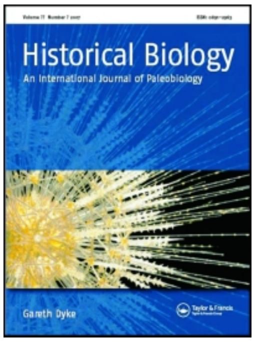

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Historical Biology
An International Journal of Paleobiology

ISSN: 0891-2963 (Print) 1029-2381 (Online) Journal homepage: http://www.tandfonline.com/loi/ghbi20

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To cite this article: Richard Buchmann, Taissa Rodrigues, Sabrina Polegario & Alexander W. A. Kellner (2018) New information on the postcranial skeleton of the Thalassodrominae (Pterosauria, Pterodactyloidea, Tapejaridae), Historical Biology, 30:8, 1139-1149, DOI: 10.1080/08912963.2017.1343314

To link to this article: https://doi.org/10.1080/08912963.2017.1343314

HISTORICAL BIOLOGY, 2018
VOL. 30, NO. 8, 1139–1149
https://doi.org/10.1080/08912963.2017.1343314

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New information on the postcranial skeleton of the Thalassodrominae (Pterosauria, Pterodactyloidea, Tapejaridae)

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ABSTRACT

The clade Tapejaridae is composed by pterosaurs commonly found in fossiliferous deposits in northeastern Brazil. It is constituted by two less inclusive clades: the smaller-bodied Tapejarinae and the larger Thalassodrominae. Here we describe the specimen MN 6566-V, from the Lower Cretaceous Romualdo Formation of the Araripe Basin, Brazil. The specimen is overall well preserved tridimensionally, and consists of three posterior cervical vertebrae, incomplete right and left scapulocoracoids, and the proximal portion of a right humerus. Comparisons to specimens described in the literature enable its identification as a thalassodromine, whose postcranial material is still poorly known despite the large amount of pterosaurs known from this unit.

ARTICLE HISTORY
Received 19 May 2017
Accepted 13 June 2017

KEYWORDS
Tapejaridae; Thalassodrominae; Romualdo Formation; Lower Cretaceous; Araripe Basin

Introduction

The Tapejaridae is a group of cosmopolitan pterosaurs, known from Cretaceous deposits in Brazil (Kellner 1989; Kellner and Campos 1994; Campos and Kellner 1997; Kellner and Campos 2002; Sayão and Kellner 2006; Eck et al. 2011; Kellner 2013; Aires et al. 2014; Manzig et al. 2014; Vila Nova et al. 2015), China (Wang and Zhou 2003a; Lü and Yuan 2005), Spain (Vullo et al. 2012), Hungary (Ősi et al. 2011; Andres et al. 2014), Morocco (Wellnhofer and Buffetaut 1999), and possibly also the United States (Kellner 2004) (but see Averianov 2014; who interprets the material from Hungary and Morocco as belonging to the Azhdarchidae). They are edentulous pterosaurs with, normally, large sagittal cranial crests. These pterosaurs belong in the more inclusive clade Azhdarchoidea. According to Kellner (2003), tapejarids are diagnosed by the confluent naris and nasoantorbital fenestra, which together make up for more than 45% of the skull length, and the presence of a premaxillary crest beginning at the anterior portion of the skull and extending posteriorly, over the occipital region.

Both the monophyly and the composition of the Tapejaridae are disputed. The clades Thalassodrominae (or Thalassodromidae), Tapejarinae, and Chaoyangopterinae (or Chaoyangopteridae) are normally recovered as monophyletic in the literature, but there are several, disparate proposals on their phylogenetic relationships to each other and to other pterosaurs, such as the Azhdarchidae and the Dsungaripteridae. Kellner (2003, 2004) found tapejarids to be the sister group of the Azhdarchidae, while Unwin (2003) recovered *Tapejara* as the sister group of *Tupuxuara* + Azhdarchidae, i.e. a paraphyletic Tapejaridae, a view that found support by Martill and Naish (2006), who also recovered a tree with a paraphyletic Tapejaridae with respect to the Azhdarchidae. The discovery and further recognition of a related clade, the Chaoyangopteridae, known mostly from Chinese deposits (Wang and Zhou 2003b; Lü et al. 2008) and allegedly one species from Brazil (Witton 2008), brought further discussion on their phylogenetic relationships. Analyses based mostly on Kellner's (2003) characters have consistently recovered tapejarines and thalassodromines as sister groups, closely related to a clade formed by chaoyangopterids and azhdarchids (Vullo et al. 2012; Wang et al. 2012; Aires et al. 2014; Manzig et al. 2014). Lü et al. (2008) presented an analysis largely based on Unwin's (2003) characters, and recovered either thalassodromines as a sister-group of azhdarchids, in a polytomy with tapejarines and chaoyangopterids (in an Adam Consensus tree), or thalassodromines and tapejarines as successive sister-groups of azhdarchids + chaoyangopterids (in a 50% majority-rule consensus tree). Other analyses recovered thalassodromines as a sister-group to tapejarines + chaoyangopterids (i.e. proposing that the Chaoyangopteridae should be considered a subfamily within the Tapejaridae; Pinheiro et al. 2011), or even thalassodromines + dsungaripterids as the sister-group of chaoyangopterids + azhdarchids, and tapejarines as the sister-group of this clade (Andres et al. 2014) (Figure 1). Such disparate proposals, besides methodological differences in the analyses, are mostly

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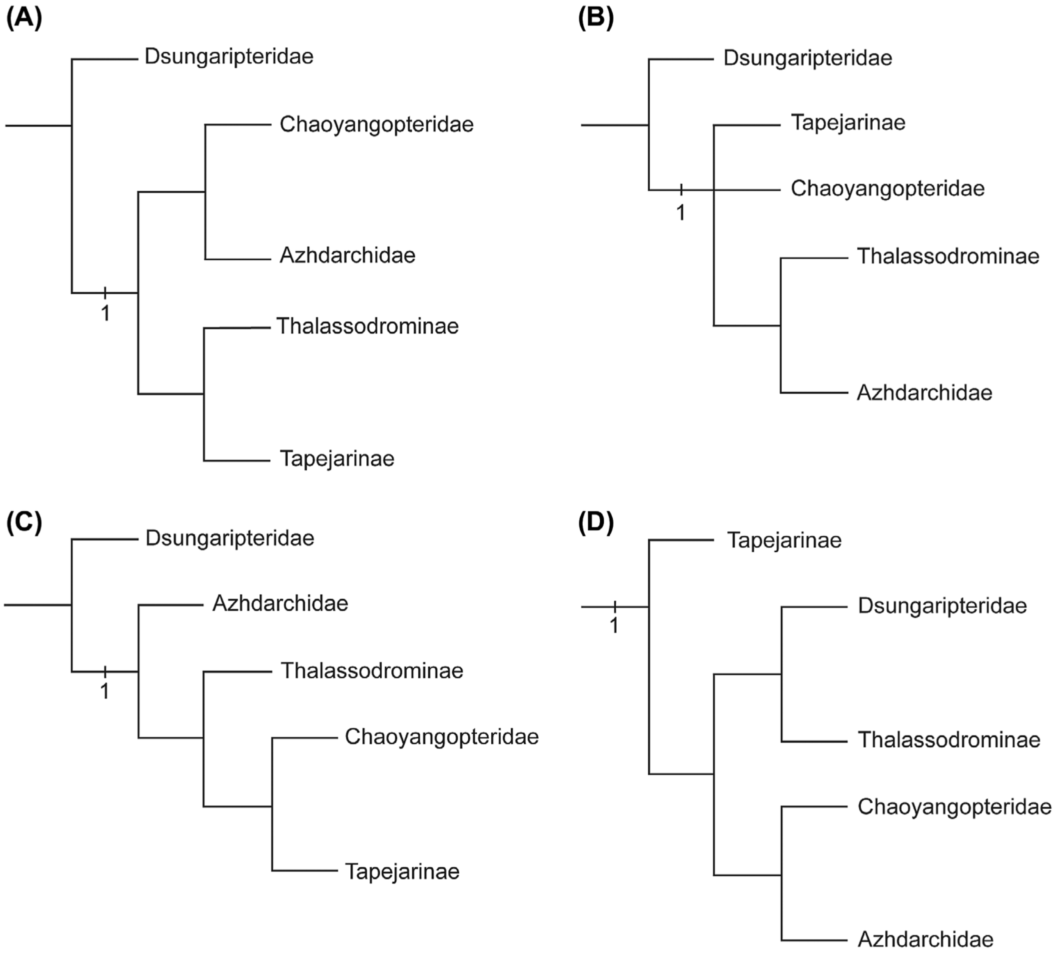

Figure 1. Most recent phylogenetic proposals of the ingroup relationships of the Azhdarchoidea. (A) Vullo et al. (2012); (B) Adams consensus tree from Lü et al. (2008); (C) Pinheiro et al. (2011); (D) Andres et al. (2014). 1. Clade Azhdarchoidea *sensu* Kellner (2003).

due to the incompleteness of several fossils, including the ones from the Romualdo and Crato formations, which are known mostly by skull material. As a discussion on this matter is beyond the scope of the present work, the taxonomy presented by Kellner and Campos (2007) is followed.

Among the tapejarids known from the Romualdo Formation, thalassodromines are comparatively larger than tapejarines, and are represented by two genera typical from this deposit, *Tupuxuara* and *Thalassodromeus* (Kellner & Campos 2007). Postcranial material attributed to Thalassodrominae is not unknown but is nonetheless scarce; therefore the description of new material can contribute to the clarification of the phylogenetic position of the group. Here, we describe a specimen (MN 6566-V) referable to the clade consisting of three cervical vertebrae, two partial scapulocoracoids, and a partial humerus.

Institutional abbreviations

AMNH, American Museum Natural History, New York, USA; CMN, Canadian Museum of Nature, Ottawa, Canada; MN, Museu Nacional / Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; NSM, National Science Museum, Tokyo, Japan; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany.

Anatomical abbreviations

con, condyle; cor, coracoid; cot, cotyle; dpc, deltopectoral crest of the humerus; fopn, foramen pneumaticum; fotr, foramen transversarium; glfo, glenoid fossa; hyp, hypapophysis; mus, muscle scar; nc, neural canal; ns, neural spine; poex, postexapophysis; poz, postzygapophysis; prcor, coracoid process; prsca, scapular process; prz, prezygapophysis; sca, scapula; sglpr, supraglenoid process; tpr, transverse process; tucor, coracoid tuberculum; uc, ulnar crest of the humerus.

Geological setting

The Santana Group pertains to the Araripe Basin, which crops out in the Brazilian northeast, between the states of Ceará, Pernambuco and Piauí (Neumann and Cabrera 1999; Assine 2007). It is divided in three formations, named, from bottom to top, Crato, Ipubi and Romualdo. The Crato and Romualdo Formations stand out for their fossiliferous richness, being Aptian-Albian in age (see Kellner et al. 2013 for a discussion of nomenclatural issues).

The material herein described comes from the Romualdo Formation, which is composed of shales, marls and limestones (Assine 2007). In the shales, carbonate concretions containing well-preserved fossils are observed, normally in three dimensions.

Table 1. Dimensions presented by the cervical vertebrae of MN 6566-V.

	Centrum length in mm (zygapophyses excluded)	Centrum width at mid-length in mm	Length:width ratio
Cervical vertebra VII	52.2	37.6	1,4
Cervical vertebra VIII	27.4	36.7	0,7
Cervical vertebra IX	25.8	?	?

From these, marine fishes are found in abundance, and pterosaurs figure as the most common tetrapods (Maisey 1991).

Systematic paleontology

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Azhdarchoidea Nessov, 1984
Tapejaridae Kellner, 1989
Thalassodrominae Kellner & Campos, 2007

Material

Specimen MN 6566-V consists of three posterior cervical vertebrae, identified as the seventh, eighth, and ninth; both incomplete, fused scapulocoracoids; and the proximal portion of a right humerus. The material was enclosed in calcareous concretions and suffered mostly from erosion, but vertebra IX was also weakened due to preparation in acid. The material is curated at the paleovertebrate collection of the Museu Nacional/UFRJ, Rio de Janeiro, Brazil.

Description and comparison

Cervical vertebrae

The three vertebrae found in specimen MN 6566-V are consistent with the last three cervicals (VII, VIII and IX), based on morphological comparison to vertebral sequences already described in the literature (Wellnhofer 1991; Bennett 2001; Aires et al. 2014; Vila Nova et al. 2015), with the posteriormost cervicals (VIII and IX) presenting morphology similar to dorsal vertebrae, while cervical VII resembles the mid-cervical pattern, as observed in pteranodontoids (Wellnhofer 1991; Bennett 2001) and other thalassodromines (Aires et al. 2014; Vila Nova et al. 2015). The material shows a VII > VIII > IX centrum length pattern (Table 1), similarly to other azhdarchoid cervicals (Averianov 2010; Aires et al. 2014; Vila Nova et al. 2015).

Cervical VII is 52.22 mm long. Part of the bone surface on the right side of the vertebra is broken off, revealing the matrix and the inner trabeculae, but the left side is better preserved (Figure 2). Anteriorly, the cortex of the cotyle is broken off, but its overall shape can be observed. It is considerably compressed dorsoventrally, with a convex dorsal margin and a concave ventral margin, which is divided in the middle by a blunt hypapophysis. Two lateral pneumatic foramina (sensu Vila Nova et al. 2015) are observed on the left side of the centrum, and while only one is visible on the right side, this difference in this specimen is likely due to the breakage in this region. The lateral pneumatic foramina present on the right side is 11.8 mm long, while the equivalent on the left side is 10.2 mm. The articular condyle has lost most of its outer surface. It is short and projected posteriorly, forming a convex surface, resulting in a procoelous centrum, as common in pterosaur vertebrae. Anteriorly, three adjacent pneumatic foramina (sensu Vila Nova et al. 2015) are present around the neural canal: one dorsally and two laterally, similar to the condition seen in Azhdarchidae and Thalassodrominae (Averianov 2010; Rodrigues et al. 2011; Aires et al. 2014; Vila Nova et al. 2015). Regarding the prezygapophyses, the left articular surface is broken but the right one is well preserved. The prezygapophyses are located anterolaterally in the vertebra and are divergent from one another. The articular surfaces face medially. The transverse foramina are present just below the prezygapophyses. There is a small prezygapophyseal turbercle ventrally to each transverse foramen, which probably represents a vestige of a cervical rib shaft, as described previously in azhdarchid and thalassodrominae material (i.e. Company et al. 1999; Pereda Superbiola et al. 2003; Averianov 2010; Rodrigues et al. 2011; Vila Nova et al. 2015). The posterior portion of the vertebra is not as well preserved as the anterior, and several parts of the bone cortex are missing, so the neural canal can be observed, but it is not clear if there were adjacent pneumatic foramina surrounding it. Among the postzygapophyses, the right one is better preserved. They are directed caudolaterally, are also divergent in relation to one another. The postzygapophyses are positioned much more dorsally than the prezygapophyses, as observed in *Tapejara wellnhoferi* (SMNK PAL 1137; Eck et al. 2011) and in other thalassodromines (AMNH 22567, 22568; Aires et al. 2014; Vila Nova et al. 2015). The postexapophyses form a concave ventrocaudal margin between them, extending posterolaterally relative to the condyle, as is observed in other thalassodromine mid-cervicals (Aires et al. 2014; Vila Nova et al. 2015). The neural spine is well preserved, except for a breakage in the posterior region. The spine is tall, blade-like, and laterally compressed, as seen in other specimens referred to the Tapejaridae (Eck et al. 2011; Aires et al. 2014; Vila Nova et al. 2015).

Cervical VIII is better preserved than the preceding one. Differently from the preceding vertebra, the centrum is reduced in relation to the neural arch and the neural spine is taller (Figure 3). The centrum is 27.39 mm long and 36.72 mm wide, thus much shorter than cervical VII. The cotyle is saddle-shaped and is less expanded than in the preceding vertebra, and has a shallow dorsal depression. The hypapophysis is short and blunt. On left side of the centrum, two lateral pneumatic foramina are observed, as in other thalassodromine vertebrae (Vila Nova et al. 2015). However, on the right side, these structures appear to be much reduced. The condyle, which lost its outer cortex, is posteriorly expanded and slightly dorsoventrally compressed. The right postexapophysis has a dorsolaterally directed articular surface. Anteriorly, the neural canal is well defined, but as the bone surface around it has been broken off, it is not possible to point out adjacent pneumatic foramina with certainty. However, the visible inner structure of the vertebra reveals that it is highly pneumatized. The right prezygapophysis is damaged, but the left one is well preserved and shows a smooth, oval articular surface that faces dorsomedially. The prezygapophyses are slightly smaller than in the preceding vertebra. The transverse foramina are well preserved, located ventrally to the prezygapophyses. Both present a small prezygapophyseal tubercle beneath it, as also seen in cervical VII. In posterior view, the neural canal can be

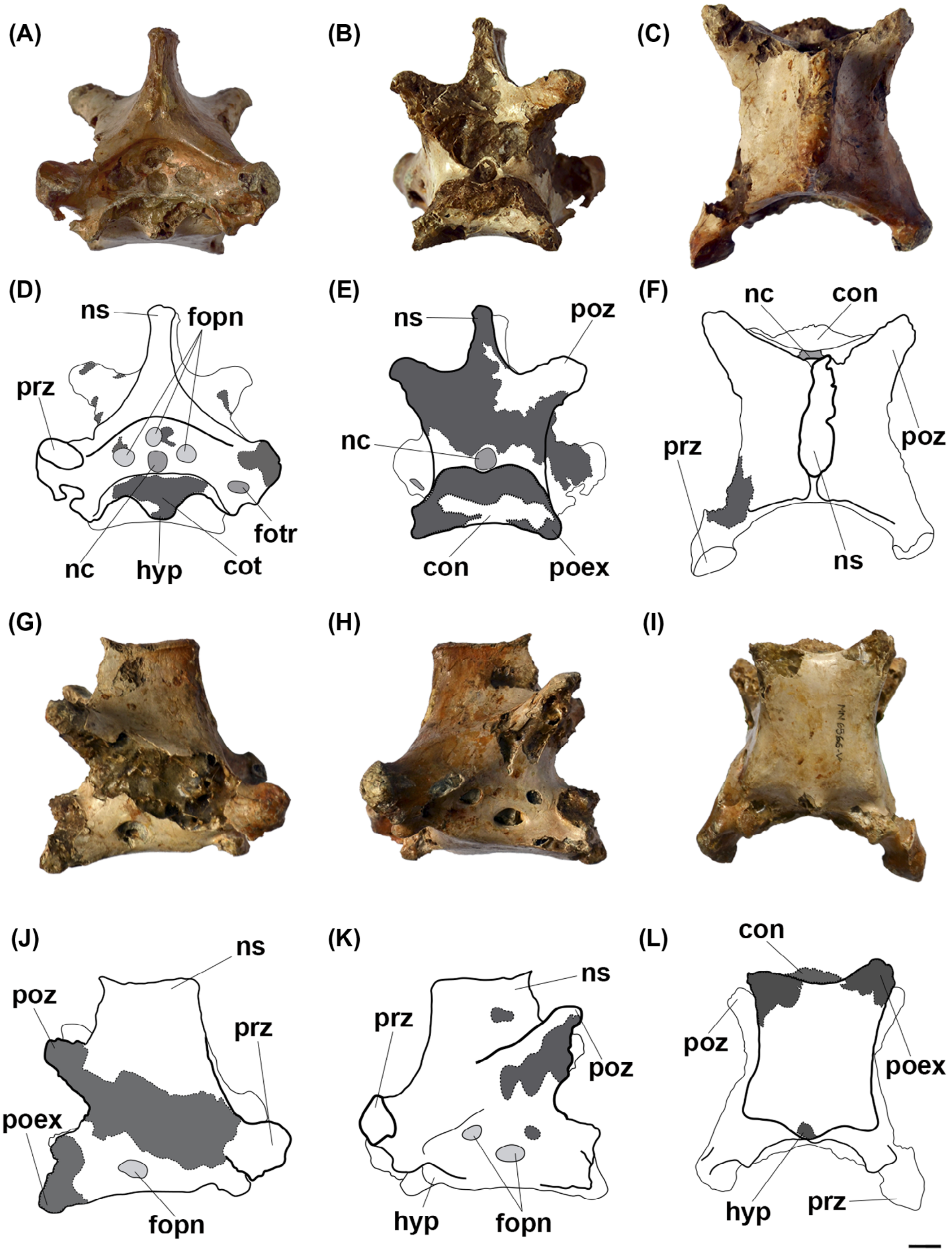

Figure 2. MN 6566-V, cervical vertebra VII. Photographs and interpretative drawings in (A, D) anterior, (B, E) posterior, (C, F) dorsal, (G, J) right lateral, (H, K) left lateral, and (I, L) ventral views. Breakages are in dark grey.
Note: Scale bar: 10 mm.

observed, but no adjacent pneumatic foramina are present, thus differing from other thalassodromine material (Aires et al. 2014; Vila Nova et al. 2015). There is a comparatively large, median pneumatic foramen, located dorsally, between the transverse processes, not seen in other thalassodromines (Aires et al. 2014; Vila Nova et al. 2015). The postzygapophyses are well preserved and show smooth articular surfaces, facing ventrolaterally. A possible pneumatic foramen is observed on the base of the right postzygapophysis. Dorsally to the postzygapophyses, the transverse processes are well developed, horn-shaped and divergent from one another.

Cervical IX is the smallest preserved vertebra from this sequence, and it is not well preserved. Its general morphology is also similar to a typical dorsal vertebra, with a centrum shorter than that of the preceding ones. In general, significant parts of the bone cortex are lost, enabling the view of the interior part of

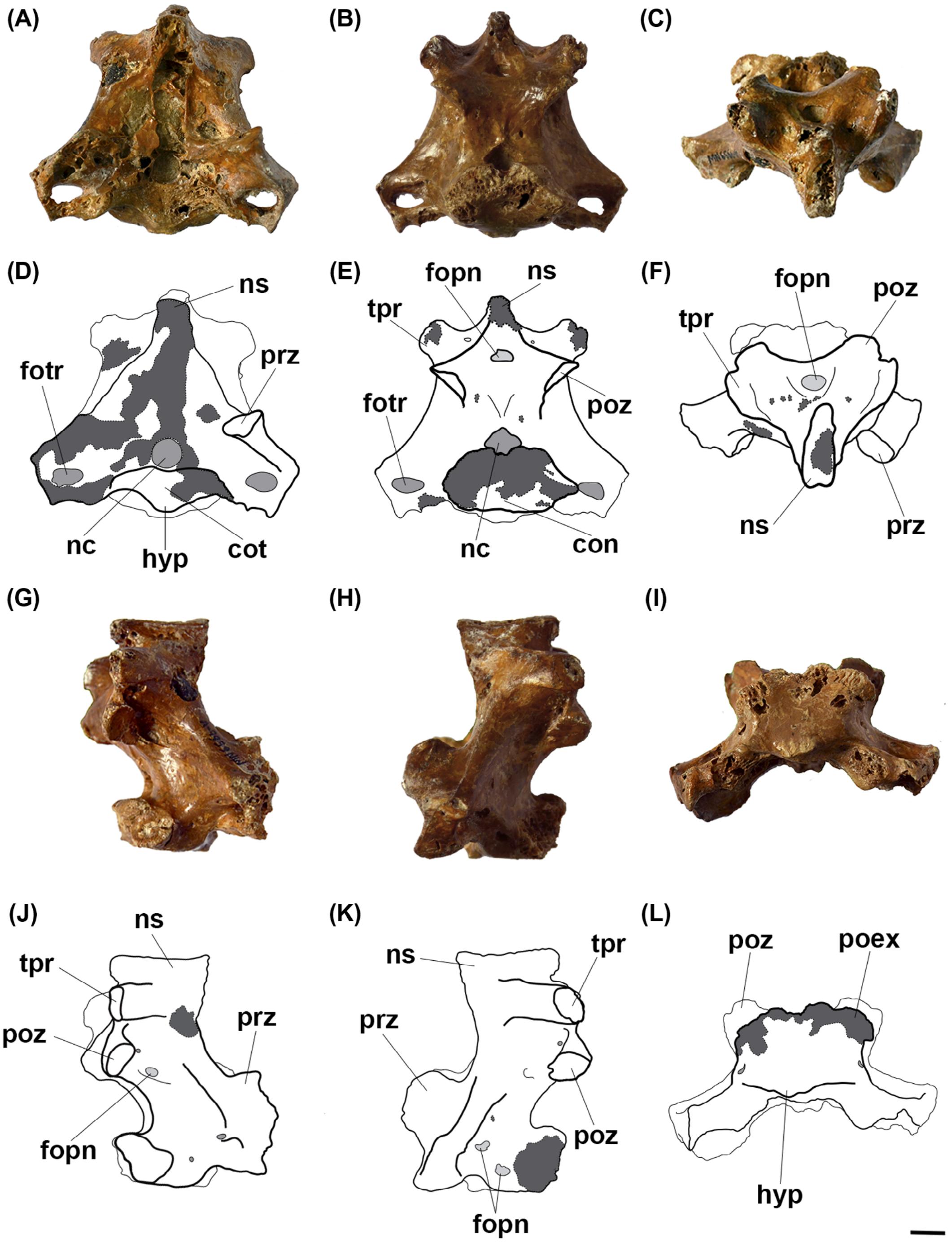

Figure 3. MN 6566-V, cervical vertebra VIII. Photographs and interpretative drawings (A, D) anterior, (B, E) posterior, (C, F) dorsal, (G, J) right lateral, (H, K) left lateral, and (I, L) ventral views. Breakages are in dark grey.
Note: Scale bar: 10 mm.

the vertebra, which possesses several extremely thin trabeculae (Figure 4). The cotyle is quite broken, but a slightly concave margin is observed. The region where the hypapophysis would be present was almost entirely lost. There is a small right lateral foramen on the centrum; on the left side the cortical surface is missing so the foramen cannot be seen. The condyle is less expanded than in the preceding vertebrae, and the postexapophyses are blunt. Anteriorly, there is a large neural canal, with one large adjacent pneumatic foramen on each side, as seen in other thalassodromine material (Vila Nova et al. 2015). The right prezygapophysis is directed anterolaterally. No postzygapophyses are preserved.

Scapulocoracoids

Both scapulocoracoids are fused, indicating at least the beginning of osteological maturity (Bennett 1993), referable to the ontogenetic stage 4 (OS4) of Kellner (2015). With the fusion, this structure takes roughly the form of a ‘U’, a common shape in pterosaurs. The right scapulocoracoid is more complete than the left one (Figure 5). As preserved, the coracoid is larger than the scapula (Table 2), but as both ends are missing, exact measurements cannot be taken and this proportion might be different if the bones were complete. The left scapulocoracoid has a comparatively large oval pneumatic foramen at the base of the

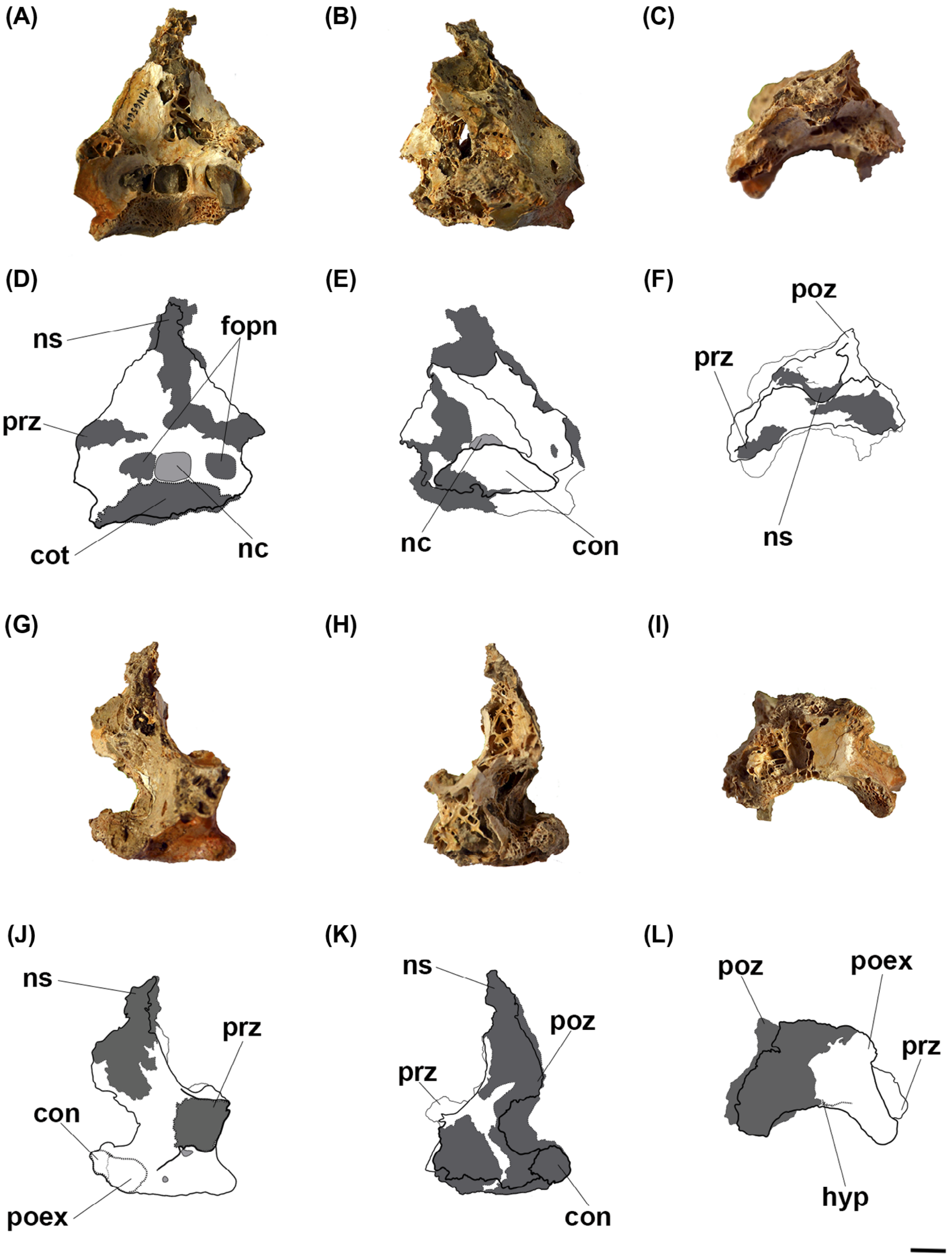

Figure 4. MN 6566-V, cervical vertebra IX. Photographs and interpretative drawings in (A, D) anterior, (B, E) posterior, (C, F) dorsal, (G, J) right lateral, (H, K) left lateral, and (I, L) ventral views. Breakages are in dark grey.
Note: Scale bar: 10 mm.

coracoid process and next to the glenoid fossa (Figure 6). Such foramen is also observed in the anhanguerid *Anhanguera piscator* (NSM-PV 19892; Kellner & Tomida 2000) and the tapejarine *Caupedactylus ybaka* (MN 4726-V; Kellner 2013). The glenoid fossa is well developed and is bound by the coracoidal and supraglenoidal processes. In medial view, there is a large, elongate pneumatic foramen on the suture between scapula and coracoid, similarly to that observed in other dsungaripteroid pterosaurs, such as the anhanguerid *Tropeognathus* cf. *T. mesembrinus* (MN 6594-V; Kellner et al. 2013), the azhdarchid *Montanazhdarcho minor* (McGowen et al. 2002) and the tapejarine *Caupedactylus ybaka* (Kellner 2013).

In the scapula, the supraglenoid process is similar to that seen in other tapejarids (Kellner 2013; Aires et al. 2014). The scapular process is smaller than in *Anhanguera piscator* (Kellner & Tomida 2000), more similar to a ridge, as in the tapejarines *Tapejara wellnhoferi* (Eck et al. 2011) and *Caupedactylus ybaka* (Kellner 2013) and in another thalassodromine specimen (Aires et al. 2014).

In the coracoid, a large coracoidal tubercle is present on its proximal portion. The tubercle is notably more developed

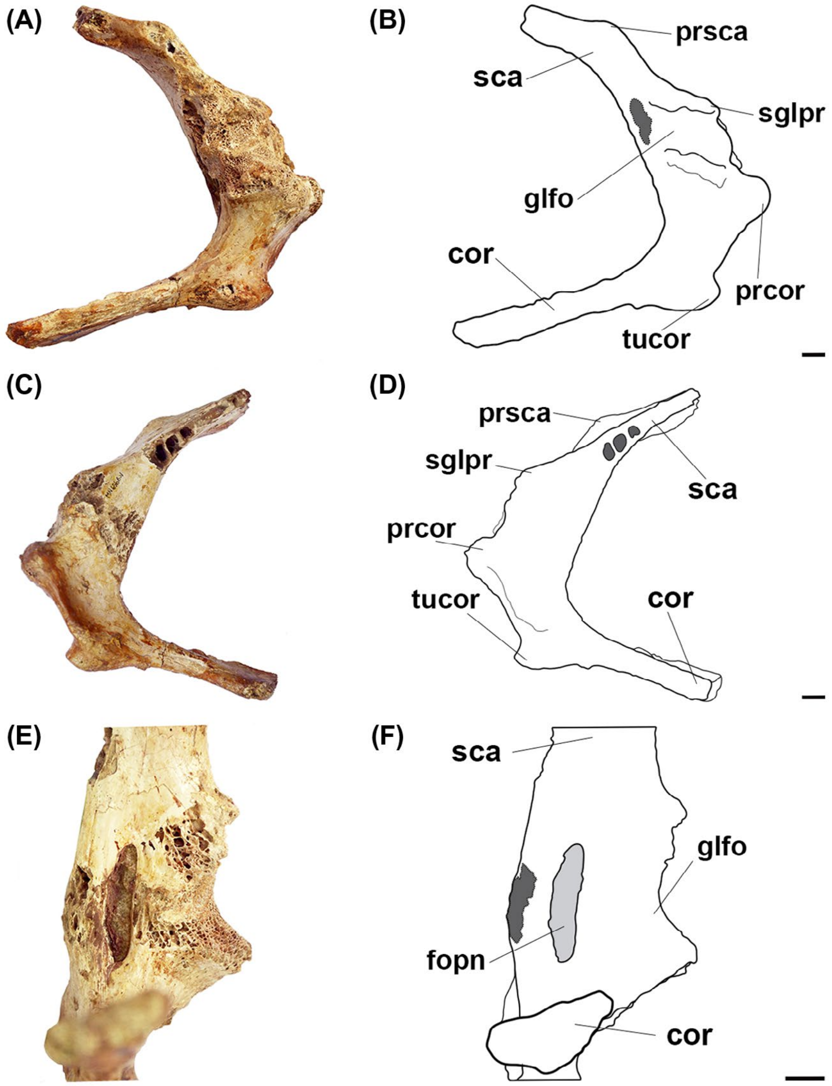

Figure 5. MN 6566-V, right scapulocoracoid. Photographs and interpretative drawings in (A, B) posterior, (C, D) anterior, and (E, F) medial views. Breakages are in dark grey. Note: Scale bar: 10 mm.

Table 2. Dimensions presented by the right scapulocoracoid of MN 6566-V.

	Length in mm (as preserved)
Scapula	>103.4
Coracoid	>138.1

than in *Anhanguera piscator* (Kellner & Tomida 2000) and its shape is similar to that seen in other tapejarids, such as *Tapejara wellnhoferi* (Eck et al. 2011), *Caupedactylus ybaka* (Kellner 2013) and an unidentified thalassodromine (Aires et al. 2014). The coracoid process is blunt and well developed, but smaller than in *Anhanguera piscator* (Kellner & Tomida 2000), again being more similar to *Caupedactylus ybaka* (Kellner 2013) and to AMNH 22567 (Aires et al. 2014).

Humerus

The right humerus is well preserved, but presents only the proximal portion (Figure 7). It is broken off in the diaphysis, revealing a circular cross-section. The humeral head is saddle-shaped, as usual in pterosaurs. There is a large, ventral pneumatic foramen, located between the humeral head and the deltopectoral crest, as seen in other azhdarchoids (Averianov 2010; Eck et al. 2011; Rodrigues et al. 2011; Kellner 2013; Aires et al. 2014). On the humeral shaft, there is a well-developed muscle scar, as also seen in a specimen referred to the Azhdarchidae (CMN 50814; Rodrigues et al. 2011).

About half of the deltopectoral crest is preserved; it is placed proximally and gently curves ventrally. The ulnar crest is comparatively large and massive. These features are similar to what is observed in other azhdarchoids, such as thalassodromines (Aires et al. 2014), tapejarines (e.g. *Caupedactylus*, *Tapejara*; Eck et al. 2011; Kellner 2013), and azhdarchids (such as *Quetzalcoatlus*; casts MN 4715-V; MN 6952-V).

Discussion

MN 6566-V can be confidently identified as a pterodactyloid pterosaur. Howse (1986), and posteriorly Kellner (2003), lists the absence of ribs in the mid-cervical vertebrae as one of the synapomorphies of the Pterodactyloidea, and they are found as

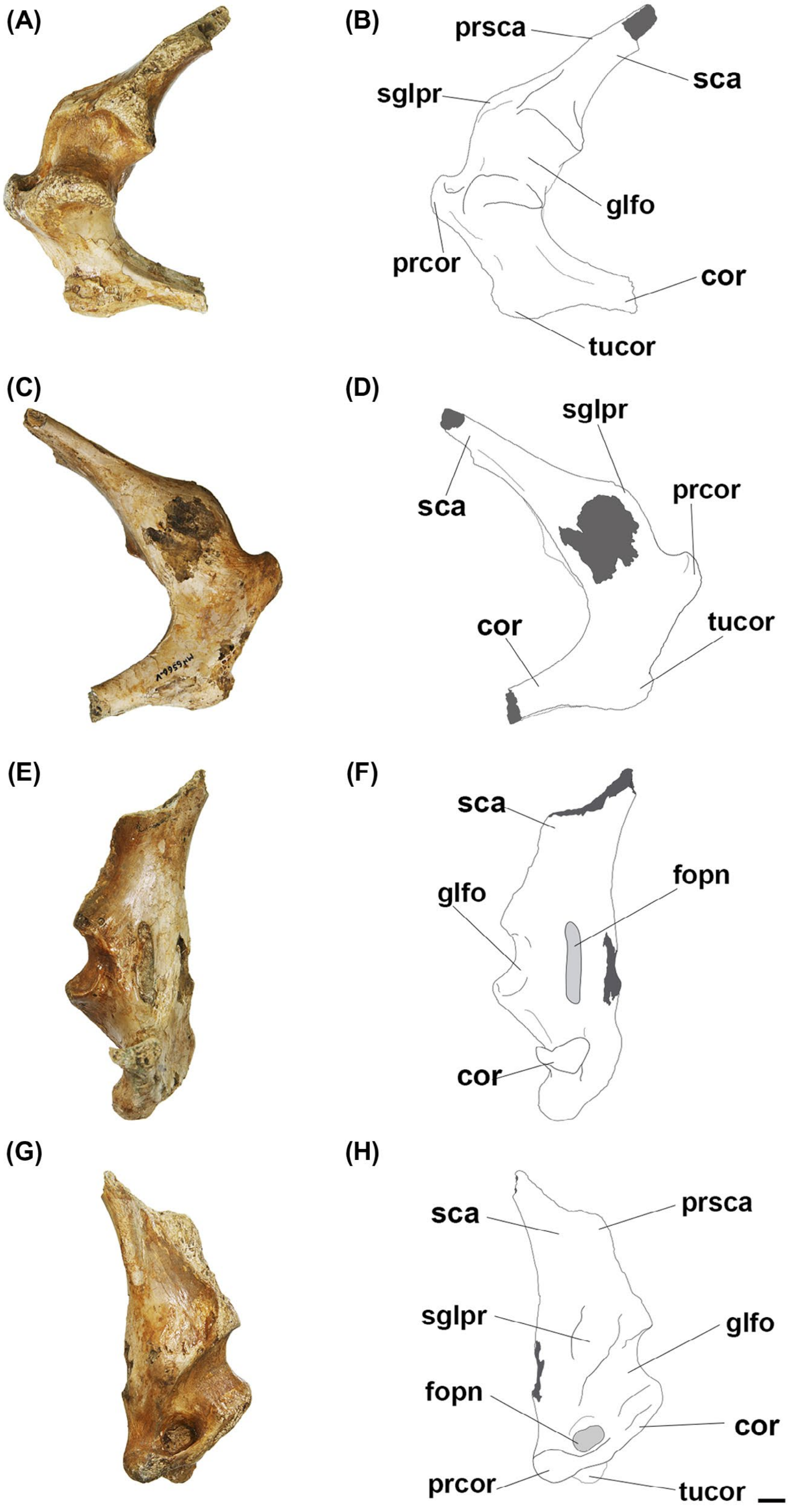

Figure 6. MN 6566-V, left scapulocoracoid. Photographs and interpretative drawings in (A, B) posterior, (C, D) anterior, (E, F) medial, and (G, H) lateral views. Breakages are in dark grey.
Note: Scale bar: 10 mm.

vestigial structures in a few specimens, such as in the seventh and eighth cervical vertebrae of MN 6566-V. In the humerus, the long, proximally located and ventrally curved deltopectoral crest is also considered a synapomorphy of the Pterodactyloidea (Kellner 2003). Among pterodactyloids, the presence of postexapophyses in the cervical vertebrae and the presence of a proximal pneumatic foramen on the humerus, both observed in MN 6566-V, are synapomorphies of the less inclusive clade

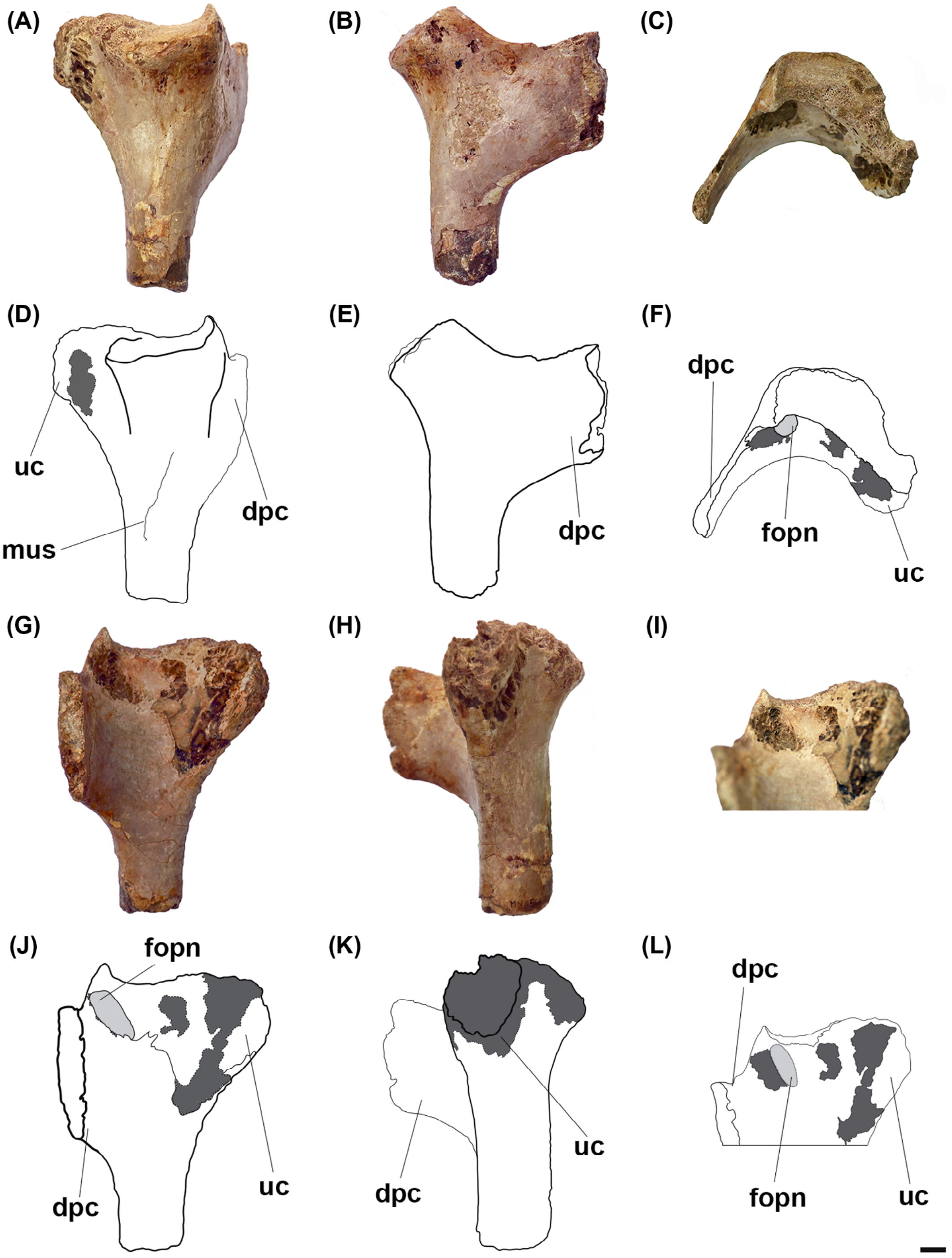

Figure 7. MN 6566-V, right humerus. Photographs and interpretative drawings in (A, D) dorsal, (B, E) lateral, (C, F) proximal, (G, J) ventral, (H, K) and medial views, and (I, L) detail of the pneumatic foramen. Breakages are in dark grey.
Note: Scale bar: 10 mm.

Dsungaripteroidea. As the Romualdo Formation pterosaurs can be roughly divided in pteranodontoids and azhdarchoids, the discussion below will focus mostly on these two dsungaripteroid clades.

In the scapulocoracoid, the presence of a broad and well-developed coracoidal tubercle, as observed in MN 6566-V, is considered a synapomorphy of the Tapejaridae (Kellner 2004). Regarding the humerus, the deltopectoral crest differs drastically from the warped shape seen in the Pteranodontoidea (Kellner and Tomida 2000; Bennett 2001), which can thus be excluded. The massive medial crest, with a developed proximal ridge, is a synapomorphy of the Tapejaroidea (Kellner 2003), and the shape of the deltopectoral crest observed in this specimen is similar to the morphology present in the Azhdarchoidea (Averianov 2010; Eck et al. 2011; Kellner 2013; Aires et al. 2014). A pneumatic foramen present ventrally, between the humeral head and the deltopectoral crest, is also observed in other azhdarchoids (Averianov 2010; Eck et al. 2011; Rodrigues et al. 2011; Aires et al. 2014), although in *Tapejara wellnhoferi* it is observed both dorsally and ventrally (Eck et al. 2011). Again, it differs from the condition seen in the pteranodontoid *Anhanguera*, in which the pneumatic foramen lies dorsally on the proximal part of the humerus (Kellner 2003).

The cervical vertebrae can be used to provide a more precise identification of the taxon to which the material belongs. The three adjacent pneumatic foramina bordering dorsally and laterally the neural canal, observed in cervical VII in anterior view, are commonly seen in dsungaripteroid mid-cervicals (Nessov 1984; Wellnhofer 1991; Kellner and Tomida 2000; Bennett 2001; Averianov 2010; Eck et al. 2011; Rodrigues et al. 2011; Aires et al. 2014; Vila Nova et al. 2015) and thus this character is not diagnostic of any clade in particular. The presence of lateral pneumatic foramina on the centrum in mid-cervicals has been previously considered a synapomorphy of the Ornithocheiroidea (Kellner 2003), and Vila Nova and colleagues (2015) have argued that they can be used to differentiate azhdarchoid taxa: in the Azhdarchidae and the Chaoyangopteridae there are no lateral pneumatic foramina on the centrum, while in Tapejarinae there is one foramen on each side and in the Thalassodrominae, two. In this respect, MN 6566-V can be referred to the latter.

The neural spines of the mid-cervicals are also diagnostic. In the Anhangueridae, they are tall and spike-like (Wellnhofer 1991; Kellner and Tomida 2000), while in the Azhdarchidae they are very reduced to absent (Averianov 2010), thus differing from the laminar neural spine observed in MN 6566-V, which is consistent with the tapejarid condition (Eck et al. 2011; Aires et al. 2014; Vila Nova et al. 2015). Vila Nova et al. (2015) pointed out that in the Chaoyangopteridae the neural spines are lower than in the Thalassodrominae and, in particular, Aires et al. (2014) discussed that in the latter the neural spine of the mid-cervicals is laterally flat and with a slight posterior curvature, a character named 'hatched-shaped' by Vila Nova et al. (2015). This is consistent with the observed condition in the specimen here described, although the posteriormost part of the neural spine of cervical VII is broken off.

Another potential difference pointed out by Vila Nova et al. (2015: Fig. 15) resides in the ventral margin of the mid-cervicals, when seen in lateral view. In the Tapejarinae, the hypapophysis is well-developed, giving the ventral margin of the vertebra a gentle curve; in the Thalassodrominae, the hypapophysis is short, so this margin is straight. The latter in seen in MN 6566-V.

The size of the vertebrae here described is consistent with other material referred to the Thalassodrominae (Aires et al. 2014; Vila Nova et al. 2015), being substantially larger than in the Tapejarinae (Eck et al. 2011). The length to width ratio of cervical VII (a mid-cervical), 1.4, is more similar to the Thalassodrominae than to the Tapejarinae (Vila Nova et al. 2015). The Azhdarchidae are readily discernible for the very elongate centra (Averianov 2010; Rodrigues et al. 2011) and, while postcranial material of the Chaoyangopteridae still needs more detailed descriptions, the mid-cervicals are also more elongate than in MN 6566-V (e.g. *Chaoyangopterus*; Wang & Zhou 2003b).

However, MN 6566-V presents two features so far unique among known thalassodromine specimens, both present in cervical VIII: the presence of a pneumatic foramen dorsally, between the postzygapophyses, and the lack of pneumatic foramina adjacent to the neural canal in posterior view. Such differences in the pneumatization suggest that it might represent a different taxon from the material that has been described previously (Aires et al. 2014; Vila Nova et al. 2015) or argue for individual variations in the vertebral pneumatization.

Conclusion

Specimen MN 6566-V is composed by cervical vertebrae VII, VIII, and IX, both incomplete scapulocoracoids, and part of the right humerus. The fused scapulae and coracoids demonstrate that this is an individual that had at least began its osteological maturity and can be referred to the ontogenetic stage 4 of Kellner (2015), and all of these bones present features consistent with the Thalassodrominae. This specimen also confirms earlier observations made on the diagnostic value of cervical vertebrae for the distinction of clades within the geographically widespread Azhdarchoidea. Within the pterosaurs from the Romualdo Formation, the Thalassodrominae are easily recognisable for the much larger size when in comparison to the Tapejarinae, and the size of the bones here described are consistent with a large pterosaur.

Acknowledgements

We would like to thank Dr. Luciana Carvalho (Museu Nacional/UFRJ) for the availability of receiving us in the collection. Dr. Leonardo Avilla (UNIRIO) and Dr. Lázaro Laut (UNIRIO) are thanked for hosting RB in their laboratories in Rio de Janeiro. Dr. Bruno Vila Nova and an anonymous reviewer made valuable comments on the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico [grant number #304780/2013-8 to AWAK]; Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro [FAPERJ #E-26/202.893/2015 to AWAK]; and Fundação de Amparo à Pesquisa e Inovação do Espírito Santo [grant number #52986870/2011 to TR].

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References

Aires ASS, Kellner AWA, Müller RT, Da Silva LR, Pacheco CP, Dias-Da-Silva S. 2014. New postcranial elements of the Thalassodrominae (Pterodactyloidea, Tapejaridae) from the Romualdo Formation (Aptian-Albian), Santana Group, Araripe Basin, Brazil. Palaeontology 57:343–355.

Andres B, Clark JM, Xu X. 2014. The earliest pterodactyloid and the origin of the group. Curr Biol. 24:1–6.

Assine ML. 2007. Bacia do Araripe [Araripe Basin]. Boletim de Geociências da Petrobras 15:371–389. Portuguese.

Averianov AO. 2010. The osteology of *Azhdarcho lancicollis* Nessov, 1984 (Pterosauria, Azhdarchidae) from the Late Cretaceous of Uzbekistan. Proc Zool Inst RAS. 314(3):264–317.

Averianov A. 2014. Review of taxonomy, geographic distribution, and paleoenvironments of Azhdarchidae (Pterosauria). ZooKeys 432:1–107.

Bennett SC. 1993. The ontogeny of *Pteranodon* and other pterosaurs. Paleobiology 19:92–106.

Bennett SC. 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Paleontogr Abt A. 260:1–112.

Campos DA, Kellner AWA. 1997. Short note on the first occurrence of Tapejaridae in the Crato Member (Aptian), Santana Formation, Araripe Basin, Northeast Brazil. An Acad Bras Ciênc. 69:83–87.

Company J, Ruiz-Omeñaca JI, Pereda Superbiola X. 1999. A long-necked pterosaur (Pterodactyloidea, Azhdarchidae) from the Upper Cretaceous of Valencia, Spain. Geol Mijnbouw. 78:319–333.

Eck K, Elgin RA, Frey E. 2011. On the osteology of *Tapejara wellnhoferi* Kellner 1989 and the first occurrence of a multiple specimen assemblage from the Santana Formation, Araripe Basin, NE-Brazil. Swiss J of Palaeontol. 130:277–296.

Howse SCB. 1986. On the cervical vertebrae of the Pterodactyloidea (Reptilia: Archosauria). Zool J Linn Soc. 88:307–328.

Kaup JJ, 1834. Versuch einer Einteilung der Saugethiere in 6 Stämme und der Amphibien in 6 Ordnungen. [An attempt to classify the mammals in 6 phyla and the amphibians in 6 orders.] Isis 3:311–315. German.

Kellner AWA. 1989. A new edentate pterosaur of the Lower Cretaceous from the Araripe Basin, Northeast Brazil. An Acad Bras Ciênc. 61(4):439–445.

Kellner AWA. 2003. Pterosaur phylogeny and comments on the evolutionary history of the group. London: Geol Soc Spec Publ. 217:105–137.

Kellner AWA. 2004. New information on the Tapejaridae (Pterosauria, Pterodactyloidea) and discussion of the relationships of this clade. Ameghiniana 41:521–534.

Kellner AWA. 2013. A new unusual tapejarid (Pterosauria, Pterodactyloidea) from the Early Cretaceous Romualdo Formation, Araripe Basin, Brazil. Earth Env Sci T R So. 103:1–13.

Kellner AWA. 2015. Comments on Triassic pterosaurs with discussion about ontogeny and description of new taxa. An Acad Bras Ciênc. 87:669–689.

Kellner AWA, Campos DA. 1994. A new species of *Tupuxuara* (Pterosauria, Tapejaridae) from the Early Cretaceous of Brazil. An Acad Bras Ciênc. 66:467–473.

Kellner AWA, Campos DA. 2002. The function of the cranial crest and jaws of a unique pterosaur from the Early Cretaceous of Brazil. Science 297:389–392.

Kellner AWA, Campos DA. 2007. Short note on the in group relationships of the Tapejaridae (Pterosauria, Pterodactyloidea). Bol Mus Nac. 75: 1–14.

Kellner AWA, Campos DA, Sayão JM, Saraiva AAF, Rodrigues T, Oliveira G, Cruz LA, Costa FR, Silva HP, Ferreira JS. 2013. The largest flying reptile from Gondwana: a new specimen of *Tropeognathus* cf. *T. mesembrinus* Wellnhofer, 1987 (Pterodactyloidea, Anhangueridae) and other large pterosaurs from the Romualdo Formation, Lower Cretaceous, Brazil. An Acad Bras Ciênc. 85:113–135.

Kellner AWA, Tomida Y. 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), Northeastern Brazil. National Science Museum, Monographs, Tokyo 17:1–135.

Lü J, Unwin DM, Xu L, Zhang X. 2008. A new azhdarchoid pterosaur from the Lower Cretaceous of China and its implications for pterosaur phylogeny and evolution. Naturwissenchaften 95:891–897.

Lü J, Yuan C. 2005. New tapejarid pterosaur from western Liaoning, China. Acta Geol Sin-Engl. 79:453–458.

Maisey JG, editor. 1991. Santana fossils: An illustrated atlas. Vol. 1. Neptune (NY): T. F. C. Publications; p. 1–459.

Manzig PC, Kellner AWA, Weinschütz LC, Fragoso CE, Vega CS, Guimarães GB, Godoy LC, Liccardo A, Ricetti JHZ, de Moura CC. 2014. Discovery of a rare pterosaur bone bed in a Cretaceous desert with insights on ontogeny and behavior of flying reptiles. PLoS ONE. 9:e100005.

Martill DM, Naish D. 2006. Cranial crest development in the azhdarchoid pterosaur *Tupuxuara*, with a review of the genus and tapejarid monophyly. Palaeontology 49:925–941.

McGowen MR, Padian K, De Sosa MA, Harmon RJ. 2002. Description of *Montanazhdarcho minor*, an azhdarchid pterosaur from the Two Medicine Formation (Campanian) of Montana. Paleobios 22:1–9.

Nessov LA. 1984. Upper Cretaceous pterosaurs and birds from the Central Asia. Paleontol Zh. 1:47–57. Russian.

Neumann VH, Cabrera L. 1999. Uma nueva propuesta estratigráfica para la tectonosecuencia post-rifte de la cuenca de Araripe, nordeste de Brasil. [A new stratigraphic proposal for the post-rift tectonic sequence of the Araripe Basin, northeast Brazil.] Boletim de resumos do Simpósio sobre o Cretáceo Brasileiro 5:279–285. Spanish.

Ősi A, Buffetaut E, Prondvai E. 2011. New pterosaurian remains from the Late Cretaceous (Santonian) of Hungary (Iharkút, Csehbánya Formation). Cretaceous Res 32:456–463.

Pereda Superbiola X, Bardet N, Jouve S, Iarochène M, Bouya B, Amaghzaz M. 2003. A new azhdarchid pterosaur from the Late Cretaceous phosphates of Morocco. London: Geol Soc Spec Publ. 217:79–90.

Pinheiro FL, Fortier DC, Schultz CL, De Andrade JAFG, Bantim RAM. 2011. New information on the pterosaur *Tupandactylus imperator*, with comments on the relationships of Tapejaridae. Acta Paleontol Pol. 56:567–580.

Plieninger F 1901. Beiträge zur Kenntnis der Flugsaurier. [Contribution to the knowledge of pterosaurs.] Palaeontographica 48:65–90. German.

Rodrigues T, Kellner AWA, Mader BJ, Russell DA. 2011. New pterosaur specimens from the Kem Kem Beds (Upper Cretaceous, Cenomanian) of Morocco. Rivista Italiana di Paleontologia e Stratigrafia 117:149–160.

Sayão JM, Kellner AWA. 2006. Novo esqueleto parcial de pterossauro (Pterodactyloidea, Tapejaridae) do Membro Crato (Aptiano), Formação Santana, Bacia do Araripe, Nordeste do Brasil. [New partial skeleton of a pterosaur (Pterodactyloidea, Tapejaridae) from the Crato Member (Aptian), Santana Formation, Araripe Basin, northeast Brazil.] Estudos Geológicos 16:16–40. Portuguese.

Unwin DM. 2003. On the phylogeny and evolutionary history of pterosaurs. London: Geol Soc Spec Publ. 217:139–190.

Vila Nova BC, Sayão JM, Langer MC, Kellner AWA. 2015. Comments on the cervical vertebrae of the Tapejaridae (Pterosauria, Pterodactyloidea) with description of new specimens. Hist Biol. 27:770–780.

Vullo R, Marugán-Lobón J, Kellner AWA, Buscalioni AD, Gomez B, de la Fuente M, Moratalla JJ. 2012. A new crested pterosaur from the Early Cretaceous of Spain: the first European tapejarid (Pterodactyloidea: Azhdarchoidea). PLoS ONE. 7:e38900.

Wang X, Zhou Z. 2003a. A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy. Chinese Sci Bull. 48:116–123.

Wang X, Zhou Z. 2003b. Two new pterodactyloid pterosaurs from the early Cretaceous Jiufotang Formation of western Liaoning, China. Vertebrat Palasiatic. 1:34–41.

Wang X, Kellner AWA, Jiang S, Cheng X. 2012. New toothed flying reptile from Asia: close similarities between early Cretaceous pterosaur faunas from China and Brazil. Naturwissenschaften 99:249–257.

Wellnhofer P. 1991. Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. [Additional pterosaur remains from the Santana Formation (Aptian) of the Chapada do Araripe, Brazil.] Palaeontogr Abt A. 215:43–101. German.

Wellnhofer P, Buffetaut E. 1999. Pterosaur remains from the Cretaceous of Morocco. Paläontol Z. 73:133–142.

Witton MP. 2008. A new azhdarchoid pterosaur from the Crato formation (Lower Cretaceous, Aptian?) of Brazil. Paleontology 51:1289–1300.