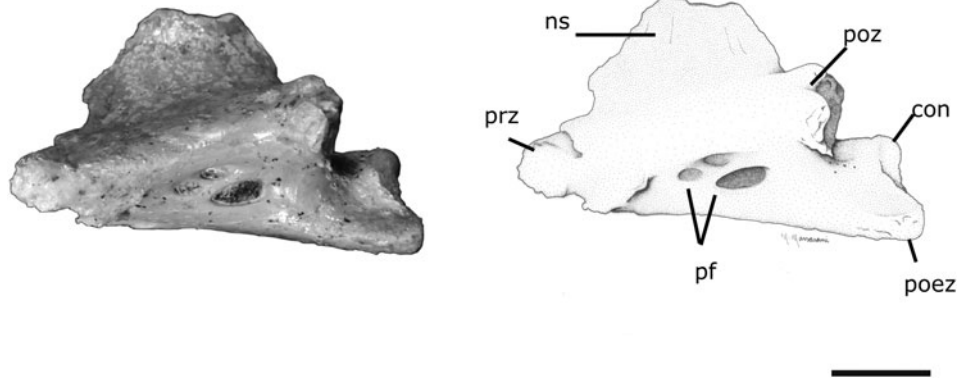
Figure 4.   AMNH 22568 cervical vertebra V in left lateral view. Notice the three lateral foramina. See text for anatomical abbreviations. Scale bar 30 mm.

are 'dorsalised', more similar to the dorsal pattern than the cervical, despite still being neck elements. This condition is seen in many pterodactyloids (Kellner and Tomida 2000; Bennett 2001). The preserved vertebrae length formula is V > VI > VII > VIII > IX. In all vertebrae, the non-articular portions of the pre- and postzygapophyses are spread, forming angles of 60° to the sagittal line in dorsal view (Figure 4). The postzygapophyses are positioned dorsal to the level of the prezygapophyses. The hypapohysis is small and does not project ventrally beyond the preexapophyseal surfaces. The neural spines are relatively long and robust, increasing in size towards the more posterior portion of the vertebrae. The neural canal is flanked on each side by a small, circular foramen, seen in both anterior and posterior views, as observed by Aires et al. (2014) in another specimen. Vertebrae V, VI and VII also have a large pneumatic foramen above the neural canal, crossing the vertebrae in the antero-posterior direction.

The estimated length (from the middle portion of the cotyle to the condyle) to width (at the centrum most constricted part) ratio of cervical V is somewhat above 1.0 (Table 1 on Supplementary Material for measures). The maximum lateral constriction of the vertebra is near its middle, slightly closer to the anterior end. The elongate prezygapophyses diverge anteriorly, with slightly ante-rodorsally convex oval articular surfaces. The prezygapophyseal tubercles emerge from the concave medial faces of the prezygapophyses. The procoelous centrum has a transversely ovoid cotyle that is almost three times wider than high (Figure 5). The anterior end of the hypapophysis is well preserved in all elements, showing a lateromedially elongated concavity as seen in other tapejarids (Eck et al. 2011; Aires et al. 2014). The ventral surface of cervical vertebra V is almost flat, with the hypapophysis forming a small elevation in the anterior portion (Figure 3). Different from other cervical vertebrae of the series, cervical vertebra V has three lateral pneumatic foramina on the left side of the centrum, one more than all other cervical

elements of MN 4728-V (Figure 4) and those described by Aires et al. (2014). Given that no complete cervical series of thalassodromines is known, it is not clear if this is a general feature of the group or a specific trait of this individual. The neural spine is well developed and hatchet like, differing from that of Azhdarchidae, a closely related group, and Anhangueria, another group present in the fossil deposits of the Araripe Basin (Rodrigues and Kellner 2013). It starts at the level of the cotyle and expands posteriorly until the beginning of the postzyga-pophyses. The highest point of the neural spine is at the middle portion of the vertebra. The postexapophyses are large and the postzygapophyseal articulation surfaces are obliquely oriented. The condyle is higher than the neural canal and has a convex dorsal margin. It is very developed, raising the postzygapophyses above the level of the prezygapophyses. The ventral margin of the centrum is
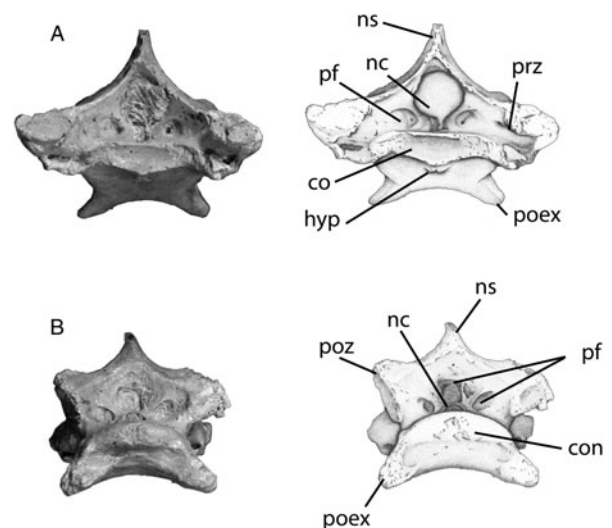

Figure 5.   AMNH 22568 cervical vertebra VI in (A) anterior and (B) posterior views. See text for anatomical abbreviations. Scale bar 30 mm.

convex between the postexapophyses; the complete cross section of its middle section was probably sub-circular and slightly wider than high.

Cervical vertebra VI is mostly similar to the previous element. Yet, it has only two pneumatic foramina on the sides of the centrum, a trait here interpreted as the typical condition for thalassodromines (see 'Discussion' section). As in cervical vertebra V, cervical vertebra VI has a larger pneumatic canal above the neural canal, so that four openings are seen both anteriorly and posteriorly (Figure 5). The neural spine is well developed, clearly hatchet shaped, with a small projection on the anterior portion. This projection is not seen in cervical vertebra V, probably due to erosion. In lateral view cervical vertebra VI differs from the previous one by a more concave ventral profile and a much lower condyle relative to the postzygapophyses. The postexapophyses are set forming a stepper angle relative to the centrum than in cervical vertebra V. Both vertebrae have postexapophyses of similar size, but the displacement of the postzygapophyses in relation to the prezygapophyses is stronger in cervical vertebra VI. Also, the hypapophysis is more evident in this vertebra than in any other of the series. However, this does not change the flat profile of its ventral surface. As in cervical vertebra V, its maximum lateral constriction is near the middle of the vertebra, slightly closer to the anterior end.

Cervical vertebra VII is the last of the mesocervical series, and has almost half the length of the two preceding elements. Its general shape is very similar to that of the cervical vertebra VII described by Aires et al. (2014). This suggest that, despite size difference, these specimens may correspond to the same taxon closely related taxa. The neural spine is more developed than in any other mesocervical vertebra. It points posteriorly and has a large base. The distal portion is broken, and the full size of the spine is uncertain, but it seems to be at least of the same height as the centrum. The distance between the postzygapophyses and the postexapophyses is larger than in any other mesocervical of the series, suggesting that its posterior articulation was more flexible. The presence of only two pneumatic foramina is evident on both sides of the centrum. This vertebra also has a well-developed *foramen transversarium* below each prezygapophysis, which is absent in the preceding elements.

Cervical vertebra VIII is dorsalised, as also seen in both *Pteranodon* (Bennett 2001) and *Azhdarco* (Averianov 2010). It possesses a developed neural spine (forming at least 60% of the vertebral height) and a comparatively small centrum (Figure 6). The caudal surface of the neural spine is high, triangular in outline, and is slightly depressed. The centrum is very compact, and smaller than the neural spine. Since the top of the neural spine is not preserved, the ratio could be even lower. Nonetheless, there are two lateral pneumatic foramina on each side of
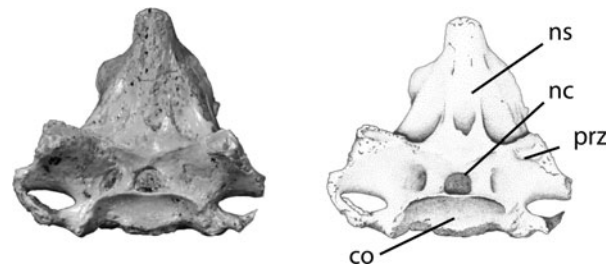

Figure 6.   AMNH 2258 cervical vertebra VIII in anterior view, showing well developed neural spine and reduced centrum. Scale bar 30 mm.

the centrum, as well as one adjacent to each side of the neural canal. Contrary to the mesocervical elements, the main articular surfaces of cervical vertebra VIII are the cotyle and the condyle, and the postexapophyses are much reduced. Yet, the pre- and postzygapophyses are still present, forming a large part, but not most of the articulation. The transverse process is positioned anteriorly, at the same plane as the postzygapophyses. The lateral pneumatic foramina are larger than the neural canal in posterior view, but smaller in anterior view.

As the following element, cervical vertebra IX is dorsalised, with almost one-third of the anteroposterior length of cervical vertebrae V or VI. Similar to cervical vertebra VIII, it has a short centrum and a comparatively high neural spine. Also, the caudal surface of the neural spine is high, triangular in outline, with an even more evident depression on its centre. In anterior view, one small pneumatic foramen is placed adjacent to each side of the neural canal, but these are not seen in posterior view (Figure 7). The transverse processes are more developed than in cervical vertebra VIII. The right rib is still connected to the vertebra, forming a large opening delimited by the *processus transversus* and the *tuberculum costae*. The pre- and postzygapophyses are very short, not distinctly set as in the mesocervical vertebrae. This suggests that this vertebra allowed a greater range of mobility than the anterior ones.

Genus and species indet 2 – MN 4728-V

Description and comparison

MN 4728-V comprises a small portion of the skull occipital region, fragments of both wings, and three cervical vertebrae. Here we will focus only on the cervical series only and the description of other elements is going to be done elsewhere. Despite the small size, MN 4728-V represents a member of the Thalassodrominae (Figure 8) since all comparable cervical elements are similar to those of AMNH 22568. The preserved wing shows an unfused carpal, hinting that this is a juvenile individual. Comparison to previously described cervical vertebrae
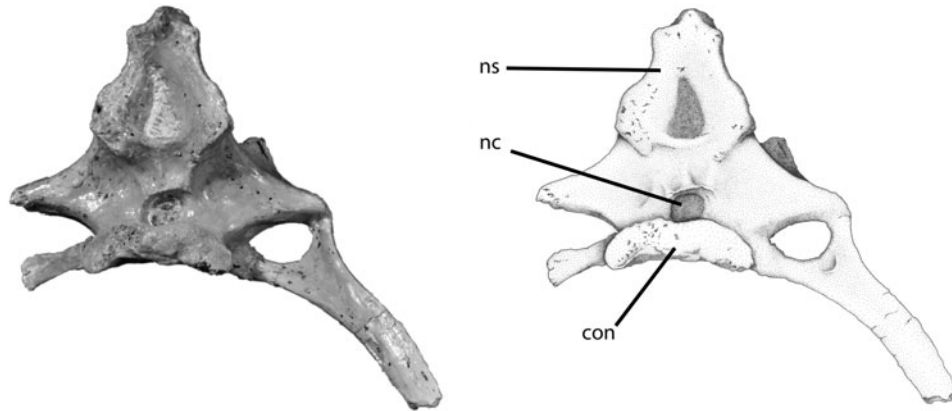
Figure 7.   AMNH 22568 cervical vertebra IX in posterior view, showing the absence of adjacent pneumatic foramina. Scale bar 30 mm.
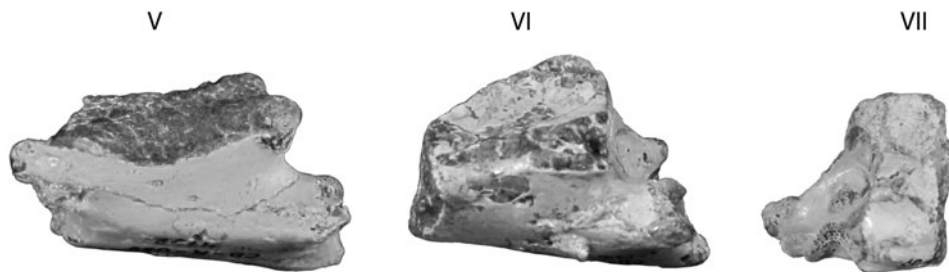

Figure 8.   MN 4728-V cervical series in left lateral view. Scale bar 10 mm.

indicates that those preserved in the present specimens probably correspond to cervical vertebrae V–VII. Their length/width ratio is higher than that of AMNH 24445 (1.8, vs. 2.3; length measured from the middle of the cotyle concavity to the middle of the condyle convexity; width measured at the middle portion of the centra – see Table 2 of Supplementary Material for measures), but resemble that of AMNH 22568 (1.5). Cervical vertebrae V and VI possess two small pneumatic foramina on the sides of the centrum, and a well-developed neural spine. These features suggest that MN 4728-V and AMNH 22568 represent taxa that are closely related with respect to AMNH 24445. It also differs from the cervical elements attributed to *Tapejara wellnhoferi* by Eck et al. (2011). Despite the similar size, the *Tapejara wellnhoferi* meso-cervical vertebrae show a larger hypapophyses and less pronounced postzygapophyses than MN 4728-V. Eck et al. (2011) also identified a single foramen on the sides of the centrum, while MN 4728-V presents two.

The cervical vertebra V pre- and postzygapophyses are incomplete, appearing to be smaller when compared to those of *Tapejara wellnhoferi* (e.g. AMNH 2445). The centrum is well developed, as anteroposteriorly long as the neural spine plus articular processes. This resembles more the condition of thalassodrominids (e.g. AMNH 22568) than of AMNH 24445, despite the great difference in size

between the two series. The presence of two small, albeit evident, pneumatic foramina on the centrum (Figure 9) sides suggests that this specimen represents a taxon that is closely related to AMNH 22568.

Cervical vertebra VI is almost identical to the preceding one, and its neural spine is better preserved. It has a very robust centrum, despite its anterior portion not being fully preserved. Both the cotyle surface and the prezygapophyses are not preserved. The condyle articular surface is well preserved, and the postzygapophyses are more robust compared to the condyle, indicating that the range of movement of this vertebra was shorter than those of AMNH 24445. Also, contrary to cervical vertebra VI of AMNH 24445, that of MN 4728-V has three pneumatic foramina adjacent to the neural canal in posterior view, one on each side and one above it.
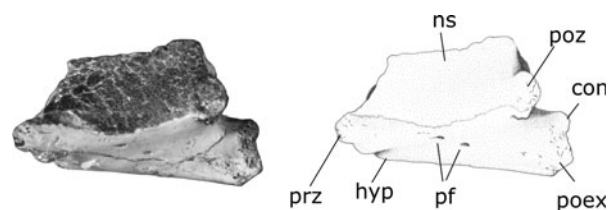

Figure 9.   MN 4728-V cervical vertebra V, showing neural spine, only partially preserved. Scale bar 10 mm.
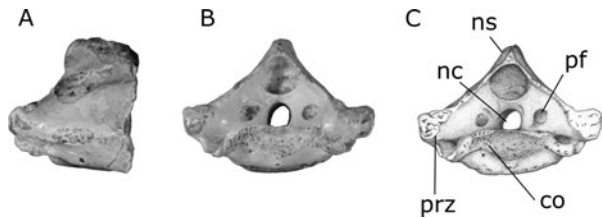
Figure 10. MN 4728-V cervical vertebra VII. (A) Left lateral view showing the preserved portion, reduced only to the anterior region. (B, C) Anterior view. The cotyle concave surface is almost completely preserved. Scale bar 10 mm.
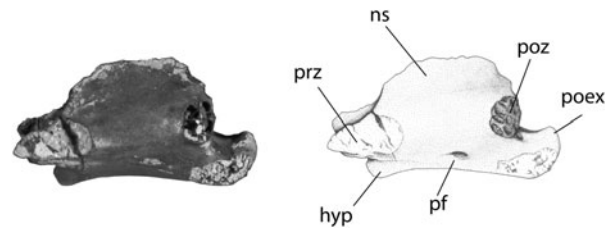

Figure 12. AMNH 24445 cervical vertebra IV in left lateral view. Notice the well-preserved prezygapophyses, showing an extensive articular projection, more oblique than the postzygapophysis. Scale bar 10 mm.

Only the anterior portion of cervical vertebra VII is preserved, with the cotyle surface almost intact (Figure 10 (A)). The prezygapophyses are present, but their articular surfaces were eroded. The prezygapophyses have the same morphology as those of the cervical vertebra VI, indicating a similar range of movement. In anterior view (Figure 10 (B),(C)), cervical vertebra VII has only two pneumatic foramina near the neural canal, one on each side. Yet, there is a depression above the canal, almost forming another foramen.

TAPEJARINAE Kellner and Campos, 2007
Tapejara cf. *Tapejara wellnhoferi* Kellner, 1989

Description and comparison

AMNH 24445 comprises three cervical vertebrae of a small pterosaur (Figure 11). It can be assigned to Tapejarinae due to the small size, elongated profile, hatchet-like low neural spine, and well-developed post-zygapophyses. The vertebrae are completely preserved and almost the same size as one another. Kellner (1995) defined the cervical length formula for *Tupuxuara* (a Thalassodrominae) as III < IV = V > VI > VII, and this appears to be the case in the preserved portion of AMNH 24445. Based on the comparison to AMNH 22568, they are probably cervical vertebrae IV–VI. Compared to the cervical vertebrae described by Eck et al. (2011), there are no anatomical or size differences, and therefore we tentatively assign AMNH 24445 to *Tapejara* cf. *Tapejara wellnhoferi*.

The neural spine of cervical vertebra IV is broken at the base, but stretches from the anterior portion of the centrum to the posterior margin, at the base of the postzygapophyses. This differ from the low, almost inexistent neural spine of Azhdarchidae such as *Azhdarcho* (Averianov 2010) or *Phosphatodraco* (Pereda-Suberbiola et al. 2003), and also from the Chaoyangopterinae pattern, which is as elongated as the tapejarinae cervical vertebrae, but with less pronounced neural spines. The postzygapophyses are extremely well developed, with dorsally oriented articulations. The anterior end of the centrum is partially eroded, which hampers the observation of the cotyle articular concavity. However, the prezygapophyses are well preserved, showing an extensive articular projection, more oblique than those of the postzygapophyses (Figure 12). This makes each cervical vertebrae to bend more than the previous. One foramen can be seen on either side, on the posterior portion of the centrum, somewhat close to the condyle, at a similar position as observed in the cervical vertebrae described by Eck et al. (2011). This is also seen on the following two vertebrae. These also share a well-developed condyle, enhancing the neck mobility, with the postexapophyses extending below the articulation surface. The hypapophysis is well developed, enhancing the ventral surface concavity and differing from the flat pattern observed on the previous specimens.

Cervical vertebra V is almost identical to the preceding one, with differences mostly due to the lack of preservation of a few structures, such as the neural spine and the cotyle. The pre- and postzygapophyses are smaller and less projected, suggesting an articulation not as limited as that of cervical vertebra IV. Cervical vertebra V is the only of AMNH 24445 with a third pneumatic foramen
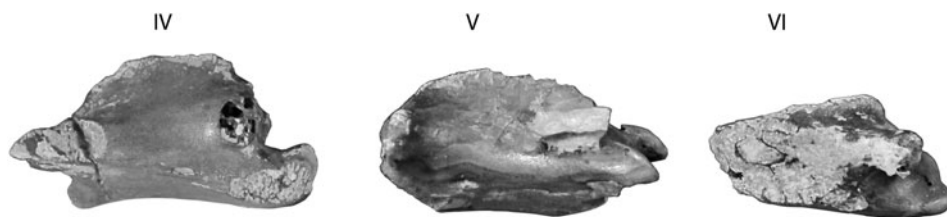

Figure 11. AMNH 24445 cervical series in left lateral view. Scale bar 10 mm.

above the neural canal, as seen in posterior view (Figure 13). The other vertebrae bear only two foramina, one on each side of the neural canal. This pattern differs from that of AMNH 22568, which has three pneumatic foramina surrounding the neural canal in cervical vertebrae V–VII.

Only the posterior portion of the last vertebra of AMNH 24445 is preserved (Figure 14). Its condyle is more developed and the postzygapophyses smaller than those of the preceding vertebrae. Cervical vertebra VI also shows a lateral pneumatic foramen on the posterior portion of the centrum, in a similar position as those of cervical vertebrae IV and V. There is also a feeble neural spine base, enhancing the similarity to the other vertebrae of the series. The left side is better preserved, but the centrum is incomplete.

Discussion

The presence of pneumatic foramina in the lateral surface of tapejarid centra has been reported before (e.g. Eck et al. 2011), and Averianov (2010) used the absence of such foramina as a diagnostic feature of *Azhdarcho*, following previous studies (Kellner 2003; Andres and Ji 2008; Costa et al. 2014). Among tapejarid specimens with the cervical series partially preserved, those of the holotype of *Sinopterus dongi* are badly crushed, hampering the observation of possible lateral foramina (Wang and Zhou 2003; Vila Nova, pers. obs.). A depression in the posterior region of the centrum of cervical vertebra VII of *Sinopterus dongi* can be inferred as a small foramen, as

also seen in cervical vertebra VI of AMNH 24445 and in one of the mesocervical vertebrae of *Tapejara wellnhoferi* (SMNK PAL 1137 – Eck et al. 2011). The presence or absence of pneumatic foramina has been used as a diagnostic trait for some pterosaur groups (Kellner 2003; Unwin 2003; Andres and Ji 2008). Eck et al. (2011) stated that some Tapejaridae lack pneumatic lateral openings, and that the presence of these elements should be used to diagnose *Tapejara wellnhoferi*. However, we here demonstrate that those foramina are more widespread within the group than previously thought. For clarity, we will refer to the pneumatic foramina surrounding the neural canal in anterior and posterior view as 'adjacent foramina', and those on the lateral surface of the neural centrum simply as 'lateral foramina'. Within this diversity, Thalassodrominae typically has two lateral foramina, while Tapejarinae has only one lateral foramen.

The neural spines of AMNH 22568 cervical vertebrae tend to become more robust towards the posterior end of the neck. This allows identifying the first cervical element of SMNK PAL 1137 (figure 4(f)–(j) of Eck et al. 2011) as probably cervical vertebra III or IV, whereas the second element (figure 4(k)–(o) of Eck et al. 2011) may correspond to cervical vertebra VI. In AMNH 22568, the neural spine of cervical vertebra VII is restricted to the centrum, as also seen in the holotype of *Sinopterus*, despite size differences. However, the overall anatomy of the cervical vertebrae of that holotype is more similar to AMNH 24445 cervical vertebrae.

The vertebral articular surfaces (pre-, postzygapophyses, hypapophyses and exapophyses) are well developed in all three specimens described in the present paper. It appears that, although they increase in size towards the posterior end in both groups, the hypapophyses of tapejarines are more pronounced than those of thalassodromines. This condition, associated with the centrum and postexapophyses shapes, creates a concave ventral surface in the Tapejarinae (Figure 15), although the postexapophyses remain the most ventral structure. In the Thalassodrominae the ventral surface is flat. The hypapohyses increase in size towards the posterior end of the series, reaching the largest size at cervical vertebra VII. As in the *Bakonydraco* cervical vertebrae described
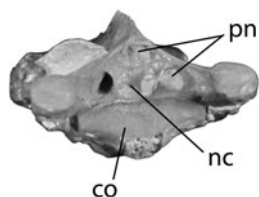

Figure 13. AMNH 24445 cervical vertebra V in anterior view. Notice the third pneumatic foramen above the neural canal. Scale bar 10 mm.

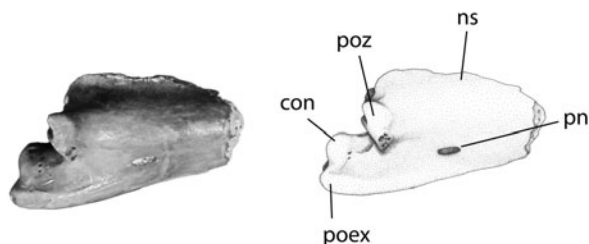Figure 14. AMNH 24445 cervical vertebra VI in right lateral view. Notice the lateral pneumatic foramen. Scale bar 10 mm.
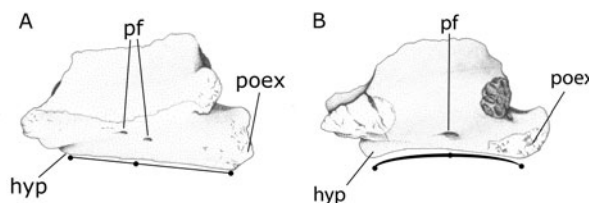

Figure 15. Tapejarids cervicals, showing the oblique straight ventral limit of Thalassodrominae (A) and the concave ventral limit of Tapejarinae (B).

by Ösi et al. (2005), the articular surfaces of the pre- and postzygapophyses in the vertebrae described here are not parallel. This feature is more evident in MN 4728-V and is also seen in other tapejarids such as in AMNH 22567 regarded as a Thalassodrominae indet (Aires et al. 2014) and *Tapejara wellnhoferi* (Eck et al. 2011). Given that this feature is not known in the Dsungaripteridae, we cannot assert if it is present in all Azhdarchoidea or only in the Tapejaridae and Azhdarchidae. Although the articular surfaces of the prezygapophyses face nearly dorsally, those of the postzygapohyses face posteroventrally, as in azhdarchids cervical vertebrae (e.g., Company et al. 1999; Pereda-Suberbiola et al. 2003). This pattern, allied with the posteriorly elongated postexapophyses, is regard to prevent the downward bending of the vertebral series, as was also inferred for *Azhdarcho* (Averianov 2013).

It is evident that the specimens described here fall into two different patterns of cervical vertebrae, one represented by AMNH 22568 and MN 4728-V and the second shown by AMNH 24445. They are all, however, more similar to one another than to the cervical vertebrae of the Anhangueria, a pterosaur group commonly found in the Araripe Basin (Vila Nova and Sayão 2012; Rodrigues and Kellner 2013), and of the Azhdarchidae, the sister-group of Tapejaridae (*sensu* Kellner 2003). The phylogenetic relationships of the Tapejaridae have been debated, with most authors favouring a close relationship with the Azhdarchidae (e.g. Kellner 2003; Andres and Ji 2008; Pinheiro et al. 2011; Wang et al. 2012; Andres et al. 2014) but others regarding *Tupuxuara* as closer to Azhdarchidae than to *Tapejara* (e.g. Unwin 2003; Martill and Naish 2006; Lü et al. 2008). This matter is even more complex, because another toothless pterosaur clade, the Chaoyangopteridae, was since described and regarded as a member of the Azhdarchoidea, but its relations to *Tapejara*, *Tupuxuara* and the Azhdarchidae was not resolved (Lü et al. 2008). Andres and Ji (2008) and Wang et al. (2012) regarded *Chaoyangopterus* and related species in sister group relationship with the Azhdarchidae, while Pinheiro et al. (2011) suggested that chaoyangopterids are part of the Tapejaridae. AMNH 22568 shows that the larger thalassodromines possess a robust neural spine, similar to those of tapejarines, and contrary to the condition in azhdarchids. This structure is partially preserved in the holotype of *Chaoyangopterus* (Wang and Zhou 2003), which also shows more elongated vertebrae than those of thalassodromines, and perhaps also tapejarines. The *Chaoyangopterus* cervical vertebrae possess long prezygapophyses, well-pronounced postexapophyses and large postzygapophyses. They also possess very low neural spines, and lack pneumatic foramina on the lateral surface of the centrum. These features match the cervical vertebrae of the Azhdarchidae, where the neural spines are even more reduced and separated into two short and low ridges confined to the anterior and posterior ends of the

neural arch (Nessov 1984; Averianov 2010). If confirmed, this cervical similarity hints into a close affinity between the Chaoyangopteridae and Azhdarchidae, instead of that between thalassodromines and azhdarchids, as proposed by Martill and Naish (2006), and that between chaoyangopterids and tapejarines, as proposed by Pinheiro et al. (2011).

Eoazhdarcho differs from tapejarids (including *Tapejara*, *Tupuxuara* and *Sinopterus*) in various features of the cervical vertebrae. The length/width ratio of the mesocervical elements is approximately 3.5 in *Eoazhdarcho* (Lü and Ji 2005), but approximately 1.0 in *Tupuxuara* (an almost square outline in dorsal view). The cervical vertebrae of *Tapejara* are similar, but slightly more elongated (Eck et al. 2011). These ratios are similar to those of MN 4728-V (cervical vertebrae V and VI) and AMNH 22568 (cervical vertebra VII). *Eoazhdarcho* is a member of Azhdarchidae, a group characterised by extremely elongated neck vertebra (Nessov 1984; Howse 1986; Wellnhofer 1991a; Kellner 2003; Ösi et al. 2005). Although somewhat elongated, cervical vertebrae of *Tapejara* are definitively not as elongated as those of azhdarchids.

In all mesocervical vertebrae described here, the prezygapophyses project anteriorly to the cotyle, and the postzygapophyses do not project posteriorly to the condyle, as reported in *Azhdarcho* (Averianov 2010). Averianov (2010) noted that in *Azhdarcho* the adjacent pneumatic foramina are subequal in size to the neural canal, the same ratio observed in the specimens described here. However, these are distinctly smaller in *Azhdarcho* when compared to the overall size of the vertebra, but the development of the adjacent pneumatic foramina in the cervical vertebrae of Azhdarchidae is regarded as being size related (Godfrey and Currie 2005; Averianov 2010).

The relative length of the *Azhdarcho* cervical vertebrae is the same as that of other short-necked pterodactyloids: I + II < III < IV < V > VI > VII > VIII > IX. The same cervical length formula was likely characteristic of all azhdarchids (Steel et al. 1997; Kellner 2010). This differs slightly from the pattern proposed by Kellner (1995) and observed in AMNH 24445: III < IV = V > VI > VII. It remains uncertain if the size differences from cervical IV to V is phylogeny related or mere stochastic variation.

Conclusions

Cladistic analyses of pterosaurs including azhdarchids, tapejarines, thalassodromines and chaoyangopterids have consistently nested them in a single clade, the Azhdarchoidea (Kellner 1995, 1996, 2003, 2004; Unwin 1996, 2003; Junchang and Unwin 1997; Wang et al. 2005; Lü et al. 2006). The cervical anatomy discussed here confirms these results, but no anatomical information is presently

known in the cervical series of those clades that allows confidently establish the relationships among them. In any case, this paper provides more information on the tapejarid cervical vertebrae, helping to establish the differences in morphology within the tapejarin and thalassodromin neck and with other derived pterodactyloids.

Disclosure statement

No potential conflict of interest was reported by the authors.

Notes

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