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Cryodrakon boreas gen. et sp. nov. a Late Cretaceous Canadian azhdarchid
pterosaur

DAVID W. E. HONE,^{1,*} MICHAEL B. HABIB,² FRANCOIS THERRIEN³

1 School of Biological and Chemical Sciences, Queen Mary University of London, London,
United Kingdom, d.hone@qmul.ac.uk;

2 Keck School of Medicine, University of Southern California, Los Angeles, CA, United
States of America, habibm@usc.edu;

3 Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada,
francois.therrien@gov.ab.ca

RH: HONE ET AL.—A NEW CANADIAN AZHDARCHID PTEROSAUR

*Corresponding author

ABSTRACT—Azhdarchid pterosaurs have been known from the Upper Campanian deposits of Alberta, Canada since 1972. Originally represented by only very fragmentary remains tentatively assigned to the genus *Quetzalcoatlus*, additional material uncovered over the years has revealed that the taxonomic identity of the Alberta pterosaur material is at odds with this in the light of the growing understanding of azhdarchid diversity. Here we describe previously undocumented pterosaur remains from Alberta and reassess previously studied material. The specimens collected from the Dinosaur Park Formation can be assigned to a new genus and species *Cryodrakon boreas* gen. et sp. nov. The largest elements referable to this taxon suggests that this genus reached sizes comparable to other giant azhdarchids.

INTRODUCTION

Azhdarchids were a diverse and broadly distributed clade of generally large Cretaceous pterosaurs. These animals included the largest flying animals of all time with upper estimates of adults reaching >10 m in wingspan and c. 250 kg in mass (Witton, 2013), although smaller species are known (c. 2.8 m wingspan at adult e.g. *Zhejiangopterus* Cai and Wei, 1994). Despite being diverse, azhdarchids are known primarily from limited and fragmentary remains, which makes understanding their taxonomy and paleobiology a difficult task.

Unlike most pterosaur groups, azhdarchids are known primarily from terrestrial settings (Witton and Naish, 2008) and, despite their likely capacity to cross oceanic distances in flight (Habib, 2010), they are broadly considered to be terrestrially capable animals that were adapted for, and lived in, inland environments. This preference for inland environments, coupled with the thin-walled and highly pneumatic bones typical of these derived pterosaurs

(Elgin and Hone, 2013), has likely contributed to their limited fossil record. Despite their large size and a distribution across North and South America, Asia, Africa and Europe (Witton, 2013), few taxa are known from more than fragmentary remains and the majority of taxonomic work has focused on rostral morphology, cervical vertebrae, and humeri.

A lack of descriptions of key taxa has also contributed to these taxonomic issues. The only largely complete and formally described azhdarchid is the Chinese *Zhejiangopterus* (Cai and Wei, 1994). However, the specimen is largely compressed into two dimensions and the description of the material is brief. Historically, *Quetzalcoatlus* from Texas, USA has been a critical taxon since its description (Lawson, 1975) as there is considerable material and much of it well preserved. However, the material of the type species *Quetzalcoatlus northropi*, which is represented by a single partial wing, has never been described in detail or given a detailed diagnosis. A second taxon that has been referred to as *Quetzalcoatlus* sp., which encompasses multiple largely complete skeletons, has received limited attention (e.g., see Kellner and Langston, 1996) and it remains possible that this putative species may represent a unique genus. This taxonomic identity of this material is currently under revision currently.

Collectively, these issues have led to a lack of understanding of azhdarchid taxonomy and contribute to some of the problematic referrals of various isolated specimens. In particular, various azhdarchid pterosaur remains from the Late Cretaceous of Alberta, Canada have been excavated (Russell, 1972; Currie and Russell, 1982) and some have been referred to *Quetzalcoatlus* (Godfrey and Currie, 2005), despite the limited description of the Texas taxon. However, as the Canadian material is the nearest to *Quetzalcoatlus* in both time and space, it is of great importance for our understanding of azhdarchid diversity and evolution.

Here we describe previously unreported and some exceptionally well preserved skeletal material, especially cervical vertebrae, of Upper Cretaceous (Upper Campanian) azhdarchid pterosaurs from the Dinosaur Park Formation of Alberta, Canada. Comparison to

other azhdarchid taxa suggests that the Albertan material may all be referred to a single taxon distinct from all currently known azhdarchid taxa. Thus a new genus and species is erected for this material: *Cryodrakon boreas*.

Institutional Abbreviations

TMM, Texas Memorial Museum, Austin, Texas, USA; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

DESCRIPTION

Numerous cervical elements and various limb elements of pterosaurs have been recovered from the upper Campanian Dinosaur Park Formation of southern Alberta over the years, (see Godfrey and Currie, 2005). In agreement with previous assignments (e.g. Currie and Russell, 1982; Currie and Jacobsen, 1995; Godfrey and Currie, 2005), all remains are here identified as belonging to azhdarchid pterosaurs. Despite varying degrees of completeness, all cervical vertebrae show some or all of the characteristic features of members of the clade: a low centrum, greatly reduced ‘bifid’ neural spine (that is, one that has separate anterior and posterior components with a space in between), and dorsoventrally flattened zygapophyses, pneumatic foramina lateral to the neural canal, greatly elongated mid cervicals (e.g., Kellner, 2003; Naish and Witton, 2017; Vidovic and Martill, 2017).

Wellnhofer (1970) suggested that the cervical vertebrae of azhdarchids elongate during ontogeny (i.e. show positive allometry). If correct, this can make identification of individual positions of individual vertebrae, and comparisons between specimens and taxa difficult, when specimens are small. This is especially the case for issues such as length-width ratios, which are commonly used in azhdarchid descriptions. Azhdarchids are well

known for elongate middle cervicals although recently animals with proportionally short and robust vertebrae have been described (Vremir et al., 2015; Naish and Witton, 2017), further complicating the issues of length-width ratios. However, recent papers (Averianov, 2010; Naish and Witton, 2017) have suggested characteristics that can help identify isolated azhdarchid cervicals and are followed here. We identify the Dinosaur Park pterosaur cervical material as one cervical IV (complete), three Vs (one of which is complete), one VI, and finally one which may be IV or VI (see below for details).

Most of the specimens here have been previously described and beautifully illustrated (e.g. Godfrey and Currie, 2005) and therefore we focus here primarily on key features of the better preserved and more complete cervical elements that relate to data on their position in the vertebral series or taxonomic identity.

TMP 1992.83.07

This specimen is a complete and very well preserved middle cervical element (Fig 1) with only very limited wear or crushing, measuring 142 mm long (see Supplementary data 1). The specimen is overall typical of azhdarchids in being proportionally long and with a centrum that is confluent with the neural arch. The neural spine is bifid and missing in the middle part of the centrum, though the anterior and posterior parts of the spine are worn and largely absent. The prezygapophyses extend well anteriorly of the centrum into a broad expansion and posteriorly there are short postexapophyses situated ventrally. There is a slight keel along the long axis on the ventral face of the vertebra.

There is no indication of pneumatic openings on the centrum but there are a series of pneumatopores associated with the neural canal. On the anterior face of the neural arch there are three pneumatopores, each of which is similar in size and all are slightly smaller than the neural canal. There is one on each side of the neural canal, though the ventral margin of each

is lower than the ventral margin of the canal and there is also a single accessory pneumatopore above the neural canal in a central position. The condition and orientation of the lateral pneumatopores are identical on the posterior face of the vertebra (Godfrey and Currie, 2005 incorrectly illustrate these as being in a dorsal position) although the accessory dorsal pneumatopore is absent.

This specimen is identified as cervical (hereafter C) IV. The vertebra is not a CIII as the neural spine does not extend along the full length of the centrum (Naish and Witton, 2017), but it is proportionally too short to be considered a CV (only c. 3.6 times longer than wide) compared to large azhdarchids (Averianov, 2010). Although both the anterior and posterior parts of the neural spine have been eroded and are incomplete, the anterior portion is larger, which supports an interpretation of this vertebra as a CIV over a CVI.

Importantly this specimen belongs to a partial skeleton (Currie and Jacobsen, 1992), which includes a humerus (Fig 2), a rib, pteroid, metacarpals, and a tibia (all under TMP 1992.83 – Fig 3, S2).

TMP 1996.12.369

This specimen is a nearly complete and very well preserved vertebra that shows wear on various extremities, in particular the anterior part (Fig 4, S2). The element is very small (total length of the centrum 10.6 mm); however despite its small size, it is proportionally the most elongate of the Dinosaur Park vertebrae with a length:width ratio of 7.82. Given its small size, this vertebra would likely have become proportionally even longer as the animal grew. This element is provisionally identified as belonging to a non-adult animal based on its small size and the striated bone surface, which is indicative of young age in pterosaurs (Bennett, 1996).

As with TMP 1992.83.07, this specimen shows postexapophyses with small pedestals and ventrally facing articular surfaces. However, there are some differences in the pneumatopores between the two specimens. On the anterior face of TMP 1996.12.369, the arrangement of pneumatopores is as described for TMP 1992.83.7, with pneumatopores situated lateral to the neural canal but in a lower position and an accessory foramen above the neural canal. On the posterior face, the lateral pair of foramina are very small, barely pinpricks, and sit in fossae. The upper part of the neural arch is worn, but there is no obvious indication of a dorsally positioned accessory foramen. We suggest that the small size of the lateral pneumatopores seen in TMP 1996.12.369 may represent an ontogenetic feature. It would seem unlikely that these openings retained this small size as the animal grew and these depressions and openings do seem to be incipient of the larger pneumatopores seen in other specimens.

The specimen is identified as a fifth cervical vertebra. In addition to being elongate, the midpoint of the neural spine is so reduced as to be effectively confluent with the centrum, which is an indicator of a CV position (Naish and Witton, 2017). Although worn, the bases of both the anterior and posterior parts of the neural spine are present and are similar in size, which excludes identification as CIV. The length of this element is almost identical to that of CV of a *Zhejiangopterus* specimen (Cai and Wei, 1994), suggesting an animal of similar size, namely with a wingspan of c. 2 m, although the *Zhejiangopterus* specimen is an adult whereas TMP 1996.12.369 is inferred to be a juvenile.

TMP 1981.16.107

This specimen represents the anterior part of a small cervical vertebra (Fig 5). It is badly broken with much of the element missing, including the left prezygopophysis. As preserved, the centrum is 29.5 mm long with a width at the midshaft break of 9.75 mm

(length:width ratio of 3.03). This specimen is strikingly similar in size, proportions, and morphology to TMP 1996.12.369 and is therefore interpreted as a fifth cervical vertebra.

There are, however, some differences between these small elements. Although broken, the remaining part of the anterior neural spine in TMP 1981.16.07 is somewhat larger than that of TMP 1996.12.369. There is also some variation in the pneumatic foramina on the anterior faces of these elements. In TMP 1981.16.01, the laterally positioned openings, although still small and set into depressions, are larger than those of TMP 1996.12.369. However, although the lateral foramina are larger, there is no indication of the presence of an accessory foramen dorsal to the neural canal.

TMP 1980.16.1367

This specimen, incomplete and poorly preserved, was previously identified as a large femur (Godfrey and Currie, 2005) but closer examination reveals that it consists of a large partial midshaft of a cervical vertebra lacking both the anterior and posterior articulations (See S2). This is based on the extremely large diameter but exceptionally thin bone walls, which are characteristic of many azhdarchid pterosaur cervical vertebrae. As the vertebra is proportionally very long and there is no trace of the neural spine along the preserved midportion, this specimen is identified as a CV.

The specimen is large, over 400 mm in length as preserved, and would have been considerably larger when complete (likely at least 500 mm). This would make it by far the largest pterosaur cervical vertebra known from Alberta. Although an exact size is hard to estimate given the lack of features on the bone, TMP 1980.16.1367 is comparable to *Arambourgiania* at c. 600 mm (Frey and Martill, 1996), suggesting a large and presumably adult animal.

TMP 1989.36.254

This specimen is not very well preserved, suffering numerous cracks and damage to the cortex and crushing, but is nearly complete (Fig 5). The centrum of this specimen measures 249 mm in length with a midshaft breadth of 60 mm for a length:width ratio of 4.15.

On the anterior face of the element, the laterally positioned pneumatopores are situated a little more dorsally than those of the other Dinosaur Park specimens. Their dorsal margins are at the same height as the dorsal margin of the neural canal, although this latter opening has its dorsal margin crushed and would have been a little taller in life. There is a dorsally positioned accessory pneumatopore, which is larger than those described in other specimens, being larger than the neural canal. This observation supports our previous suggestion that the size of these openings may change with ontogeny. The posterior face is badly damaged, making it difficult to recognize features although there does appear to be one large lateral pneumatopore on the right side.

The specimen is clearly proportionally shorter than the three aforementioned specimens described as CVs and is generally close in morphology to TMP 1992.83.07 (cf. Fig 1), suggesting that it represents either a CIV or CVI. The anterior neural spine appears to have been quite large but the posterior part is too worn to provide any useful comparisons between the two parts. Given that the specimen is overall somewhat less elongate than TMP1980.16.1367 (despite a larger overall size), TMP 1989.36.254 is considered to be most likely a CIV, though this is a tentative assignment.

TMP 1993.40.11

This specimen is badly crushed and incomplete (Fig 5). The posterior part of the vertebra is missing and there is little information available on the more anterior part. The

midline length of the preserved part is 161 mm and thus is somewhat larger than TMP 1996.12.369 but smaller than the two largest specimens (TMP 1980.16.1367 and TMP 1989.36.254).

The identity of this element is difficult to determine given the damage it has suffered. The overall proportions (length:width ratio of approximately 3.6) suggest that it is a middle cervical, and not one of the most anterior or posterior elements. It is not a CIII as it does not have a reduction in the neural spine to make it bifid unlike other azhdarchids, and it is not a VII or VIII as the cotyle appears to be smaller than the neural arch (see Naish and Witton, 2017). It could potentially be a CIV-VI, though CV would seem unlikely as, despite the missing portions, it is not as elongate as the elements identified CVs above. It is therefore tentatively considered a CVI as it looks different from TMP 1996.12.369, which we consider a CIV.

Other Cervical Elements

Several other poorly preserved cervical elements are known from the Dinosaur Park Formation of Alberta. TMP 2005.39.8 and TMP 1998.68.100 are very complete articular ends of small cervical vertebrae, which contain limited information about their affinities or anatomy although they both are from azhdarchid pterosaurs. TMP 1980.16.1506 lacks both articular ends and the midshaft is not well preserved, but it does preserve an accessory pneumatic cavity above the neural canal and a pair of lateral foramina that are positioned close to the ventral margin of the neural canal, which matches the features described above for other Dinosaur Park pterosaur vertebrae.

The specimens studied share features that suggest they belong to the same taxon – namely a dorsally positioned accessory pneumatopore, the lateral pneumatopores having a relatively low position, and when present, short postexapophyses (Figs 1, 4, 5). While Ósi et al. (2011, p. 462) accurately cautioned that “[t]he presence or absence of a pneumatic foramen on a cervical vertebra does not necessarily reflect taxonomical differences”, the consistency in foramina arrangement among the studied specimens indicates these features are taxonomically useful in this instance and can be used to diagnose the taxon. Although the specimens are assigned to different positions in the cervical series, Averianov (2010) has showed that multiple features (including pneumatic foramina) are consistent in their position along an azhdarchid cervical vertebral series. Since these specimens share a unique set of features (which differ from all other azhdarchids), they can be assigned to a new taxon, *Cryodrakon boreas* gen. et sp. nov. A previously-described partial azhdarchid skeleton recovered from the Dinosaur Park Formation (Currie and Jacobsen, 1995; Godfrey and Currie, 2005), includes the vertebrae describe above (TMP 1992.83) and also preserves a humerus (TMP 1992.83.4) that is notably different from that of other azhdarchid pterosaurs (Figures 1-3). This skeleton, as well as all other previously described azhdarchid material from the same formation (Figs 4-5) are assigned to *Cryodrakon boreas*.

All small azhdarchid specimens can be referred to juvenile individuals as opposed to belonging to small adult individuals (or taxa). For example, the tibia of TMP 1992.83 shows no co-ossification of the tibia to the fibula or proximal tarsals (Godfrey and Currie, 1995) which is normal for adult pterosaurs suggesting that it is immature. Normally archosaur vertebrae show fusion between the neural arch and centrum late in ontogeny, however in azhdarchids, where there are both juvenile and adult cervical vertebrae known (e.g. *Azhdarcho* - Averianov, 2010), fusion apparently occurs very early, such that the suture is obliterated by even a very young age. This condition is observed in our specimens, with no

suture visible in even the smallest specimens, and so this fusion does not confer adult status. The similarity in juvenile and adult azhdarchid vertebrae is also reflected here by the consistency of the traits seen between specimens of very different sizes implying that they are part of a consistent series with smaller specimens (that do show the juvenile trait of grainy bone texture – Bennett, 1996) representing juveniles.

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

AZHDARCHOIDEA Nessonov, 1984

AZHDARCHIDAE Nessonov, 1984

CRYODRAKON BOREAS gen. et sp. nov.

Holotype—Specimen TMP 1992.83, an associated partial skeleton consisting of a fourth cervical vertebra (TMP 1992.83.7), a rib (TMP 1992.83.5), a humerus (TMP 1992.83.4), a pteroid (TMP 1992.83.3), a wing metacarpal IV (TMP 1992.83.1), a tibia (TMP 1992.83.2), and a metatarsal (TMP 1992.83.6).

Referred Material—Cervical vertebrae (TMP 1996.12.369, TMP 1981.16.107, TMP 1980.16.1367, TMP 1989.36.254 and TMP 1993.40.11), a scapulocoracoid (TMP 1981.16.182), an ulna (TMP 1965.14.398), wing metacarpals (TMP 1979.14.24, TMP 1987.36.16, and TMP 2005.12.156), wing phalanges (TMP 1972.1.1, TMP 1982.19.295, and TMP 1992.36.936), and a femur (TMP 1988.36.92).

Etymology—*Cryodrakon* derived from the Ancient Greek for ‘cold’ and ‘dragon’, *boreas* from the Greek god of the north wind. This is therefore the ‘cold dragon of the north winds’.

Horizon and Locality—All material is from exposures of the Dinosaur Park Formation in Dinosaur Provincial Park, Alberta, Canada which was laid down between 76.7

Ma and 74.3 Ma (Eberth et al., 2017). Although the material comes from various localities dispersed within the formation, the holotype was discovered 2 m above the base of the formation.

Definition and Diagnosis—Azhdarchid pterosaur that differs from other azhdarchids by the presence of the following diagnostic features:

1) The lateral pneumatic foramina are positioned in a relatively ventral position, their ventral margins are at similar level to (or even below) the ventral margin of the neural canal in both anterior and posterior view. While the foramina do not quite have this arrangement in some specimens, e.g. TMP 1981.16.107, they still do not approach the dorsal margins of the neural canal which is normal in other azhdarchids. This feature of low pneumatopores is also possibly present in *Eurazhdarcho* and the cervical vertebrae of an unnamed azhdarchid (see below).

2) Ventrally directed postexpophyses on short pedestals. The articular facets of the postexpophyses are distinctly orientated ventrally and further, are well-separated from the articular surface of the centrum (cotyle).

Comparisons to Other Azhdarchid Pterosaurs

In addition to the autapomorphies stated above, *Cryodrakon boreas* also demonstrates the presence of other traits in combination that further distinguish it from all other azhdarchids as a distinct taxon. Note that a number of azhdarchids are known only from material that does not overlap with our remains – especially jaw material (e.g. *Aerotitan*, *Volgadraco*, see Averianov, 2014) and so comparisons with these are not possible.

Alanqa—Some cervical material has been referred to this taxon (Averianov, 2014) although the holotype specimen is represented only by cranial material (Ibrahim et al., 2010) and this may not be an azhdarchid (Longrich et al., 2018). The specimen is a highly

incomplete posterior end of a cervical vertebra and few details can be ascertained though unlike *Cryodrakon*, it has only short postexpophyses.

Aralazhdarcho—This taxon possesses reduced pneumatopores that lie lateral to the neural canal on the anterior faces of midcervical vertebrae (Averianov, 2007, 2014). This is also true of the two midcervicals of the Dinosaur Park azhdarchid, but these are from young animals. Based on the large size of pneumatopores in animals closer to (or possibly at) adult size of *Cryodrakon* (and including the holotype), this condition would be distinct from *Aralazhdarcho*.

Arambourgiania—The cervical vertebrae of *Arambourgiania* are nearly circular in cross-section (Martill *et al.* 1998), which is different from the dorsoventrally-compressed condition observed in the Dinosaur Park azhdarchid. The pneumatopores positioned lateral to the opening of the neural canal are considerably larger than the neural canal itself in *Arambourgiania* (Martill *et al.* 1998)(Fig 6), contrary to the Alberta material. Although above we suggest that the pneumatopores may increase in size during ontogeny, the lateral pneumatopores are still considerably smaller than the neural canal even in the larger specimens *Cryodrakon*. Furthermore, *Arambourgiania* lacks a dorsally positioned pneumatic foramen above the neural canal. Cervical vertebra V in *Arambourgiania* is also greatly elongate and proportionally far longer than any of the Alberta specimens studied.

According to Suberbiola *et al.* (2003), *Arambourgiania* has ventrally orientated postexpophyses, as in *Cryodrakon*. However, this condition is far from clear based on the descriptions and illustrations of Frey and Martill (1996) and Martill *et al.*, (1998), so it is not considered to affect the diagnosis given above. Even if they share this feature, the two taxa are clearly distinct given the other differences presented. Additional material that may be referable to the holotype has recently been described (Martill and Moser, 2018) but this, unfortunately, does not reveal any further details or comparisons with *Cryodrakon*.

Azhdarcho—Several features distinguish *Cryodrakon* from *Azhdarcho*. There is no pneumatopore situated dorsal to the neural canal on the anterior face in cervicals III and IV of *Azhdarcho* (although one is present in cervicals VI and VII) (Averianov, 2010), whereas a large pneumatopore is present on the anterior face of the cervical IV in the Dinosaur Park azhdarchid. The middle of the dorsal margin of the cotyle in *Cryodrakon*, as seen in anterior view, shows a distinct dip such that this allows the opening of the neural canal to be seen in posterior view (Fig 5E), a feature not seen in *Azhdarcho* (Averianov, 2010, his Fig 11). The postexapophyses in *Cryodrakon* are also considerably broader than those of *Azhdarcho*. Finally, the latter also has proportionally narrower and taller centra in cervicals III and IV than *Cryodrakon*.

Bakonydraco—The diagnosis of this taxon is based on features of the rostrum (Ősi et al., 2005), however two middle cervical vertebrae can potentially be referred to this taxon. Although crushed, both cervical vertebrae appear to have a well-defined small ridge that forms the middle part of the neural spine in dorsal view, but this ridge is larger and sharper in *Bakonydraco* than in other azhdarchids (Ősi et al., 2005, their Figs 4-5), including *Cryodrakon*. The postexapophyses in the *Bakonydraco* midcervical vertebrae also face ventrally and neither of them have an accessory pneumatopore dorsal to the neural canal (Fig 6), which differs from the conditions seen in *Cryodrakon*. Although one of the two poorly preserved midcervical vertebrae of *Bakonydraco* appears to have low positioned lateral pneumatopores (Ősi et al., 2005, their Fig 5, specimen B) as in *Cryodrakon*, crushing has compressed the apparent height and position of the neural canal and this similarity is likely an artefact of the distortion of the material rather than a true representation of the character state. Some studies (e.g., Andres and Myers, 2012) have suggested that this taxon is not an azhdarchid, though if this is the case it would further distance this from *Cryodrakon*.

Eurazhdarcho—This taxon has been described as having ventrally located pneumatopores lateral to the neural canal (Vremir et al., 2013), however these are not illustrated (their Fig 6) and their position is difficult to confirm. If present, this would be a feature shared by *Eurazhdarcho* and *Cryodrakon*, but several other features clearly distinguish the two taxa. *Eurazhdarcho* has a considerably longer anterior part of the neural spine on cervical vertebra IV (nearly 30% of the length of the dorsal margin of the neural arch) than *Cryodrakon* (less than 25%). Although poorly preserved, it has been suggested that the posterior part of the neural spine is similarly sized to the anterior part in *Eurazhdarcho* and that the anterior and posterior parts nearly meet in the midline (Vremir et al., 2013, their Fig 6). In contrast, the posterior neural spine of *Cryodrakon* is much smaller than the anterior one, and the two are well separated. The prezygopophyses seem unusually large in *Eurazhdarcho* and is unlike those of other azhdarchids (Fig 6).

Hatzegopteryx—Until recently cervical material was unknown for this genus, but a large and unusually short cervical has now been referred to this taxon (see Naish and Witton, 2017). This middle cervical is proportionally much shorter than that of other azhdarchids, including *Cryodrakon* which has the ‘traditional’ azhdarchid elongate cervicals IV to VII. In addition, the articular surface of the prezygapophyses is large in *Hatzegopteryx* compared to the length of the supporting arms whereas it is considerably smaller (i.e., the arms are relatively long) in *Cryodrakon*.

There are also differences in the humerus between the two taxa. Although the deltopectoral crest *Hatzegopteryx* is unwarped (Buffetaut et al. 2003), *Cryodrakon* does show slight curvature of the distal end of the crest in dorsal view not seen in the former (see Witton and Habib, 2010, their Fig 1). In anterior or posterior view, the lateral margin of the humerus is straight in *Cryodrakon* but this shows a distinctive convexity in *Hatzegopteryx* (Witton and Habib, 2010, their Fig 1).

Mistralazhdarcho—This taxon is known from a large number of elements from across the skeleton though only limited vertebral material (Vullo et al., 2018). *Mistralazhdarcho* lacks the accessory dorsal pneumatic foramina on mid cervicals seen in *Cryodrakon*, and also has less divergent prezygapophyses than seen on the TMP material (Vullo et al., 2018). There are also differences in the humeral head as noted by Vullo et al. (2018): “it appears not as saddle-shaped” as in the in *Cryodrakon*.

Finally, it is rare to be able to compare pteroids between azhdarchids, but Vullo et al., (2018) noted that the overall shape of this element is different between TMP 1992.83 (*Cryodrakon*) and *Mistralazhdarcho* and that the latter has a smaller pneumatic foramen than the former. Collectively therefore, the two are distinct taxa.

Phosphatodraco—Three characteristics differentiate *Phosphatodraco* from the Dinosaur Park azhdarchid. First, the prezygapophyses are proportionally longer in *Cryodrakon* than in *Phosphatodraco* (Suberbiola et al., 2003). Secondly, the cervical vertebrae V to VII of *Phosphatodraco* are similar in length and overall proportions to one another (Pereda Suberbiola et al., 2003), whereas cervical vertebra V is clearly the proportionally longest of the series in *Cryodrakon*. Finally, the anterior face of cervical vertebra VI of *Phosphatodraco* lacks pneumatic foramina (Suberbiola et al. 2003), a clear distinction with the material referable to *Cryodrakon* (Fig 6).

Quetzalcoatlus—Some of the Dinosaur Park pterosaur material had been assigned previously to the large North American azhdarchid *Quetzalcoatlus* (Godfrey and Currie, 2005). Two species are currently known for this genus (Lawson, 1975; Kellner and Langston, 1996), although limited detail has been published to date. Nevertheless, it is possible to separate *Cryodrakon* from *Quetzalcoatlus* based on several differences.

The pedestals for the postexpophyses in *Quetzalcoatlus* are considerably smaller than in *Cryodrakon*, to the extent where the articular surfaces of the postexpophyses contact

the articular surface of the centrum (Witton and Naish, 2008, their Fig 4) in cervicals III-V. *Quetzalcoatlus* also lacks an additional pneumatic foramen (or depression) situated dorsal to the neural canal that is present in *Cryodrakon*.

The cervical IV for *Quetzalcoatlus* is 215 mm long (Habib, pers obs) and the corresponding element in *Cryodrakon* (TMP 1992.83.07) is about 66% of the length (143 mm). However, the midshaft diameter in TMP 1992.83.07 is a fraction larger than the corresponding element in *Quetzalcoatlus* suggesting the elements of *Cryodrakon* are generally more robust (see Supplementary data 1).

The humerus of *Quetzalcoatlus* differs also from that of the Alberta taxon. The humeral length-to-midshaft breadth ratio is considerably higher in *Cryodrakon* than in *Quetzalcoatlus northropi* (7.06 versus 6.02 – Habib, pers obs), indicative of an overall proportionally thinner element in the Dinosaur Park azhdarchid. The humeral head of *Cryodrakon* is more robust in dorsal view than in *Q. northropi* (see Witton and Habib, 2010, their Fig 3), whereas in contrast, the distal end of the deltopectoral crest and distal condyle are more greatly expanded in *Q. northropi* than in *Cryodrakon* (Wellnhofer, 1990, figure top of p141).

There are also well preserved humeri of *Quetzalcoatlus* sp., including TMM 47180 and TMM 42138. The two specimens are undistorted and differ from TMP 1992.83.4 in length by less than 0.5%, making them effective for comparison with *Cryodrakon*. The breadth and shape of the deltopectoral crests in *Quetzalcoatlus* sp. and *Cryodrakon* are essentially identical (53.9 mm vs 53.8 mm). The humeri of *Quetzalcoatlus* sp. are slightly shorter than in *Cryodrakon* (by about 8%), but they are slightly larger in diameter (8% larger in diameter, at mid shaft, in the dorsoventral direction is 2% larger in diameter, at mid shaft, in the mediolateral direction). The humerus of *Quetzalcoatlus* sp. also flares slightly more than that of *Cryodrakon* proximally to distally: the humeral head of *Quetzalcoatlus* sp. is only

2% larger in maximum breadth, but the distal end of the humerus is 11% wider in maximum breadth. The humerus of *Quetzalcoatlus* sp. is therefore somewhat more robust in external dimensions (slightly shorter length combined with slightly greater diameter, especially distally).

Volgadraco—Averianov et al. (2008) named this taxon based on jaw fragments and some incomplete cervical vertebrae. The best preserved of the latter was a third cervical, which lacks any accessory pneumatic foramina lateral to the neural canal which is a clear distinction from the material described here serving to separate *Cryodrakon* from this genus.

Zhejiangopterus—The cervical series of this taxon has not been described or illustrated in detail (Cai and Wei, 1994), making comparison with the Dinosaur Park azhdarchid difficult. However, cervical vertebrae IV – VI are shown to be considerably longer than wide and are proportionally longer than the Alberta specimens described herein, suggesting the two taxa are distinct.

The humerus of *Zhejiangopterus* can be seen only in one view, so comparisons are limited. However, *Cryodrakon* shows a clear ‘step’ on the dorsal part of the deltopectoral crest where it connects to the shaft of the humerus, whereas there is a smooth grading from the crest to the shaft in *Zhejiangopterus*. The latter also shows a slight ventral expansion to the distalmost part of the deltopectoral crest not seen in *Cryodrakon*.

Azhdarchidae indet.—Watabe et al. (2006) described a series of azhdarchid remains from Mongolia that included a well-preserved cervical vertebra. The specimen lacks an accessory pneumatopore on both the anterior and posterior faces of the vertebra (Fig 6), which clearly separates it from *Cryodrakon* as does the relatively dorsally positioned lateral pneumatores on the element.

Vremir et al., (2015) described a partial cervical vertebra IV from the Late Cretaceous of Transylvania, which was suggested to belong to a new taxon, but was not named. This

specimen does show pneumatic openings lateral to the neural canal on the anterior surface in a low position, similar to the condition described in the Dinosaur Park azhdarchid. However, the anterior floor of the neural arch is considerably more exposed in dorsal view in the Transylvanian specimen than in *Cryodrakon*. Although very incomplete, the Transylvanian specimen can be measured to show it has a maximum length of the anterior pre- to posterior postzygopophyses to minimum width ratio of 4.2, which contrasts sharply with that of TMP 1992.83.07 (also a CIV) of 3.4, suggesting the two specimens belong to different taxa.

Cohen et al. (2018) describe an isolated azhdarchid wing metacarpal of Turonian age from Utah. The specimen belongs to an individual of estimated 4.7 m in wingspan and with a morphology close to that of both TMP 87.36.16 and TMP 1992.83.1. However, we agree with Cohen et al. (2018) that there are differences in morphology between the two and that this unnamed azhdarchid is not likely to be the same taxon as represented by the *Cryodrakon* material.

Longrich et al. (2018) show a single small and elongate azhdarchid mid cervical. This shows a dorsal accessory pneumatopore and apparently ventrally positioned lateral ones (though the specimen is badly crushed) similar to *Cryodrakon*. However, it shows considerable constriction in the diameter of the centrum proximal to the distal cotyle, has a depression on the ventral surface, and is described as somatically mature despite being only c. 150 mm in length, all of which point to this being different to *Cryodrakon*.

Montanazhdarcho—Although this taxon has been referred to the Azhdarchidae (Padian *et al.*, 1995; McGowen *et al.*, 2002), recent work suggests that it is probably not an azhdarchid (Carroll, 2015). This taxon is not known from any cervical material, but the humerus is clearly distinct from that of *Cryodrakon*. The humerus TMP 1992.83.4 shows a much greater boss in the middle of the proximal face of the humerus (seen in anterior view) and there is also a distinct process to the proximodorsal margin of the ulnar crest, neither of

which is seen in *Montanazhdarcho* (McGowen et al., 2002). While Godfrey and Currie (2005) accurately recognized that the wing metacarpals from the Alberta pterosaur were consistent in size and morphology with *Montanazhdarcho*, the distinctive features of the humerus demonstrate that these taxa are distinct.

DISCUSSION

The Dinosaur Park pterosaur material described herein has been referred previously to several different azhdarchid and related taxa. Some elements, such as TMP 1980.16.1367 and TMP 1981.16.107, have been referred to *Quetzalcoatlus* (Currie and Russell, 1982). Godfrey and Currie (2005) suggested that the wing metacarpals were consistent with *Montanazhdarcho*, although they noted the difficulty of assigning the known pterosaur material to any single azhdarchid taxon based on the lack of available data on their anatomy and the temporal difference with other known azhdarchids. The fact that *Montanazhdarcho* may not represent an azhdarchid rules out this assignment. The azhdarchid taxonomic situation has improved considerably in recent years with the discovery and description of numerous new specimens allowing for more detailed comparisons. Despite the previous referrals, the Dinosaur Park azhdarchid material is clearly distinct from any previously described taxon.

The occurrence of *Cryodrakon* in the upper Campanian Dinosaur Park Formation, which was deposited between 76.7 Ma and 74.3 Ma (Eberth et al., 2017), makes this taxon one of the geologically oldest azhdarchids known from North America. Although the exact stratigraphic position of most pterosaur element within the formation is unknown, the holotype was discovered only 2 m above the base of the Dinosaur Park Formation (Currie and Koppelhus, 2005, CD supplement), confirming the presence of giant azhdarchids in

North America since at least ~76.5 Ma. A partial pterosaur limb fragment, TMP 1987.77.128, likely azhdarchid based on bone wall thickness, has been recovered from exposures of the upper Campanian Oldman Formation at the Devil's Coulee fossil locality, roughly 160 km to the SW of Dinosaur Provincial Park. This fossil site, famous for the preservation of abundant dinosaur nests and embryos, has been dated to ~75 Ma (Horner and Currie, 1994) and is largely contemporaneous with exposures of the Dinosaur Park Formation in Dinosaur Provincial Park. Given the temporal and geographic proximity of the two sites, it is plausible that the Oldman specimen may belong to the same taxon but confirmation awaits additional discoveries. The presence of a common pterosaur taxon in both is therefore considered plausible - despite the limited remains of azhdarchids, they are known from a wide number of locations in the northern continents (Witton, 2013) and at least some localities appear to host multiple taxa (e.g. Vremir et al., 2013; Naish and Witton, 2017), although to date, most have only a single recognised azhdarchid present. Note that one scrap of pterosaur material, TMP 1987.77.128, was recovered from the Oldman Formation, which underlies the Dinosaur Park Formation, and is likely also azhdarchid based on the thickness of the bone wall and its close temporal and geographic position to the above formations, but little else can be said out this.

Several authors have suggested the presence of at least two azhdarchid taxa in the Dinosaur Park Formation of Alberta. Sullivan and Fowler (2011) referred two wing phalanges, TMP 1972.1.1 and TMP 1982.19.295, to *Navajodactylus boerei*, a medium-sized pterosaur from the upper Campanian Kirtland Formation of New Mexico, USA. However, this referral is problematic as both Alberta specimens are poorly preserved and appear to lack the diagnostic characters of *Navajodactylus*, and even appear to differ in having an extended ridge rather than a dorsal boss on the dorsal cotyle as seen in the *Navajodactylus* holotype (Sullivan and Fowler, 2011, their Fig 4B) and in lacking the pneumatic foramen. In turn, Vremir et al., (2013) also suggested the presence of two taxa based on two cervical vertebrae,

TMP 1992.83.7 and TMP 1980.16.1367 (which they erroneously referred to using the outdated catalogue number ‘PMA P80.16.1367’) – the large and very incomplete cervical. However, no justification was given for this suggested distinct identification and, as noted above, there is no obvious reason to think TMP 1980.16.1367 is a separate taxon, although it is so incomplete that it is difficult to say much about the nature of this specimen. The respective size difference between these elements likely reflect individuals of different age and does not support recognition of two taxa on the basis of size alone given the wide range of sizes of adult animals seen in other pterodactyloid pterosaurs (Bennett, 2001). Despite other referrals, there is no convincing evidence of other taxa being present in the Dinosaur Park Formation based on the available data and thus all material here is referred to *Cryodrakon boreas* pending revisions based on further finds and in particular more articulated material. There may well be more than one taxon present here, but currently this cannot be supported.

The fragmentary nature of the material available, and possible ontogenetic trajectories, prevents us from conducting a cladistic analysis to determine the phylogenetic relationships of *Cryodrakon boreas*. Nevertheless, certain characteristics permit a preliminary assessment of the phylogenetic position of the taxon within Azhdarchidae. For example, it does lack distinct cervical zygapophyses for the middle cervicals, a trait which suggests it does not lie within basalmost Azhdarchidae, but instead within the *Jidapterus-Quetzalcoatlus* clade (Vidovic and Martill, 2017). This is consistent with the Late Cretaceous age of the material. The confirmation that the Dinosaur Park material is not referable to *Quetzalcoatlus* limits the geographic and temporal range of this taxon.

Bauplan

Until recently, azhdarchids were considered to be generally homogenous with a single bauplan being universal across the group, a phenomenon common in pterosaurs as they are generally highly conservative in form within clades. The azhdarchid bauplan in particular was distinctive for a greatly elongate neck, with very long mid-cervical vertebrae. This is seen in particular in the near complete skeleton of *Zhejiangopterus* but is apparent in any long-necked azhdarchid such as *Phosphatodraco* or *Arambourgiania*. However, it has been suggested that azhdarchids may be more variable than this (Unwin, 2005) and recent finds (Vremir et al., 2015; Naish and Witton, 2017) suggest that, in fact, some azhdarchids had proportionally short and robust necks and were likely rather different, showing that there may have been multiple azhdarchid morphs.

In the case of *Cryodrakon*, this taxon clearly has elongate midcervical vertebrae and would fit into the better-known morph of long-necked azhdarchids. The longest well preserved vertebrae here have centra that are approximately five times longer than wide which is considerably greater than those of the short-necked *Hatzegopteryx* (Naish and Witton 2017). *Cryodrakon* is broadly comparable to *Quetzalcoatlus* with the humerus and some vertebrae being of similar sizes and proportions to *Quetzalcoatlus* sp. and the giant, if badly incomplete, cervical of *Cryodrakon* is comparable to the larger cervicals of the *Quetzalcoatlus northropi*.

Anatomical comparisons suggest that, in general, *Cryodrakon* may have been slightly more robust than *Quetzalcoatlus*. A break in the humerus of *Quetzalcoatlus* sp. (TMM 47180) reveals that cortical bone thickness is near identical to that of *Cryodrakon* (for which cortical bone thickness data were obtained by CT imaging). The cortical bone is very thin in the humeri of both taxa, as would be expected for azhdarchid taxa. The cortical bone thickness in *Cryodrakon* is slightly higher as it ranges from 1.1 mm to 1.3 mm, but it is 1.07 mm in TMM 47180 (where it can be measured). Based on these differences in cortical bone

thickness, the humerus of *Cryodrakon* is slightly stronger in bending than that of *Quetzalcoatlus*. Overall, the humeri of *Cryodrakon* and *Quetzalcoatlus* are quite similar, varying in most proportions within the range that would be expected for intraspecific comparisons. The greatest difference in overall shape is the slightly exaggerated flaring of the humerus distally in *Quetzalcoatlus*.

These similarities confirm that *Cryodrakon* and *Quetzalcoatlus* were likely of very similar size and build, and the two species likely shared similar flight performance characteristics and flight muscle fractions. Combined with the somewhat greater length of the humerus in *Cryodrakon*, it is likely that *Cryodrakon* was slightly heavier than *Quetzalcoatlus* but that their overall mass was likely similar. These similarities further enhance the contrast in the cervical vertebrae morphology between the two species. The cervical vertebrae of *Cryodrakon* are absolutely more robust than those of *Quetzalcoatlus*. Assuming, based on humeral characteristics, that *Cryodrakon* was of very similar mass, the relative robustness of the neck in *Cryodrakon* was also significantly greater. In short, *Cryodrakon* had a long neck, but within this morph, it may have been a relatively robust animal.

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Supplementary Files

Table S1.

Additional figures S2.

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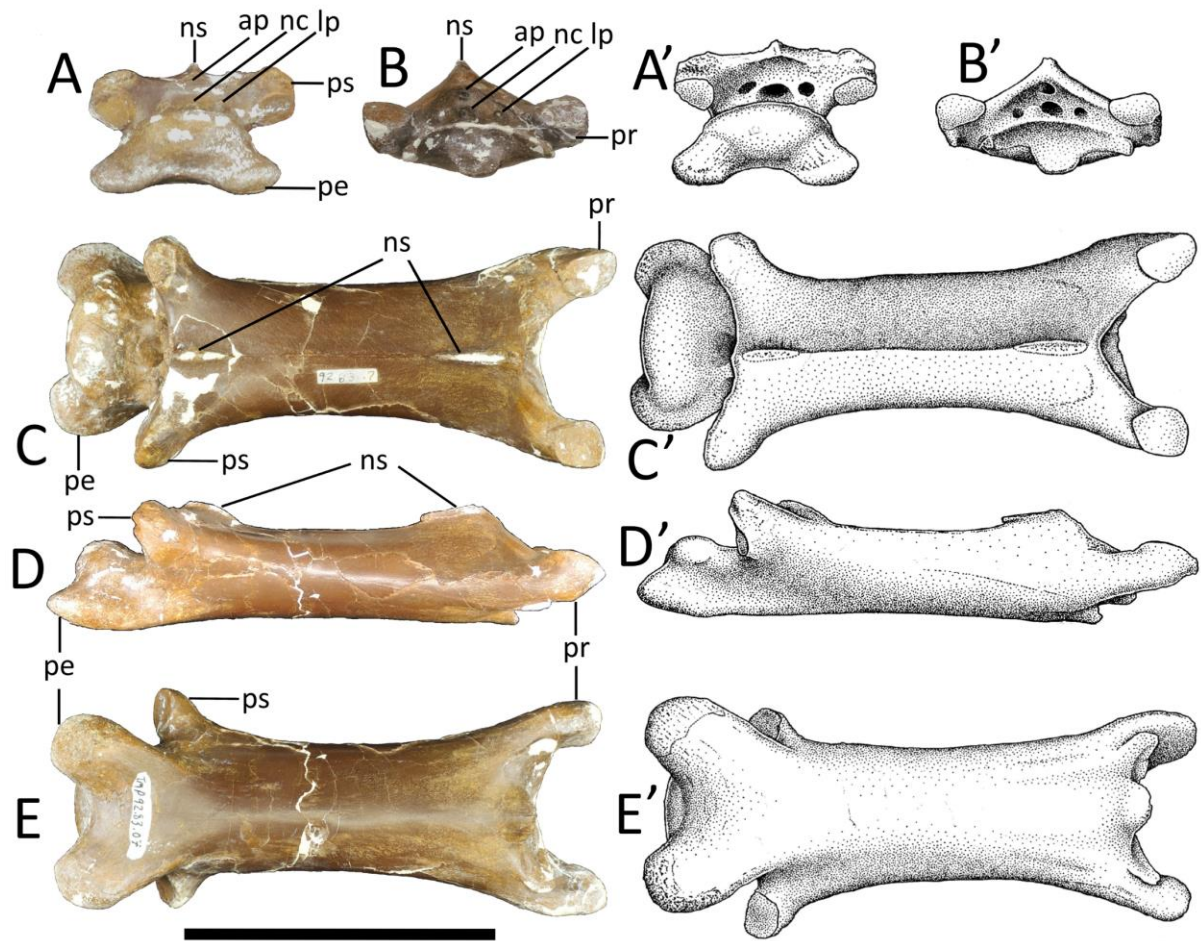


Figure captions

FIGURE 1. Cervical vertebra of specimen TMP 1992.83.07 in **A)** anterior view, **B)** posterior view, **C)** dorsal view, **D)** right lateral view and **E)** ventral view. Abbreviations: **ap** accessory pneumatopore, **lp** lateral pneumatopore, **nc** neural canal, **ns** neural spine, **pe** postexapophyses, **pr** prezygopophyses, **ps** postzygopophyses. Scale bar is 10 cm. Companion drawings (by S. Godfrey) of the element in these same views are presented as A'-E'. Full page width.

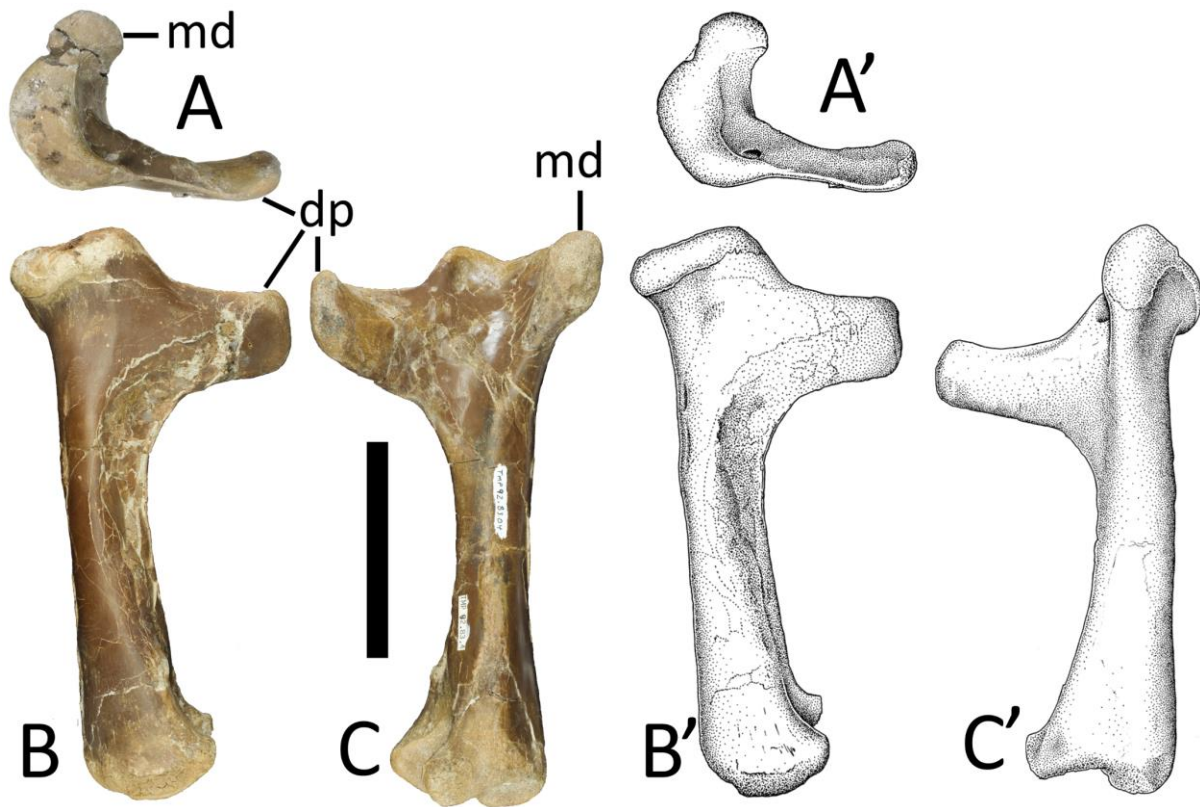


FIGURE 2. Humerus of specimen TMP 1992.83 in **A**) dorsal view, **B**) posteriolateral view and **C**) medioanterior view. Abbreviations **dp** deltopectoral crest, **md** medial crest. Scale bar is 10 cm. Companion drawings (by S. Godfrey) of the element in these same views are presented as **A'** and **B'** with **C'** showing the humerus in anterior view. Full page width.

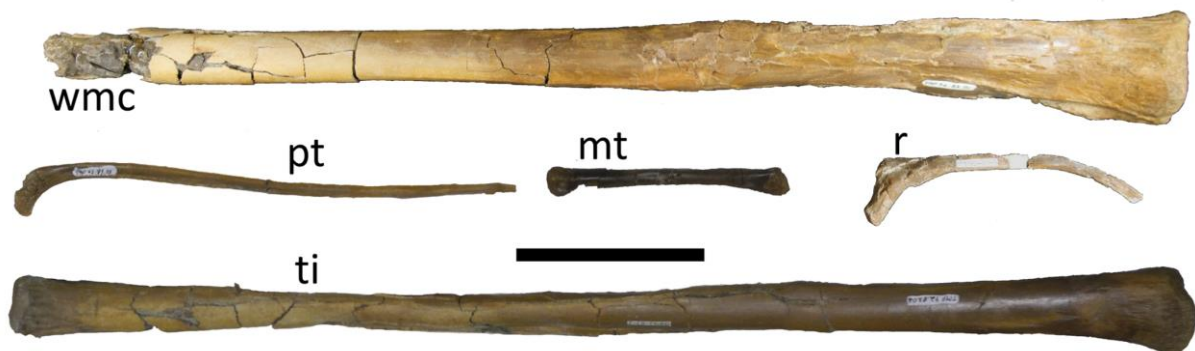


FIGURE 3. Additional material of specimen TMP 1992.83. Abbreviations: **mt** metatarsal, **pt** pteroid, **r** rib, **ti** tibia, **wmc** wing metacarpal. Scale bar is 10 cm. Page width.

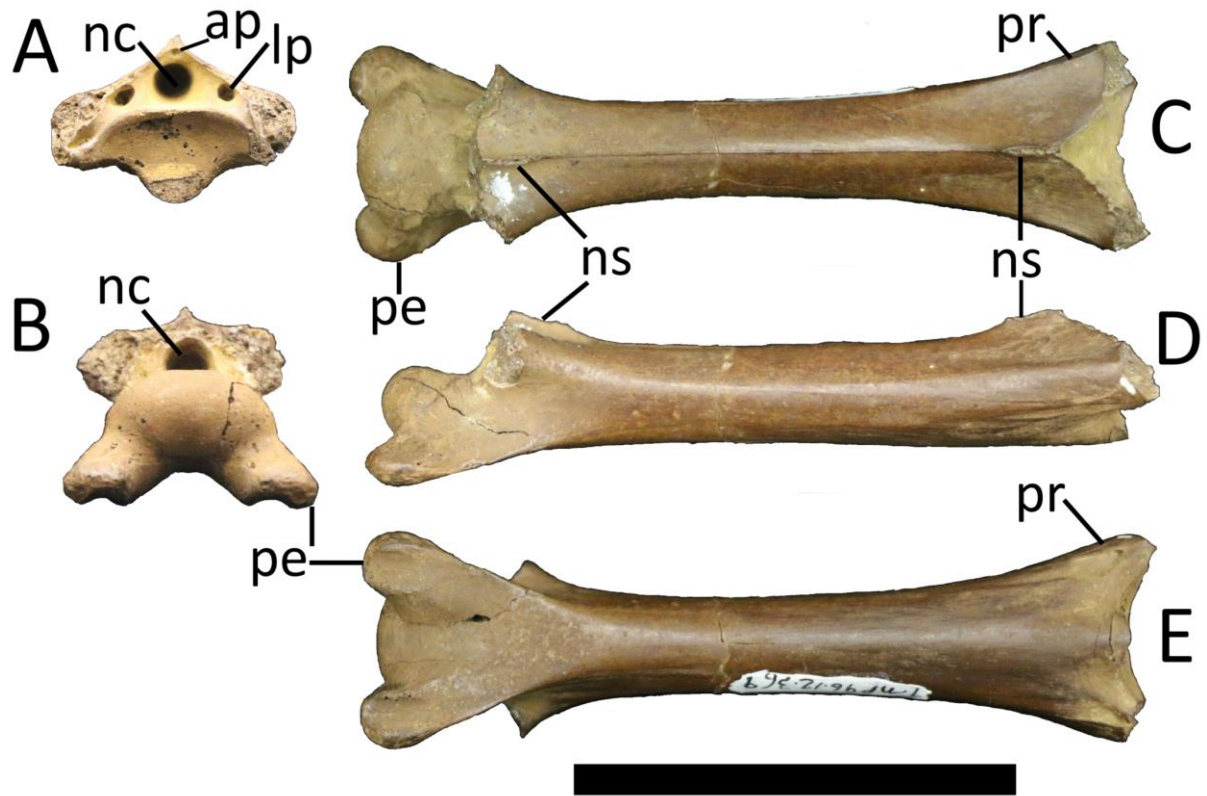


FIGURE 4. Cervical vertebra of specimen TMP 1996.12.369 in **A**) posterior view, **B**) anterior view, **C**) dorsal view, **D**) right lateral view and **E**) ventral view. Abbreviations as figure 1: Scale bar is 5 cm. Page width.

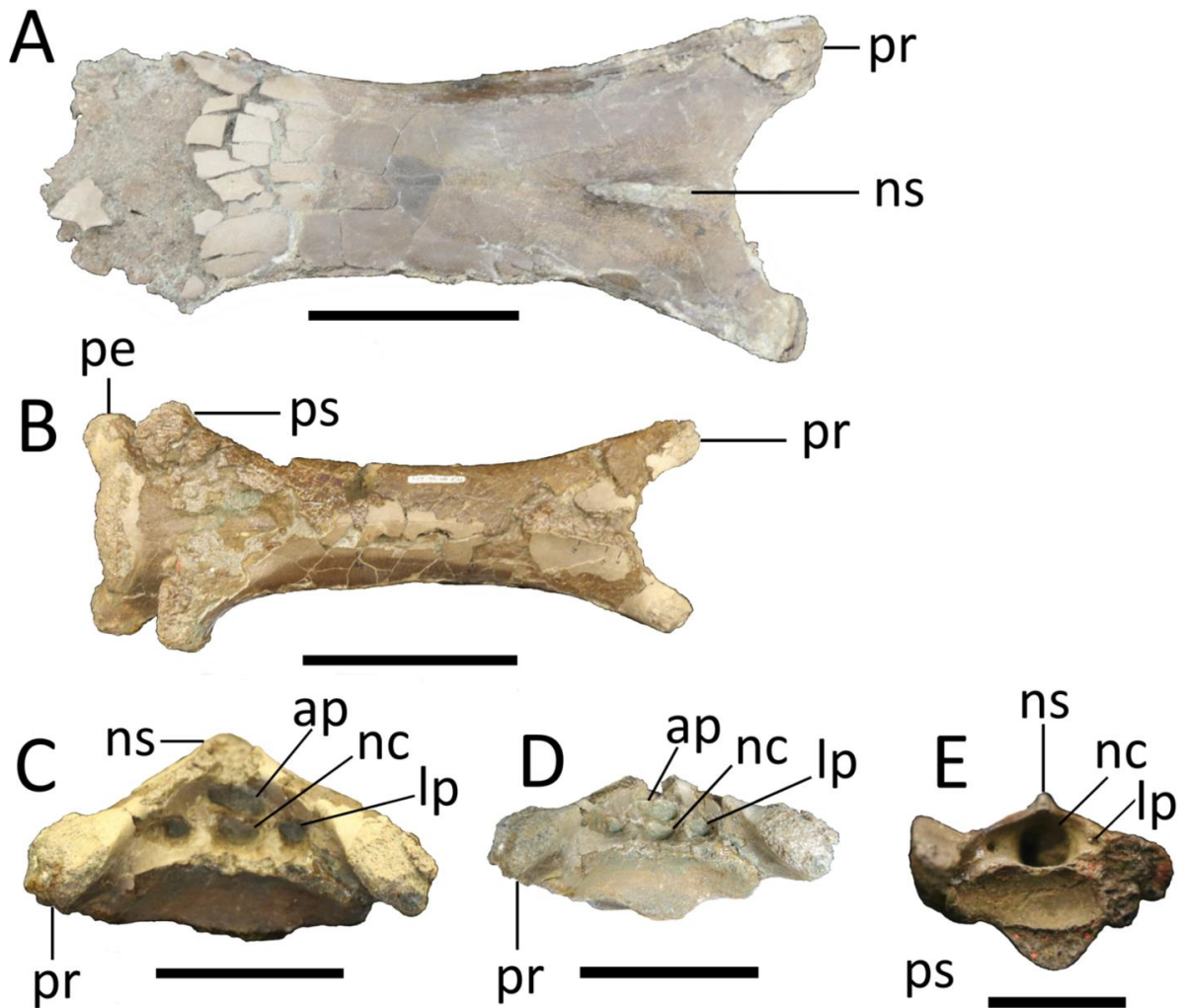


FIGURE 5. Cervical vertebra of Dinosaur Park azhdarchid pterosaurs. **A)** specimen TMP 1993.40.11 in dorsal view, scale bar 5 cm **B)** specimen TMP 1989.36.254 in dorsal view, scale bar is 10 cm **C)** specimen TMP 1989.36.254 in anterior view, scale bar is 5 cm **D)** specimen TMP 1989.36.254 in anterior view, scale bar is 5 cm **E)** specimen TMP 1981.16.107 in posterior view, scale bar is 1 cm. Abbreviations as figure 1. Two thirds width.

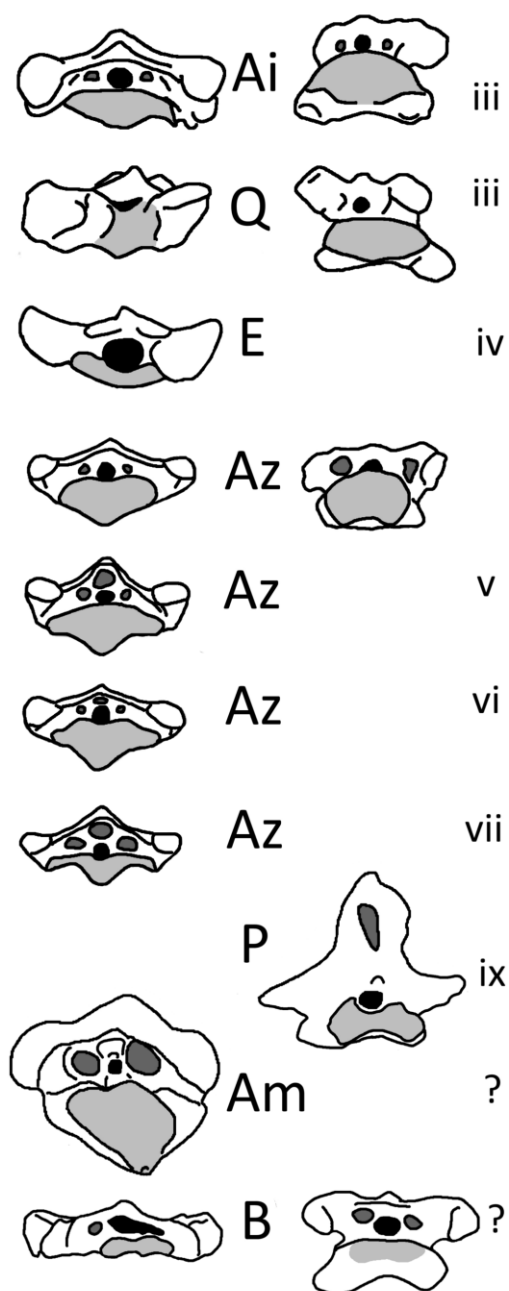


FIGURE 6. Simplified traces of the anterior (left column) and posterior (right column) views of selected other azhdarchid cervical vertebrae. Abbreviations and sources are as follows: **Q** *Quetzalcoatlus* (Witton and Naish, 2008), **Am** *Arambourgiania* (Martill et al., 1998), **Az** *Azhdarcho* (Averianov, 2010), **B** *Bakonydraco* (Ósi et al., 2005), **E** *Eurazhdarcho*, (Vremir et al., 2013), **P** *Phosphatodraco* (Suberbiola et al., 2003), **Ai** *Azhdarchidae* indet (Watabe et al., 2006). Numbers indicate the position of the element in the series, or a ‘?’ indicates unknown

or uncertain position. Illustrations not to scale and these are scaled to approximately equal condylar widths. Neural canals are solid black, pneumatic openings are dark grey, condylar faces are in pale grey. Single column width.