Neck biomechanics indicate that giant Transylvanian azhdarchid pterosaurs were short-necked apex predators (#12797)

First submission

Please read the **Important notes** below, and the **Review guidance** on the next page.
When ready **submit online**. The manuscript starts on page 3.

Important notes

Editor and deadline

Mathew Wedel / 3 Sep 2016

Files	9 Figure file(s) Please visit the overview page to **download and review** the files not included in this review pdf.
Declarations	No notable declarations are present

Review guidelines

Please in full read before you begin

How to review

When ready **submit your review online**. The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this **pdf** and upload it as part of your review

To finish, enter your editorial recommendation (accept, revise or reject) and submit.

BASIC REPORTING

- ✓ Clear, unambiguous, professional English language used throughout.
- ✓ Intro & background to show context. Literature well referenced & relevant.
- ✓ Structure conforms to **PeerJ standard**, discipline norm, or improved for clarity.
- ✓ Figures are relevant, high quality, well labelled & described.
- ✓ Raw data supplied (See **PeerJ policy**).

EXPERIMENTAL DESIGN

- ✓ Original primary research within **Scope of the journal**.
- ✓ Research question well defined, relevant & meaningful. It is stated how research fills an identified knowledge gap.
- ✓ Rigorous investigation performed to a high technical & ethical standard.
- ✓ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- ℹ Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- ✓ Data is robust, statistically sound, & controlled.
- ✓ Conclusion well stated, linked to original research question & limited to supporting results.
- ✓ Speculation is welcome, but should be identified as such.

The above is the editorial criteria summary. To view in full visit **https://peerj.com/about/editorial-criteria/**

Neck biomechanics indicate that giant Transylvanian azhdarchid pterosaurs were short-necked apex predators

Darren Naish Corresp., [1] , **Mark P Witton** [2]

[1] Ocean and Earth Science, University of Southampton, Southampton, UK
[2] School of Earth & Environmental Sciences, University of Portsmouth, Portsmouth, United Kingdom

Corresponding Author: Darren Naish
Email address: eotyrannus@gmail.com

Azhdarchid pterosaurs include the largest animals to ever take to the skies with some species exceeding 10 metres in wingspan and 220 kg in mass. Associated skeletons show that azhdarchids were long-necked, long-jawed predators that combined a wing planform suited for soaring with limb adaptations indicative of quadrupedal terrestrial foraging. The postcranial proportions of the group have been regarded as uniform overall, irrespective of their overall size, notwithstanding suggestions that minor variation may have been present. Here, we discuss a recently discovered giant azhdarchid neck vertebra referable to *Hatzegopteryx* from the Maastrichtian Sebeş Formation of the Transylvanian Basin, Romania, which shows how some azhdarchids departed markedly from conventional views on their proportions. This vertebra, which we consider a cervical VII, is 240 mm long as preserved and almost as wide. Among azhdarchid cervicals, it is remarkable for the thickness of its compacta (4-6 mm along its ventral wall) and robust proportions. By comparing its dimensions to other giant azhdarchid cervicals and to the more completely known necks of smaller taxa, we argue that *Hatzegopteryx* had a proportionally short, stocky neck highly resistant to ~~torque~~ and compression. This specimen is one of several hinting at greater disparity within Azhdarchidae than previously considered, but the first to demonstrate such proportional differences within giant taxa. On the assumption that other aspects of *Hatzegopteryx* functional anatomy were similar to those of other azhdarchids, and with reference to the absence of large terrestrial predators in the Maastrichtian of Transylvania, we suggest that this pterosaur played a dominant predatory role among the unusual palaeofauna of ancient Haţeg.

Neck biomechanics indicate that giant Transylvanian azhdarchid pterosaurs were short-necked apex predators

Darren Naish[1] and Mark P. Witton[2]

[1]Ocean and Earth Science, University of Southampton, National Oceanography Centre, Southampton, University of Southampton, Southampton SO14 3ZH, UK. [2]School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth, PO1 3QL, UK.

*Correspondence to [eotyrannus@gmail.com]

Abstract

Azhdarchid pterosaurs include the largest animals to ever take to the skies with some species exceeding 10 metres in wingspan and 220 kg in mass. Associated skeletons show that azhdarchids were long-necked, long-jawed predators that combined a wing planform suited for soaring with limb adaptations indicative of quadrupedal terrestrial foraging. The postcranial proportions of the group have been regarded as uniform overall, irrespective of their overall size, notwithstanding suggestions that minor variation may have been present. Here, we discuss a recently discovered giant azhdarchid neck vertebra referable to *Hatzegopteryx* from the Maastrichtian Sebeş Formation of the Transylvanian Basin, Romania, which shows how some azhdarchids departed markedly from conventional views on their proportions. This vertebra, which we consider a cervical VII, is 240 mm long as preserved and almost as wide. Among azhdarchid cervicals, it is remarkable for the thickness of its compacta (4-6 mm along its ventral wall) and robust proportions. By comparing its dimensions to other giant azhdarchid cervicals and to the more completely known necks of smaller taxa, we argue that *Hatzegopteryx* had a proportionally short, stocky neck highly resistant to torque and compression. This specimen is one of several hinting at greater disparity within Azhdarchidae than previously considered, but the first to demonstrate such proportional differences within giant taxa. On the assumption that other aspects of *Hatzegopteryx* functional anatomy were similar to those of other azhdarchids, and with reference to the absence of large terrestrial predators in the Maastrichtian of Transylvania, we suggest that this pterosaur played a dominant predatory role among the unusual palaeofauna of ancient Haţeg.

Substantial recent interest in the largest known azhdarchid pterosaurs – the Upper Cretaceous taxa *Arambourgiania philadelphiae*, *Quetzalcoatlus northropi* and *Hatzegopteryx thambema* – has shed much light on their morphology, palaeoecology, and flight capabilities (Witton and Naish 2008, 2015; Witton and Habib 2010; Habib 2013). ~~T~~his advanced pterodactyloid clade, deeply nested with the morphologically diverse Azhdarchoidea (Nessov 1984; Kellner 2003; Unwin 2003; Andres and Meyers 2013), ~~is noted for the~~ proportionally elongate, edentulous jaws, remarkably long, cylindrical neck vertebrae and often unusually large size of its ~~constituent taxa~~ (Witton and Naish 2008; Witton 2013). Although azhdarchids are ~~comparably~~ well represented in the fossil record compared to other pterosaur groups, frustratingly little is known of their skeletal anatomy. This situation is exacerbated ~~by the fact that~~ even the best represented taxa – *Zhejiangopterus linhaiensis* and *Quetzalcoatlus* sp. – remain only preliminarily described (Cai and Wei 1994; Lawson 1975; Kellner and Langston 1996). Hypotheses about flight, body mass, functional morphology, ecology and lifestyle, all of which remain controversial, are based predominantly on knowledge of inadequately described taxa (Witton and Naish 2008, 2015; Averianov 2013). Despite th~~is~~, azhdarchids have been widely assumed as uniform in anatomy and ecology (Unwin 2005; Witton and Naish 2008; Witton 2013).

Azhdarchids are primarily characterised by their elongate, often tubular neck vertebrae (Nessov 1984; Kellner 2003; Unwin 2003; Andres and Meyers 2013), and ~~it is a familiar fact of the pterosaur literature that~~ these often isolated fossils make up a substantial portion of the azhdarchid fossil record. That the giant azhdarchids had the same long necks as their smaller relatives has been verified by the discovery of several gigantic vertebrae, including University of Jordan, Department of Geology (UJA) specimen VF1: the 620 mm long holotype cervical V of *A. philadelphiae*. This specimen is argued by some authors to pertain to an animal with a c. 3 m long neck (Frey and Martill 1996; Martill et al. 1998), a dimension which would make large azhdarchids among the longest-necked animals outside of Sauropoda (Taylor and Wedel 2013) and Plesiosauria, despite their necks being formed of only nine vertebrae (Bennett 2014). However, recent discoveries of two proportionally short, isolated azhdarchid cervical vertebrae from the Maastrichtian Sebeş Formation (Transylvanian Basin) of western Romania have prompted suggestions that some azhdarchids may have been proportionally *short necked* (Vremir 2010; Vremir et al. 2015). The first of these specimens, LPV (FGGUB) R.2395, was interpreted as a cervical IV from a small azhdarchid with an estimated 3 m wingspan (Vremir et al. 2015). The second represents a gigantic azhdarchid: Transylvanian Museum Society (Cluj-Napoca, Romania) specimen EME 315 (Fig. 1). This latter bone is proportionally short and wide, of robust construction and bears relatively thick bone walls. Details of bone structure and provenance led Vremir (2010) to suggest it may represent a cervical III from *Hatzegopteryx*, a giant azhdarchid described from the middle member of the Densuş-Ciula Formation, Maastrichtian of Vãlioara, northern Haţeg basin, deposits contemporary and adjacent to the

Sebeş Formation. Vremir (2010) concluded that the size and shape of EME 315 is so distinct relative to that of other azhdarchids that it must reflect a departure from expected azhdarchid anatomy and lifestyle.

The concept of 'short necked' azhdarchids is yet to be explored in detail, despite the significance it has for our understanding of azhdarchid palaeoecology and disparity. The functional anatomy of the long, stiffened azhdarchid neck has been the most controversial element in discussions of azhdarchid lifestyles (e.g. Witton and Naish 2013, 2015; Averianov 2013, and references therein), so gaining an understanding of its variation and biomechanics is paramount to advancing palaeobiological appreciation of the group. Here, we investigate the radical morphological differences between EME 315 and other azhdarchid cervicals on two grounds. Firstly, we attempt to estimate the probable neck length of EME 315 and other azhdarchids (both giant and smaller species) to assess possible variation in their proportions and form. Secondly, we assess the bending strength of two giant azhdarchid vertebrae (EME 315 and UJA VF1) to see what influence variation in structural properties might have had on function and hence on behaviour and ecology. It is imperative to these studies that we also understand the likely identity and vertebral position of EME 315, and this is also discussed below.

Methods

Taxonomic and anatomical identity of EME 315

EME 315 possesses multiple apomorphies of azhdarchid pterosaur cervical vertebrae, including the characteristic 'bifid' neural spine, large, dorsoventrally flattened zygapophyses and a low centrum (e.g. Andres and Ji 2008; Averianov 2010; Buffetaut and Kuang 2010; Vremir et al. 2013). It can thus be referred to Azhdarchidae with confidence. We agree with Vremir (2010) that comparable size, anatomy, and geographical and geological provenance all indicate affinities with *Hatzegopteryx*, a robust giant azhdarchid first described from nearby Vălioara in the Haţeg Basin (Buffetaut et al. 2002, 2003). We draw specific attention to the ventral bone wall of EME 315: at 4-6 mm thick, it is considerably thicker than the 2.6 mm or less reported from most other giant azhdarchids (including the giant *Arambourgiania* holotype cervical – Frey and Martill 1996; Martill et al. 1998) but is comparable to bone walls of the *H. thambema* holotype humerus (Laboratory of Vertebrate Palaeontology, Geological and Geophysical Faculty, University of Bucharest, Romania) FGGUB R1083 (Buffetaut et al. 2003). A large, elongate cervical vertebra from the Maastrichtian of the French Pyrenees was also described as having thick bone walls of 2-6 mm (Buffetaut et al. 1997) so it is possible that this feature was more widespread in azhdarchids. The spongiose internal texture visible at the broken end of

EME 315 also recalls the aberrant internal structure of the skull and humerus of the *H. thambema* holotype (Buffetaut et al. 2002). We consider *Hatzegopteryx* and EME 315 to possess a bone construction atypical among pterosaurs, and a close relationship between these specimens likely. However, the Sebeş Basin material does not overlap with the *H. thambema* holotype, so we, accordingly, provisionally identify the Sebeş Basin vertebra as *Hatzegopteryx* sp. only.

Isolated azhdarchid cervicals have typically been regarded as offering little insight to their position within the cervical series, except perhaps for cervical V, which appears distinctly elongate (Frey and Martill 1996; Martill et al. 1998). Recent work on relatively complete azhdarchid cervical skeletons indicates that their vertebrae may show consistent characteristics specific to the position in the cervical series (Pereda-Suberbiola et al. 2003 (*sensu* Kellner 2010); Averianov 2010, 2013) (Fig. 2). Work in this area must be regarded as provisional given that complete azhdarchid necks, or even sufficient material to completely reconstruct entire cervical series, remain few in number. However, we consider known azhdarchid necks of consistent enough form that the likely vertebral position of well-preserved azhdarchid cervicals, such as EME 315, can be determined with some degree of confidence.

Vremir (2010) considered EME 315 as a cervical III, but we consider this unlikely. The neural spines of cervical III in *Azhdarcho lancicollis* (Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia, ZIN PH 131/44) and *Quetzalcoatlus* sp. (Texas Memorial Museum, Austin, USA, TMM 41544.16) extend for the length of the entire centrum and lack any obvious reduction in height at mid-length (Fig. 2a; Howse 1986; Averianov 2010), a significant contrast to the bifid neural spine of EME 315. Indeed, Howse (1986) reported that the *Quetzalcoatlus* cervical III neural spine is at its highest point mid-way along its length, a marked contrast to the condition in EME 315. The proportions of cervical III cotyles, which are approximately twice as wide as tall and subequal in height to the neural arch, also contrast with EME 315, as does the continuous tapering of cervical III zygapophyses when viewed in dorsal aspect. Cervical IIIs also seem generally longer-bodied than the proportionally short EME 315. We find greater similarity with other azhdarchid cervicals (below) and thus disagree with a cervical III identity for EME 315.

Azhdarchid cervicals IV and V can be up to eight times longer than wide (Lawson 1975; Howse 1986; Frey and Martill 1996). Their neural spines comprise low anterior and posterior ridges with a mid-length so reduced that they are confluent with the vertebral corpus, sometimes being represented by a faint, narrow ridge at best (Fig. 2d-f). EME 315 is not elongate relative to its width (Fig. 1E) and, though possessing a bifid neural spine, the breadth of the preserved neural spine bases suggests they were robust, tall structures. Azhdarchid cervical VIs ~~seem~~ similar to fourth and fifth elements, but have a proportionally tall posterior neural spine (Fig.

2g-h). EME 315 contrasts with most or all of these conditions, and thus likely pertains to a posterior section of the neck – that is, to cervicals VII or VIII.

Strong similarity occurs between EME 315 and cervicals VII and VIII of *Azhdarcho lancicollis* (ZIN PH 138/44 and 137/44, respectively (Averianov 2010, 2013), Fig. 2i-k), with the most notable similarity pertaining to cervical VII. The cotyle heights of these vertebrae are characteristically shallower than their neural arches, and four times wider than high (Averianov 2010). The cotyle width:height ratio of EME 315 approximates this at ca. 3.7. Both EME 315 and *Azhdarcho* cervical VII possess hypapophyses, which is lacking in cervical VIII of *Azhdarcho* (Averianov 2010). Reconstructed length:width ratios of EME 315 and the posterior cervicals of *Azhdarcho* are similar (1.36 in *Azhdarcho* cervical VII, 1.06 in cervical VIII, versus 1.25 in EME 315; based on a reconstructed EME 315 length and width of 300 mm and 240 mm, respectively), as are the presences of pneumatic foramina dorsal to the neural canal. The relatively splayed prezygapophyses of cervicals VII and VIII in *Azhdarcho* also correspond well with EME 315, although they are much smaller in *Azhdarcho* cervical VIII. The articular faces in the latter are joined to the vertebral body via a constricted bony shaft, whereas the zygapophyses of EME 315 and *Azhdarcho* cervical VII are more massive in overall form. Cervical VII in *Azhdarcho* and EME 315 are also similar in having a tapered 'waist' mid-way along the length of the centrum, whereas this feature is absent in cervical VIII of *Azhdarcho*: in contrast, it has subparallel lateral margins. The pneumatic foramina are larger than the neural canal in *Azhdarcho*'s cervical VII, which contrasts with the condition in EME 315 and cervical VIII of *Azhdarcho*. EME 315 also lacks pneumatic foramina on the lateral surface of the centrum, in contrast to *Azhdarcho*'s cervical VIII where they are present. The neural spines on the posterior cervicals of *Azhdarcho* are unknown, but those of the posteriormost cervicals of *Phosphatodraco mauritanicus* are proportionally tall and anteroposteriorly restricted (Fig. 2J; Pereda-Suberbiola et al. 2003). This condition matches the one that appears to have been present in EME 315.

EME 315 thus possesses a combination of anatomical traits that are a good match for the posterior cervical vertebrae of at least two other azhdarchid taxa, and it differs markedly from the middle or anterior neck vertebrae of any taxon. We note particular similarity with cervical VII of *Azhdarcho* and hence provisionally consider a seventh cervical position most likely for EME 315, the caveat being that additional discoveries of azhdarchid posterior cervical vertebrae are needed to bolster our identification.

Size of the EME 315 individual

We refrain from providing a specific wingspan estimate for the EME 315 individual because the relationships between wingspans and cervical vertebrae are not reliably predicted using existing data. Disagreements over the wingspan of the individual represented by the *Arambourgiania* holotype cervical (stated as having a wingspan of 7-8 m wingspan by Pereda-Suberbiola et al. 2003 and yet argued as 10 m or more by others – Frey et al. 1996; Steel et al. 1997; Martill et al. 1998) demonstrate the uncertainty surrounding size estimates of the largest pterosaurs known only from vertebral remains. Vremir (2010) indicated that the great width of EME 315 suggested a similarly expanded postcervical column and perhaps a much larger overall size than that of other giant azhdarchids. This interpretation is questionable as the cervical and anteriormost dorsal vertebrae of giant pterodactyloids are wider and more massive than the rest of the axial column (Bennett 2001; Kellner et al. 2013). A lack of study on the proportional changes in the pterosaur axial column precludes detailed commentary on the likely dimensions of the dorsal column belonging to the animal represented by EME 315, but observations of other pterodactyloid skeletons suggest it may be unwise to use cervical width as an indicator of overall body size.

Nevertheless, it is possible to provide a qualified assessment of the general size represented by this vertebra. EME 315 is the most robust pterosaur cervical yet reported and conforms proportionally in width to approximate size predictions for FGGUB R1083, a humerus estimated to represent a 10m wingspan animal (Buffetaut et al. 2003). The size of pterodactyloid cervical condyles and cotyles appears to be relatively uniform along the cervical series (e.g. *Anhanguera* (Wellnhofer 1991a); *Quetzalcoatlus* sp. (Witton and Naish 2008); *Azhdarcho* (2010)), allowing us to assume that the 150 mm wide cotyle of EME 315 is similar to the condylar and cotylar dimensions present along the preceding part of the neck. In the reconstructed neck of *Azhdarcho*, and in completely known necks of *Anhanguera*, atlas cotyle width (assumed to correspond to the dimensions of the occipital condyle) is 30-40% of condyle and cotyle width in the remainder of the neck: the 55 mm wide occipital condyle of the *H. thambema* skull therefore corresponds to the 150 mm wide cotyle of EME 315. The unprecedented width and robust construction of EME 315 also corresponds with the unusually broad skull of *H. thambema*, estimated to span 500 mm across the quadrates (Buffetaut et al. 2003). We take these comparisons to indicate that EME 315 probably represents an animal at the upper known limit of pterosaur size.

Neck length estimate

Incredibly long necks incorporating elongate, tubular mid-cervical vertebrae are a well-known feature of Azhdarchidae (e.g. Nessov 1984; Frey and Martill 1996; Kellner 2003; Unwin 2003; Witton and Naish 2008; Averianov 2013). However, published attempts to estimate the length of giant azhdarchid necks are rare and presently limited to isometric scaling of *Quetzalcoatlus* bones to the same linear proportions as the *Arambourgiania* holotype (Frey and Martill 1996;

Steel et al. 1997). Subsequent discussions of neck length in giant azhdarchids (e.g. Martill 1997; Taylor and Wedel 2013) have relied on these figures. However, pterosaur necks, like those of virtually all long-necked tetrapods, are known to scale ~~with allometry~~ (Wellnhofer 1970) meaning that it may be unwise to rely on isometric extrapolations when estimating their size.

To estimate and compare the lengths of cervicals III-VII for the EME 315 individual and other azhdarchids, we compiled vertebral length data from six azhdarchid necks: four associated and complete cervical series – representing three skeletons of *Zhejiangopterus linhaiensis* (Cai and Wei 1994), and the holotype of *Phosphatodraco mauritanicus* (Pereda-Suberbiola et al. 2003, as interpreted by Kellner 2010) – in addition to reconstructed, composite skeletons of *Azhdarcho* and *Quetzalcoatlus* sp. (Steel 1997; Averianov 2013) (Table 1). Our sample represents animals with wingspans ranging from 2.5-4.6 m and cervical III-VII lengths of 326–1495 mm. Regression analyses of these data provided reliable relationships between azhdarchid cervical vertebrae and neck length (Fig. 3). Surprisingly, we find that azhdarchid necks scale rather differently to other long necked tetrapods. In most long necked animals – examples include sauropods, giraffes, plesiosaurs and tanystropheids (Tschanz 1988; O'Keefe and Hiller 2006; Parrish 2006) – extreme neck length is often associated with a disproportionate increase in the size of cervical vertebrae (i.e. larger animals have disproportionately longer individual neck bones with respect to overall neck length). However, azhdarchid cervical vertebrae seem to scale in a manner suggestive of either negative allometry or near isometry. Cervicals III and VII show scaling exponents of 0.88 and 0.78 (respectively), while cervicals IV – VI show exponents within 0.9 – 1.11 (Fig. 3). This 'conservative' approach to scaling is discussed more below.

Bone strength analysis

Structurally, azhdarchid cervicals are essentially hollow tubes with near-circular or elliptical cross sections (Fig. 4): they are thus of a form conducive to beam loading calculations if we wish to ascertain their relative strength. We modelled the bending strength of both UJA VF1 (the holotype vertebra of *Arambourgiania*) and EME 315 based on their minimal central diameters, and using both their preserved and estimated total lengths (Table 2). To enhance comparability between these vertebrae, we also modelled a hypothetical *Hatzegopteryx* cervical V based on length projections from our azhdarchid neck dataset and the centrum dimensions of EME 315: we estimate this bone's length as 413 mm. This also provides a minimum estimate of neck strength because, as noted above, cervical V is the longest bone in the azhdarchid neck and thus the most susceptible to distortion under loading. Vertebral sections were modelled as consistent along the vertebral length and internal supporting structures were not factored into our equations. Because the vertebrae in question are elliptical in cross-section, we modelled their stresses in both dorsoventral and lateral loading. To calculate second moment of area (*I*) for each vertebral axis, we used:

2. $I = \pi/4(R_1R_2^3 - R_3R_4^3)$

Where R_1 and R_2 represents the total bone radii in perpendicular x and y axes (respective to loading regime), and R_3 and R_4 represent radii of the internal bone cavity. Bone stress was modelled using cantilever-style loading, where one end of the bone is fixed and the total length of the bone equals the moment arm. Stress values reflect those experienced at the supported end of the bone. Vertebrate bones are rarely loaded as true cantilevers in life but such a reductionist approach provides a quantified means of comparing bone structure and robustness (Witton and Habib 2010). ~~As cantilevers,~~ we calculated stresses (σ, Mpa) experienced at the supported end of the vertebrae during loading:

2. $\sigma = WL/Z$

Where *L* is bone length (mm), *W* (N) is the weight loaded onto the bone and *Z* is section modulus (second moment of area/distance to neutral ~~axis~~ of vertebra). Calculating bone strength requires some assumptions about the Young's ~~M~~odulus of pterosaur bone. We follow Palmer and Dyke (2009) in using 22 G~~p~~a – a value agreeing with several avian long bones – which seems a reasonable proxy for pterosaur bones. Following Currey (2004) and Palmer and Dyke (2010), we used the relationship between Young's ~~M~~odulus and yield stress in tension of 162 M~~p~~a. We modelled a range of values reflecting different upper limits for giant pterosaur body mass (180–250 kg) for *W* to demonstrate the sensitivity of our results and calculate Relative Failure Force (RFF~~) ~~(Witton and Habib 2010) for each model. RFF is bone failure force, in bending, divided by total body weights. Although pterosaur axial elements were unlikely to ever bear a full loading of body mass in life, it provides a useful proxy by which we might compare the results here with those of other studies (e.g. Witton and Habib 2010).

Results and discussion

Neck length of EME 315 and other azhdarchid pterosaurs

The results of our neck length estimates are summarised in Fig. 5. Our dataset shows a reasonable ($r^2=0.973$) relationship between the length of cervical VII and the combined lengths of cervicals III-VII:

1. $CIII\text{-}VII = 17.283CVII^{0.7835}$

where *CIII-VII* represents the length of cervicals III-VII (mm), and *CVII* represents the length of cervical VII (mm). Assuming EME 315 is a seventh cervical, its preserved length (240 mm) predicts a cervical III-VII length of only 1266 mm, while the estimated total length (300 mm) projects cervical III-VII values of 1508 mm. These values must be considered low given the size of EME 315 and its indications of body size similar to that of the *H. thambema* holotype. Using the estimated 770 mm length (Frey and Martill 1996), we modelled the cervical III-VII length of *Arambourgiania* at 2652 mm, a value shorter than estimates based on isometric scaling (2817 m; Steel 1997) but still 75% longer than that predicted for the EME 315 azhdarchid. This discrepancy is further borne out in our estimate of 412 mm for a *Hatzegopteryx* cervical V – almost half the estimated length of *Arambourgiania* cervical V. Indeed, predicted cervical values of EME 315 match those measured from the reconstructed neck of the 4.6 m wingspan *Quetzalcoatlus* sp. (Steel 1997): its estimated cervical V length and neck length are near identical to values measured from *Q*. sp., despite this taxon being substantially smaller (410 mm and 1495 mm, respectively) (Fig. 6).

These calculations ~~agree~~ in establishing that *Hatzegopteryx* had a proportionally short neck (Vremir 2010) c. 50-60% of the length expected for a 'typical' giant azhdarchid like *Arambourgiania*. Our estimates indicate that giant azhdarchids included both *Hatzegopteryx*-like forms with short, wide necks, and *Arambourgiania*-like species with long, gracile necks. The former befits an animal with the unusually robust cranial anatomy known for *H. thambema* and is consistent with the view that this pterosaur was robust overall (Buffetaut et al. 2002, 2003). As noted above, short necks have been postulated for a much smaller Romanian azhdarchid known from a likely cervical IV, LPV (FGGUB) R.2395 (Vremir et al. 2015). This neck of this animal, considered to have a 3-4 m wingspan, was estimated at 352–419 mm using an earlier version of the data presented above: we revise this estimate here to 460 mm. Nevertheless, this value is still shorter than that measured from smaller azhdarchids (e.g. the 2.5 m wingspan *Zhejiangopterus linhaiensis*, 502 mm measured neck length) and suggests that short necks may not be restricted to giant taxa (Vremir et al. 2015). Overall, these data suggest that there is more variation in neck proportions and robustness within Azhdarchidae than previously anticipated: the concept of the clade as one with a uniformly long-necked morphotype (e.g. Witton and Naish 2008) now warrants significant reappraisal.

Neck biomechanics in giant azhdarchids

EME 315 represents an anatomical extreme among pterosaur neck vertebrae: its size, bone wall thickness and massiveness are unprecedented among other flying reptile remains. Its functional properties, and utility within a possibly shorter variant of the azhdarchid neck, are therefore significant not only to our understanding of azhdarchid palaeobiology as a whole, but in that they represent a hitherto unreported morphological class of pterosaur anatomy.

Our bone strength analysis (Table 2) shows that *Hatzegopteryx* neck vertebrae are considerably stronger than those of *Arambourgiania*. Even at the lowest loading threshold, and in its strongest bending plane (sagittal), the holotype *Arambourgiania* cervical does not withstand the strain of one bodyweight. At most, the UJA VF1 vertebrae has RFFs of 0.57 (1765 N loading in sagittal plane), this decreasing to 0.38 in 2452 N coronal loading. *Hatzegopteryx*, however, shows consistent capacity for the withstanding of high stresses. The (reconstructed) 300 mm long EME 315 model has an RFF of 10.04 when loaded with 1765 N in the coronal pane, and maintains high RFFs (5.57) even when loaded by 2452 N on its weakest axis. The longer (412 mm) hypothetical *Hatzegopteryx* cervical IV is also consistently strong in all tests, able to withstand 4.05 - 7[illegible] RFFs in various loading regimes.

These findings confirm predictions that giant azhdarchid vertebrae are not functionally uniform (Vremir 2010), and that assessments of the detailed anatomy of giant azhdarchid cervicals provide insights into the contrasting figures generated by our bone strength analysis. *Arambourgiania* cervical V can be viewed as a giant variant on a ‘typical’ azhdarchid cervical, being a thin-walled (maximum bone wall thickness 2.6 mm), elongate tube supported internally by a network of bony trabeculae (Frey and Martill 1996; Martill et al. 1998). It mainly differs from other azhdarchid cervicals in bearing a mid-centrum section which is taller than wide (55 mm tall vs. 48 mm wide). As is well documented for other long pterosaur bones, this form is ideally suited to maximising stiffness, and thus resisting bending and torsion over long dimensions and within constrained loading regimes. The ratio of bone shaft thickness to wall thickness (bone radius/bone thickness, R/t) in UJA VF1 is 9.9, a value greater than recorded from other tetrapods but comparable to those measured from large pterosaur wing bones (Currey 2002; Fastnacht 2005). Frey and Martill (1996) suggested that the unusually tall cross section of *Arambourgiania* likely improved its resistance to dorsoventral deformation, and this is corroborated by our bending analysis. Dorsoventral expansion of a cervical vertebra is an economical evolutionary ‘method’ of increasing vertical bending strength without incurring additional mass (Frey and Martill 1996), and we might predict this to be an evolutionary response to an increase in the weight of the neck and head. Even accounting for the ‘conservative’ scaling of pterosaur necks (Fig. 3), mass compounds exponentially against length, and giant pterosaurs would thus have experienced proportionally higher loading on their neck skeleton than similarly proportioned smaller species. As with most pterosaur bones, the greatest risk of structural failure to UJA VF1 is buckling: this can be caused by high compressive loads along the long axis of the vertebra or large bending moments. This may explain why the R/t of the *Arambourgiania* cervical is not as high as those measured from other long pterosaur bones (Fastnacht 2005 reports an R/t of 20 for some pterosaur bones): lowering R/t is one way to increase buckling strength.

The structural characteristics of EME 315 frequently contrast with this configuration. As noted above, the vertebra is proportionally short overall, and although its mid-centrum section is of an elliptical shape typical for an azhdarchid, it is broader than other azhdarchid centra in all respects, being 74 mm tall by 115 mm wide. The large second moment of area created by the expanded centrum can be seen as being particularly significant as goes resisting bending through experimental modelling of a vertebra with the *Hatzegopteryx* section profile and the 770 mm length predicted for *Arambourgiania* cervical V. Even when loaded at 2452 N, this hypothetical vertebra still produces high (over 2.17) RFF scores. By contrast, the smaller, thinner-walled section of *Arambourgiania* only achieves an RFF of 1.47 when shortened to 300 mm (the predicted complete length of EME 315) and modelled with the lightest loading in our experiments.

The EME 315 bone wall is formed by a relatively thick (4-6 mm) layer of banded bone which means that – despite the size of the centrum – it has an R/t comparable to that of *Arambourgiania* at 9.45. EME 315 compromises the stiffening effect of a higher R/t in having expanded bone walls. Its larger size hypothetically permits a much higher R/t, which would be advantageous to decreasing mass against bone structural performance (see Currey 2002 for discussion). However, it may be that the thicker bone walls of this bone enhanced buckling strength without drastically altering bending strength (Currey 2002) or that its cross-sectional proportions are sufficient to provide high bending resistance alone. Such thick bone walls are not without precedent in pterosaurs – they appear in certain dsungaripterid limb bones (Fastnacht 2005), a partial vertebra from another European azhdarchid (Buffetaut et al. 1997) and the *Hatzegopteryx* type material (Buffetaut et al. 2002, 2003). Buckling resistance has been posited as an explanation for this phenomenon in at least some cases (Fastnacht 2005).

Well-preserved endosteal regions of EME 315 show that a system of camellate bone, rather than the trabeculae seen in *Arambourgiania* (Martill et al. 1998), occupied at least the ventral part of the centrum's interior. Such tissues seem pervasive throughout *Hatzegopteryx* bones, also being present in the jaw and humerus. We interpret these features as evidencing further resistance to buckling elsewhere in the skeleton. Finally, we note that the already large mid-length centrum of EME 315 is considerably expanded at the anterior and posterior ends of the vertebra. This allows for broadened cotyle/condyle articulations and a greater capacity to distribute high stresses between vertebral joints; indeed, their relatively wide, shallow profile is ideally shaped to resist torsion.

Assuming that the general characteristics and proportions of these giant azhdarchid neck vertebrae apply to their entire cervical series (which seems reasonable, given the profiles of other pterosaur vertebrae), two major structural configurations seem to have existed among giant forms. Selection pressures on *Arambourgiania* seem to have prioritised mass reduction and stiffness, which are ideal for elongating bones at the expense of loading capacity. We predict that the anterior cervical skeleton and crania of *Arambourgiania* were relatively slender and lightweight, more akin to the gracile skull of *Quetzalcoatlus* than the proportionally broad or deep skulls of *Hatzegopteryx* or the unnamed Texas Memorial Museum specimen 42489-2. EME 315 seems contrarily adapted: its cross-sectional proportions, massive features and thick bone walls are not advantageous for producing a long, lightweight neck skeleton (at least within the context of pterosaur anatomy), but better suited to resisting high bending and compressive stresses. Assuming the other neck bones of the EME 315 individual were similarly adapted, *Hatzegopteryx* must have possessed a significantly stronger neck skeleton than *Arambourgiania*, and perhaps the strongest neck of any known pterosaur. Our stress analysis accords with observations that the very large jaw bones of *Hatzegopteryx* indicate a very wide (0.5 m), and thus potentially relatively large and heavy, skull in this animal (Buffetaut et al. 2002, 2003).

Supporting and utilising the azhdarchid neck skeleton

The robustness and apparent stress resistance of EME 315 raises questions about the function of the *Hatzegopteryx* neck, particularly with respect to how it may have performed in tasks other than just supporting a large skull. Investigating this requires some appreciation of pterosaur neck musculature. Pterosaur cervical myology has not featured prominently in technical discussions of this group, but artistic representations of azhdarchids – many of them overseen by pterosaur researchers – frequently show an extremely reduced cervical musculature relative to the typical tetrapod condition. We assume that these reconstructions were compiled following observation of mid-series vertebrae, which are very long, have reduced processes, and have indications of limited arthrological range (Averianov 2013).

However, azhdarchid fossils – including the specimens discussed here – show that the assumption of a paltry, reduced neck musculature represents an oversimplification and is inconsistent with anatomical data from other animals. Our arguments can be summarised as follows: 1) azhdarchid skeletal anatomy suggests that certain muscle groups related to neck function were indeed minimised, but that many aspects of axial, skull and pectoral skeletal anatomy show potential for large muscle attachments; 2) comparisons made between azhdarchid neck skeletons and those of extant animals suggest they are not as atypical as often assumed, and that reptilian cervical musculature correlates well with large muscle attachment sites on azhdarchid cervicals; and 3), that various aspects of azhdarchid anatomy counter any proposals of a reduced degree of soft-tissue neck support. We will briefly explore these points here to further elaborate on the functional capacity of giant azhdarchid necks.

Our most general observation is that complete, associated azhdarchid neck skeletons show that they are not solely composed of simple, stiff-jointed, near-featureless tubes. As outlined in Fig. 2, cervicals III, VI, VII and (probably) VIII possess prominent neural spines, indicating differential development of epaxial musculature along the neck (Witton and Naish 2008). The ‘tubular’ morphology often ascribed to their neck skeletons only really applies to cervicals IV and V. Averianov (2013) demonstrated that intervertebral cervical articulations are variable along the neck, those of the posterior vertebrae being less restrictive than those of the anterior- and mid-sections. In these respects, azhdarchid necks are comparable to those of other amniotes. X-rays of living animals show that the middle section of the cervical series is often relatively immobile, and that the majority of movement in the neck is achieved via movement at either end of the cervical series (Vidal et al. 1986; Graf et al. 1992, 1995; Taylor et al. 2009). Relatively long-necked mammals (examples include horses, deer, giraffes and camels), as well as extinct long-necked reptiles such as tanystropheids, possess reduced processes and relative immobility associated with their mid-length cervical vertebrae (Fig. 7; Goldfinger 2004; Renesto 2005). Azhdarchid neck skeletons are thus typical in that greater complexity and robustness was present at the extreme ends of their cervical skeleton, as well as in neighbouring cranial or torso skeletal elements; this was surely associated with the anchoring of powerful neck musculature at the base and anterior end of the neck. These are optimal positions from which to support and operate long necks. In view of this, the elongate and tubular, relatively immobile mid-series vertebrae of azhdarchids should be viewed as a pronounced development of a skeletal adaptation common across tetrapods, not as an unusual or unprecedented anatomical configuration.

Azhdarchid skeletons show ample attachment sites for neck musculature. For example, the occipital face of *Hatzegopteryx* shows obvious signs of substantial soft-tissue attachment: the nuchal line is well developed and long, and its dorsolateral edges are deeply dished and marked with vertical scarring (Buffetaut et al. 2002, 2003). Comparison with extant reptile anatomy (Herrel and de Vree 1999; Cleuren and de Vree 2000; Snively and Russel 2007) suggests that these features reflect large insertion areas for transversospinalis musculature (specifically m. transversospinalis capiti and the m. epistropheo-capitis group), cervical musculature devoted to neck extension and lateral flexion. The large neural spines on posterior azhdarchid cervicals and anterior thoracic vertebrae provide potential origin sites for m. transversospinalis capiti, while the long neural spine of cervical III likely anchored m. epistropheo-capitis. The opisthotic process of *Hatzegopteryx* is poorly known but was evidently large and robust and likely facilitated attachment of large neck extensors and lateral flexors (m. semispinalis capitis/spinocapitis posticus). Similarly, the broken basioccipital tuberosities of *Hatzegopteryx* are long even as preserved: neck and head flexors anchoring to these (m. longissimus capitis profundus, m. rectus capitisventralis) would have had high mechanical advantage. The length and size of these occipital features suggest that large muscles with augmented lever arms were anchored to the azhdarchid skull. Witmer et al. (2003) and Habib and Godfrey (2010) made similar observations about the occipital faces of other pterodactyloids: at least the anterior neck skeleton of pterosaurs was likely strongly muscled.

At the other extreme of the axial column, the azhdarchid scapulocoracoid suggests that their superficial neck musculature may have been well developed. Their scapulae are large and dorsoventrally expanded compared to those of other pterosaurs (e.g. Elgin and Frey 2011), permitting broad insertions of m. levator scapulae and m. serratus (Bennett (2003) shows their likely origin in other pterosaurs). These muscles originate on the anterior cervicals in modern reptiles and can function as neck elevators if the scapulae are immobile. Azhdarchid scapulocoracoids articulated tightly with the dorsal vertebrae and sternum (Frey et al. 2003) and were buried within deep flight musculature, so were likely capable of little, if any, motion. Contraction of cervical-pectoral muscle groups would thus likely elevate the neck, and asymmetric contraction of these muscles would move the neck laterally. These muscles (or homologues thereof) are particularly large in long-necked, large-headed mammals such as horses and deer (Goldfinger 2004), and we propose that the enlarged pectoral skeleton of azhdarchids may indicate similar enhancement of the posterior neck musculature.

Comparison with the anatomy of modern reptiles suggest that both m. levator scapulae and m. serratus, as well as muscles operating within the cervical series, anchored to the lateral faces of the neural arch and zygapophyses in azhdarchids (Herrel and de Vree 1999; Cleuren and de Vree 2000; Snively and Russel 2007). This is important for consideration of azhdarchid palaeobiology, it being a clear indication that neural spine height is not the only indicator of neck muscle size. Reptilian cervical extensor musculature, such as m. longissimus cervicis and m. transversospinalis cervicis, originate and insert on cervical zygapophyses as well as the vertebral corpus (Herrel and de Vree 1999; Snively and Russel 2007). Other muscles, including those superficial muscles outlined above, originate on cervical ribs, diapophyses and transverse processes (Herrel and de Vree 1999; Cleuren and de Vree 2000; Snively and Russel 2007). These structures are reduced in azhdarchids, but not absent. Juvenile specimens show that vestigial cervical ribs occur on the ventral surfaces of their prezygapophyses (Godfrey and Currie 2005), fusing to the zygapophyses in older animals to form the ventral face of the prezygapophysis (Unwin 2003). In well preserved specimens, fused cervical ribs form prominent ventral prezygapophyseal tubercles (Company et al. 1999; Vremir et al. 2015). The retention of cervical ribs in tubercle form may indicate that these structures maintained a functional role, perhaps persisting as attachment sites for muscles ancestrally anchored to non-reduced cervical ribs, diapophyses or transverse processes. We refrain from making more specific comment on this issue until an improved understanding of pterosaur cervical musculature is achieved, but note that well-preserved azhdarchid zygapophyses have complicated morphologies with crests, prominences, concave facets and well-defined edges (e.g. Frey and Martill 1996; Company et al. 1999; Averianov 2010; Vremir et al. 2013, 2015): anatomy expected of structures that act as anchorage sites for prominent musculature. The atypically elongate, broad zygapophyses of azhdarchids (e.g. Howse 1986; Unwin 2003; Kellner 2003; Witton and Naish 2008) can be viewed with new significance if, as proposed here, they accommodated muscle attachment.

Finally, the idea that azhdarchids had thinly muscled necks is at odds with their cranial proportions, which are among the most extreme of any animal. The skulls of azhdarchids were proportionally huge (Fig. 6; Cai and Wei 1994; Kellner and Langston 1996; Witton 2013) and – even accounting for their high degree of pneumaticity – would have subjected their neck tissues to high amounts of strain and stress. A well developed epaxial muscle system was likely needed for cranial movement and support. We speculate that azhdarchid cranial proportions may have played a role in the 'conservative' neck scaling identified in our neck data series. Other long-necked animals typically have small heads and relatively large torsos, the evolution of which are presumably linked to an allometric increases in cervical length. Large headed azhdarchids, however, metaphorically faced the biomechanical challenge of exponential strain on their lengthening necks from their large ~~cranial tissues~~, and this may have limited their allometric potential. The additional neck tissues needed to support large heads on lengthening necks may have been further constrained by a general need for pterosaurs to maintain a lightweight bauplan for flight.

We thus propose that hypotheses of highly reduced neck muscles in azhdarchids are likely erroneous. The reduction of some axial structures – in particular the neural spines of the mid-series cervicals and small size of cervical rib homologues – suggest that some muscle groups were likely reduced, but other areas for muscle attachment were prominent enough to indicate that their necks were neither weak nor underpowered. Indeed, several of their likely attachment sites must be viewed as expanded compared to those of other pterosaurs, and with high mechanical advantage for operating the head and neck.

Our hypotheses regarding azhdarchid neck musculature allow us to make some provisional, general comments on the vertebral myology of giant forms. We note that areas likely to anchor muscle – such as neural spines and zygapophyses – of EME 315 are proportionally expanded. The bifid neural spine of EME 315 is broken at the base of each process, but the broken surfaces are sufficiently broad and elongate (Fig. 1) to suggest that the spines were broad, long and perhaps tall when complete. The geometry of the zygapophyses are complex. Low crests and prominent edges extend from the vertebral corpus towards their articular surfaces, and their lateral and medial faces show complex concavities and edges: we posit that these mark muscle scarring. The ventrolateral surfaces of the EME 315 corpus are also notably concave and meet the ventral face along a defined, sweeping edge. These features suggest that EME 315 was well-muscled in life. This seems appropriate given the size of the *Hatzegopteryx* skull, and those features indicating large muscle insertions on its occipital face.

The holotype cervical of *Arambourgiania* may also show some evidence of muscle scarring: a sagittal crest on its anterior ventral surface and two low crests on the dorsal surface of the prezygapophyses. These latter features are topographically similar, though less defined, to crests seen on EME 315 and other azhdarchid vertebrae. However, the overall potential area for muscle attachment in this giant vertebra is much lower than it is in EME 315. The broken section of the anterior surface of the neural spine is smaller than that seen in EME 315, indicating a shallower neural spine overall. The zygapophyses are also shorter and more gracile. These differences might be partly explained by the different likely positions of EME 315 and UJA VF1 within the cervical skeleton (a cervical V is expected to have lesser muscle attachment than preceding or following vertebrae) but better known azhdarchid necks suggest that generalities of morphology will be common in other, adjacent vertebrae along the column (Fig. 5). We therefore conclude that *Arambourgiania* likely had a relatively lightly muscled neck relative to that of *Hatzegopteryx*. This is in keeping with the reduced strength of UJA VF1 in our bending tests.

Disparity and ecological diversity in giant azhdarchids

EME 315 and the other *Hatzegopteryx* material provides the strongest evidence yet that azhdarchids were not anatomically uniform (Vremir et al. 2013; Witton 2013). Understanding the overall form of azhdarchids is hampered by a lack of associated material, but fragmentary specimens indicate that azhdarchids were variable in at least three major anatomical respects (Figs. 5 and 8). The first is neck type, since some taxa had relatively short (though perhaps not shorter than expected for other pterodactyloids), robust necks (such as *Hatzegopteryx*; R2395), and others had much longer, more gracile and mechanically weaker necks (e.g. *Quetzalcoatlus* sp., *Arambourgiania*). The second is cranial morphotype: this also comprises robust forms, with relatively short skulls and proportionally broad jaws (e.g. *Bakonydraco*, Javelina Formation specimen TMM 42489-2), and gracile forms with elongate rostra and slender jaws (*Quetzalcoatlus* sp.; *Zhejiangopterus*; *Alanqa*). Some azhdarchids also appear to have relatively slender rostra, as indicated by the concave dorsal skull margin of *Azhdarcho* (Fig. 8A, Averianov 2010). A third category concerns the wing skeletons: we note that the relatively abbreviated metacarpal IV and proximal wing phalanx of the diminutive azhdarchid *Montanazhdarcho minor* contrast markedly with the elongate distal forelimb elements of *Quetzalcoatlus* sp. and *Zhejiangopterus* (McGowan et al. 2002). It has been speculated that azhdarchids might be roughly grouped into ‘robust’ and ‘gracile’ forms based on these differences (Witton 2013). It certainly seems appropriate to consider forms like *Hatzegopteryx* ‘robust’ and others – e.g., *Quetzalcoatlus* and *Zhejiangopterus* – ‘gracile’, but some taxa show ‘mixed’ anatomies (e.g. *Montanazhdarcho* has proportionally stocky wing bones, but elongate neck bones (McGowan et al. 2002)), suggesting these categories must be considered loose. Azhdarchid body plans may have been rather more varied than imagined previously.

Our assessment of vertebral strength in *Hatzegopteryx* and *Arambourgiania* suggests that azhdarchids had drastically different functional ~~properties and biomechanical potential~~. We presume that cranial and cervical disparity reflects distinct foraging habits and prey preferences, with robust azhdarchids pre~~dating~~ relatively larger prey than their gracile counterparts. The stout, thick-walled cervicals of *Hatzegopteryx*, as well as its generally reinforced bones and wide jaws (Buffetaut et al. 2002, 2003) seem better suited to tackling larger, more powerful prey, or for using forceful foraging methods, than azhdarchid species with thin-walled bones, long, gracile necks and narrow skulls. Undescribed fossils likely referable to *Hatzegopteryx* (including additional skull and limb elements that cannot be described here) show that robust construction was consistent across its body. The high resistance to bending stresses and indications of large cervical muscles in *Hatzegopteryx* are consistent with this concept, as are the inverse findings for *Arambourgiania*.

Modern studies on azhdarchid foraging behaviour suggest that they were terrestrially-foraging generalists (Witton and Naish 2008, 2015; Carroll et al. 2013; Witton, 2016). So far as ~~it can be compared~~, giant azhdarchid anatomy is similar enough to that of the smaller, better known azhdarchids to assume that they also foraged terrestrially, albeit perhaps with a greater emphasis on faunivory. We propose that gracile giants like *Arambourgiania* consumed relatively small prey such as early juvenile and hatchling dinosaurs, large eggs and other diminutive components of Cretaceous terrestrial ecosystems (Fig. 9A). This is in keeping with proposals that some giants occupied ‘middle tier’ predatory niches in some Cretaceous ecosystems (Witton and Naish 2015). *Hatzegopteryx*, however, shows potential for tackling much larger prey items, perhaps even killing animals too large to ingest whole (modern azhdarchid analogues, such as storks, are capable of attacking large animals, and killing children, with their azhdarchid-like beaks: see Witton and Naish 2015 for discussion). ~~We note that~~ *Hatzegopteryx* is the largest terrestrial predator in Maastrichtian eastern Europe by some margin (Witton and Naish 2015): its size, robust anatomy, and the deficit of other large carnivores in well-sampled European deposits implies that it may have been an apex predator in its community (Fig. 9B). The idea that a pterosaur may have played such an important role in a terrestrial Cretaceous ecosystem is far removed from previous interpretations of azhdarchids and pterosaurs generally, and perhaps a clear sign of how far pterosaur studies have progressed in recent decades (see Wellnhofer 1991b; Witton 2013; Hone 2012 for overviews of pterosaur research).

Finally, the growing evidence for distinct bauplans within Azhdarchidae complicates assessments of pterosaur disparity at the close of the Cretaceous and ideas surrounding the extinction of the group. Azhdarchids dominate pterosaur faunas in the Maastrichtian, with only a solitary Brazilian nyctosaurid humerus representing a different clade (Price 1953). Assumptions that azhdarchids were morphologically uniform have led to proposals that Maastrichtian pterosaurs were ecologically constrained at the end of the Cretaceous, and that their extinction represents the unspectacular end of a long, gradual decline across Pterosauria (Unwin 2005; Witton 2013). The identification of clear distinctions in form and function within Azhdarchidae argues that Maastrichtian pterosaurs were not as ecologically homogenous as previously thought, and that their extinction may have coincided with their exploitation of niches previously unused in pterosaur evolution. Pterosaur extinction in the K/Pg event may thus have been more significant than traditionally considered.

Acknowledgements

This work reflects discussion with a number of individuals on azhdarchid pterosaur anatomy, animal scaling and functional anatomy. We are grateful to S. Brusatte, E. Buffetaut, G. Dyke, M. Habib, D. Hone, A. Kellner, C. Palmer, M. Norell, D. Unwin, M. Vremir and M. Wedel for their assistance in helping us develop the ideas outlined in this paper.

References

Andres, B., and Myers, T. S. 2013. Lone star pterosaurs. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 103, 383-398.

Andres, B. and Qiang, J. 2008. A new pterosaur from the Liaoning Province of China, the phylogeny of the Pterodactyloidea, and convergence in their cervical vertebrae. *Palaeontology*, 51, 453-469.

Averianov, A. O. 2013. Reconstruction of the neck of *Azhdarcho lancicollis* and lifestyle of azhdarchids (Pterosauria, Azhdarchidae). *Paleontological Journal*, 47, 203-209.

Averianov, A. O. 2010. The osteology of *Azhdarcho lancicollis* Nessov, 1984 (Pterosauria, Azhdarchidae) from the late Cretaceous of Uzbekistan. *Proceedings of the Zoological Institute RAS*, 314, 264-317.

Bennett, S. C. 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon* Part I. General description of osteology. *Palaeontographica Abteilung A*, 1-112.

Bennett, S. C. 2003. Morphological evolution of the pectoral girdle in pterosaurs: myology and function. In Buffetaut, E. and Mazin, J. M. (eds) Evolution and Palaeobiology of Pterosaurs, *Geological Society Special Publications*, 217, 191-215.

Bennett, S. C. 2014. A new specimen of the pterosaur *Scaphognathus crassirostris*, with comments on constraint of cervical vertebrae number in pterosaurs. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 271, 327-348.

Buffetaut, E. and Kuang, X. 2010. The *tuba vertebralis* in dsungaripterid pterosaurs. *Acta Geoscience Sinica*, 31, 10–11.

Buffetaut, E., Laurent, Y., Le Loeuff, J. and Bilotte, M. 1997. A terminal Cretaceous giant pterosaur from the French Pyrenees. *Geological Magazine*, 134, 553-556.

Buffetaut, E., Grigorescu, D. and Csiki, Z. 2002. A new giant pterosaur with a robust skull from the latest Cretaceous of Romania. *Naturwissenschaften*, 89, 180-184.

Buffetaut, E., Grigorescu, D. and Csiki, Z. 2003. Giant azhdarchid pterosaurs from the terminal Cretaceous of Transylvania (western Romania). In Buffetaut, E. and Mazin, J. M. (eds) Evolution and Palaeobiology of Pterosaurs, *Geological Society, London, Special Publications*, 217, 91-104.

Cai, Z., and Wei, F. 1993. On a new pterosaur (*Zhejiangopterus linhaiensis* gen. et sp. Nov.) from Upper Cretaceous in Linhai, Zhejiang, China. *Vertebrata Pal Asiatica*, 32, 181-194.

Carroll, N.R., Poust, A.W. and Varricchio, D.J. 2013. A third azhdarchid pterosaur from the Two Medicine Formation (Campanian) of Montana. In Sayão, J.M., Costa, F.R., Bantim, R.A.M., and Kellner, A.W.A. (eds) *International Symposium on Pterosaurs, Rio Ptero 2013, Short Communications*, 40–42. Universidad Federal do Rio de Janeiro, Rio de Janeiro.

Cleuren, J. and de Vree, F. 2000. Feeding in crocodilians. In Schwenk, K. (ed) *Feeding: form, function, and evolution in tetrapod vertebrates*. Elsevier Academic Press, 337-358.

Company, J., Ruiz-Omeñaca, J. I. and Pereda Suberbiola, X. 1999. A long-necked pterosaur (Pterodactyloidea, Azhdarchidae) from the Upper Cretaceous of Valencia, Spain. *Geologie en Mijinbouw*, 78, 319-333.

Currey, J. D. 2002. *Bones: structure and mechanics*. Princeton University Press.

Currey, J. D. 2004. Tensile yield in compact bone is determined by strain, post-yield behaviour by mineral content. *Journal of biomechanics*, 37, 549-556.

Elgin, R. A., and Frey, E. 2011. A new azhdarchoid pterosaur from the Cenomanian (Late Cretaceous) of Lebanon. *Swiss Journal of Geosciences*, 104, 21-33.

Fastnacht, M. 2005. The first dsungaripterid pterosaur from the Kimmeridgian of Germany and the biomechanics of pterosaur long bones. *Acta Palaeontologica Polonica,* 50, 273–288.

Frey, E., and Martill, D. M. 1996. A reappraisal of *Arambourgiania* (Pterosauria, Pterodactyloidea): One of the world's largest flying animals. *Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen*, 199, 221-248.

Frey, E., Buchy, M. C. and Martill, D. M. 2003. Middle- and bottom- decker Cretaceous pterosaurs: unique designs in active flying vertebrates. In Buffetaut, E. and Mazin, J. M. (eds) Evolution and Palaeobiology of Pterosaurs, *Geological Society Special Publications*, 217, 267-274.

Graf, W., de Waele, C. and Vidal, P. P. 1992. Skeletal geometry in vertebrates and its relation to the vestibular end organs. In Berthoz, A., Graf, G. and Vidal, P. P. (eds.) *The Head-Neck Sensory Motor System*. Oxford University Press (New York and Oxford), pp. 129–134.

Graf, W., de Waele, C. and Vidal, P. P. 1995. Functional anatomy of the head-neck movement system of quadrupedal and bipedal mammals. *Journal of Anatomy*, 186, 55–74.

Goldfinger, E. 2004. *Animal Anatomy for Artists: The Elements of Form*. Oxford University Press.

Habib, M. 2013. Constraining the air giants: limits on size in flying animals as an example of constraint-based biomechanical theories of form. *Biological Theory*, 8, 245-252.

Habib, M. and Godfrey, S. 2010. On the hypertrophied opisthotic processes in *Dsungaripterus weii* Young (Pterodactyloidea, Pterosauria). *Acta Geoscientica Sinica,* 31, 26.

Herrel, A., and Vree, F. D. 1999. The cervical musculature in helodermatid lizards. *Belgian Journal of Zoology*, 129, 175-186.

Hone, D.W.E. 2012. Pterosaur research: recent advances and a future revolution. *Acta Geologica Sinica*, 86, 1366-1376.

Howse, S. C. B. 1986. On the cervical vertebrae of the Pterodactyloidea (Reptilia: Archosauria). Zoological Journal of the Linnaean Society, 88, 307-328.

Godfrey, S. J. and Currie, P. J. 2005. Pterosaurs. In Currie, P.J., and Koppelhus, E.B. (eds) *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*. Indiana University Press, Bloomington and Indianapolis, 292-311.

Kellner A. W. A. 2003. Pterosaur phylogeny and comments on the evolutionary history of the group. In Buffetaut, E. and Mazin, J. M. (eds) Evolution and Palaeobiology of Pterosaurs, *Geological Society Special Publications*, 217, 105–137.

Kellner, A. W. 2010. Comments on the Pteranodontidae (Pterosauria, Pterodactyloidea) with the description of two new species. *Anais da Academia Brasileira de Ciências*, 82, 1063-1084.

Kellner, A. W. A. and Langston Jr, W. 1996. Cranial remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from Late Cretaceous sediments of Big Bend National Park, Texas. *Journal of Vertebrate Paleontology*, 16, 222-231.

Kellner, A. W., Campos, D. A., Sayao, J. M., Saraiva, A. A., Rodrigues, T., Oliveira, G., Cruz, L. A., Costa, F. R., Silva, H. P. and Ferreira, J. S. 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. *Anais da Academia Brasileira de Ciências*, 85, 113-135.

Lawson, D. A. 1975. Pterosaur from the Latest Cretaceous of West Texas: Discovery of the largest flying creature. *Science*, 185, 947–948.

Martill, D. M., Frey, E., Sadaqah, R. M. and Khoury, H. N. 1998. Discovery of the holotype of the giant pterosaur *Titanopteryx philadelphiae* Arambourg 1959, and the status of *Arambourgiania* and *Quetzalcoatlus*. *Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen*, 207, 57-76.

McGowan, M. R., Padian, K., de Sosa, M. A. and Harmon, R. J. 2002. Description of *Montanazhdarcho minor*, an azhdarchid pterosaur from the Two Medicine Formation (Campanian) of Montana. *PaleoBios* 22, 1-9.

Nessov L. A. 1984. [Pterosaurs and birds from the Late Cretaceous of Middle Asia]. *Paleontol. Zhurnal*, 1, 47–57. [In Russian]).

O'Keefe, F. R. and Hiller, N. 2006. Morphologic and ontogenetic patterns in elasmosaur neck length, with comments on the taxonomic utility of neck length variables. *Paludicola*, 5, 206–229.

Parrish, J. M. 2006. The origins of high browsing and the effects of phylogeny and scaling on neck length in sauropodomorphs. In Carrano, M. T., Gaudin, T. J., Blob, R. W. and Wible, J. R.

(eds). *Amniote paleobiology: perspectives on the evolution of mammals, birds, and reptiles*. University of Chicago Press, 201-224.

Palmer, C., and Dyke, G. J. 2009. Biomechanics of the unique pterosaur pteroid. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20091899.

Price, L. I. 1953. A presença de Pterosáuria no Cretáceo superior do Estada da Paraiba. *Divisão de Geologia e Mineralogia Notas Preliminares e Estudos*, 71, 1-10.

Renesto, S. 2005. A new specimen of *Tanystropheus* (Reptilia Protorosauria) from the Middle Triassic of Switzerland and the ecology of the genus. *Rivista Italiana di Paleontologia e Stratigrafia (Research In Paleontology and Stratigraphy)*, 111, 377-394.

Rieppel, O., Jiang, D. Y., Fraser, N. C., Hao, W. C., Motani, R., Sun, Y. L., and Sun, Z. Y. 2010. *Tanystropheus* cf. *T. longobardicus* from the early Late Triassic of Guizhou Province, southwestern China. *Journal of Vertebrate Paleontology*, 30, 1082-1089.

Snively, E., and Russell, A. P. 2007. Functional variation of neck muscles and their relation to feeding style in Tyrannosauridae and other large theropod dinosaurs. *The Anatomical Record*, 290, 934-957.

Steel, L., Martill, D. M., Kirk, J., Anders, A., Loveridge, R. F., Frey, E. and Martin, J. G. 1997. *Arambourgiania philadelphiae*: giant wings in small halls. *The Geological Curator*, 6, 305-313

Suberbiola, X. P., Bardet, N., Jouve, S., Iarochène, M., Bouya, B. and Amaghzaz, M. 2003. A new azhdarchid pterosaur from the Late Cretaceous phosphates of Morocco. In Buffetaut, E. and Mazin, J. M. (eds) Evolution and Palaeobiology of Pterosaurs, *Geological Society Special Publications*, 217, 79-90.

Taylor, M. P., and Wedel, M. J. 2013. Why sauropods had long necks; and why giraffes have short necks. *PeerJ*, 1, e36.

Taylor, M. P., Wedel, M. J., and Naish, D. 2009. Head and neck posture in sauropod dinosaurs inferred from extant animals. *Acta Palaeontologica Polonica*, 54, 213-220.

Tschanz, K. A. R. L. 1988. Allometry and heterochrony in the growth of the neck of Triassic prolacertiform reptiles. *Palaeontology*, 31, 997-1011.

Unwin D. M. 2003. On the phylogeny and evolutionary history of pterosaurs. In Buffetaut, E. and Mazin, J. M. (eds) Evolution and Palaeobiology of Pterosaurs, *Geological Society Special Publications*, 217, 139–190.

Unwin, D. M. 2005. *The Pterosaurs from Deep Time*. Pi Press, New York.

Vidal, P. P., Graf, W. and Berthoz, A. 1986. The orientation of the cervical vertebral column in unrestrained awake animals. *Experimental Brain Research,* 61, 549-559.

Vremir, M. 2010. New faunal elements from the Late Cretaceous (Maastrichtian) continental deposits of Sebeş area (Transylvania). *Acta Musei Sabesiensis*, 2, 635-684.

Vremir, M., Kellner, A. W. A., Naish. D. and Dyke, G. J. 2013. A new azhdarchid pterosaur from the Late Cretaceous of the Transylvanian Basin, Romania: implications for azhdarchid diversity and distribution. *PLoS ONE* 8, e54268.

Vremir, M., Witton, M., Naish, D., Dyke, G., Brusatte, S. L., Norell, M. and Totoianu, R. 2015. A Medium-Sized Robust-Necked Azhdarchid Pterosaur (Pterodactyloidea: Azhdarchidae) from the Maastrichtian of Pui (Haţeg Basin, Transylvania, Romania). *American Museum Novitates*, 3827, 1-16.

Wellnhofer, P. 1970. Die Pterodactyloidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. *Bayerische Akademie der Wissenschaften, Mathematisch-Wissenschaftlichen Klasse, Abhandlugen*, 141, 1-133.

Wellnhofer, P. 1991a. Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. *Palaeontographica* 215, 43-101.

Wellnhofer, P. 1991b. *The Illustrated Encyclopedia of Pterosaurs*. Salamander Books.

Witmer, L. M., Chatterjee, S., Franzosa, J., and Rowe, T. 2003. Neuroanatomy of flying reptiles and implications for flight, posture and behaviour. *Nature*, 425, 950-953.

Witton, M. P. 2013. *Pterosaurs: Natural History, Evolution, Anatomy*. Princeton University Press.

Witton, M. P. 2016. Pterosaurs in Mesozoic ecosystems: a review of fossil evidence. In Hone, D. W. E., Martill, D. M. and Witton, M. P. (eds) New Perspectives on Pterosaur Palaeobiology. *Geological Society Special Publications*. In press.

Witton, M. P. and Habib, M. B. 2010. On the size and flight diversity of giant pterosaurs, the use of birds as pterosaur analogues and comments on pterosaur flightlessness. *PLoS ONE*, 5, e13982.

Witton, M. P. and Naish, D. 2008. A reappraisal of azhdarchid pterosaur functional morphology and paleoecology. *PLoS ONE*, 3, e2271.

Witton, M. P., and Naish, D. (2013). Azhdarchid pterosaurs: water-trawling pelican mimics or “terrestrial stalkers”?. *Acta Palaeontologica Polonica*, 60, 651-660.

Tables and table captions

	Lengths (mm)					
Taxon	*Zhejiangopterus linhaiensis*			*Phosphatodraco mauritanicus*	*Azhdarcho lancicollis*	*Quetzalcoatlus* sp.
Reference	Cai and Wei 1994			Pereda-Suberbiola et al. 2003; Kellner 2009	Averianov 2013	Steel et al. 1997
Specimen number	M1323	M13234	M1328	OCP/DEK GE 111	Reconstruction	Reconstruction
Cervical number						
III	36	50	57	110	57.2	170.0
IV	114	82	92	190	78.1	265.0
V	142	84	98	225	156.2	410.0
VI	120	72	81	190	102.3	380.0
VII	90	38	56	150	60.0	270.0
CIII-VII neck length	502	326	384	865	453.75	1495.00
Proportion of CV/neck length	0.283	0.258	0.255	0.260	0.34	0.27
Proportion of CVII/neck length	0.179	0.117	0.146	0.173	0.13	0.18

Table 1. Azhdarchid cervical vertebrae data used in neck length estimates.

									Section modulus		Maximum stress (Mpa)		RFF	
Taxonomic ID	Specimen	Body mass (kg)	W (N)	Vertebral length (mm)	Centrum width radius (mm)	Centrum height radius (mm)	Cortical thickness (mm)	R/t	Sagittal bending	Coronal bending	Sagittal bending	Coronal bending	Sagittal bending	Coronal bending
Hatzegopteryx sp.	EME 315	250	2,452	240	57.5	37	5	9.45	25307	32830	23.25	17.92	6.97	9.04
Hatzegopteryx sp.	EME 315 (reconstructed)	250	2,452	300	57.5	37	5	9.45	25307	32830	29.06	22.40	5.57	7.23
Hatzegopteryx sp.	EME 315 (hypothetical CV)	250	2,452	412.7	57.5	37	5	9.45	25307	32830	39.98	30.82	4.05	5.26
Arambourgiania philadelphiae	UJA VF1	250	2,452	620	24	27.5	2.6	9.90	4819	4455	315.40	341.20	0.51	0.47
Arambourgiania philadelphiae	UJA VF1 (reconstructed)	250	2,452	770	24	27.5	2.6	9.90	4819	4455	391.71	423.75	0.41	0.38
Hatzegopteryx sp.	EME 315	200	1,961	240	57.5	37	5	9.45	25307	32830	18.60	14.34	8.71	11.30
Hatzegopteryx sp.	EME 315 (reconstructed)	200	1,961	300	57.5	37	5	9.45	25307	32830	23.25	17.92	6.97	9.04
Hatzegopteryx sp.	EME 315 (hypothetical CV)	200	1,961	412.7	57.5	37	5	9.45	25307	32830	31.98	24.66	5.07	6.57
Arambourgiania philadelphiae	UJA VF1	200	1,961	620	24	27.5	2.6	9.90	4819	4455	252.32	272.96	0.64	0.59
Arambourgiania philadelphiae	UJA VF1 (reconstructed)	200	1,961	770	24	27.5	2.6	9.90	4819	4455	313.36	339.00	0.52	0.48
Hatzegopteryx sp.	EME 315	180	1,765	240	57.5	37	5	9.45	25307	32830	16.74	12.90	9.68	12.55
Hatzegopteryx sp.	EME 315 (reconstructed)	180	1,765	300	57.5	37	5	9.45	25307	32830	20.93	16.13	7.74	10.04
Hatzegopteryx sp.	EME 315 (hypothetical CV)	180	1,765	412.7	57.5	37	5	9.45	25307	32830	28.79	22.19	5.63	7.30
Arambourgiania philadelphiae	UJA VF1	180	1,765	620	24	27.5	2.6	9.90	4819	4455	227.09	245.67	0.71	0.66
Arambourgiania philadelphiae	UJA VF1 (reconstructed)	180	1,765	770	24	27.5	2.6	9.90	4819	4455	282.03	305.10	0.57	0.53

Table 2. Giant azhdarchid cervical vertebra bending strength compared.

Figure captions

Figure 1. Giant azhdarchid cervical vertebra referred to *Hatzegopteryx* sp. A-D, line drawings of EME 315 in anterior (A), right lateral (B), ventral (C) and dorsal (D) views; E, proportions of EME 315 compared to other azhdarchid cervicals: note atypical combination of length/width ratio (l:w) and length compared to other azhdarchid cervicals, and especially against the only other known giant cervical, *Arambourgiania* (UJA RF1). Light shading indicates damage; dark shading indicates filler. Abbreviations: co, cotyle; hy, hypapophysis; nc, neural canal; nsa; neural spine (anterior region); nsp, neural spine (posterior region); pnf, pneumatic foramen; prz, prezygapophysis; poz, postzygapophysis; vprzt, ventral prezygapophyseal tubercle (fused cervical rib). Scale bar is 100 mm.

Figure 2. Characteristics of azhdarchid vertebrae across their cervical series, demonstrated by several azhdarchid taxa. A, *Azhdarcho lancicollis* cervical III (ZIN PH 131/44), left lateral aspect; B-C, *Quetzalcoatlus* sp. cervical III (TMM 41544.16) in dorsal (B) and left lateral (C) aspect; D, *A. lancicollis* cervical IV (ZIN PH 144/44), left lateral aspect; E, *Q.* sp. cervical V (TMM 41455.15), left lateral aspect; F, *Arambourgiania philadelphiae* cervical V (UJA VF1), dorsal aspect; G-H, *A. lancicollis* cervical VI (ZIN PH 147/44) in left lateral (G) and posterior (H) aspect (note especially large neural spine); I, *A. lancicollis* cervical VII (ZIN PH 138/44), dorsal aspect; J, *Phosphatodraco* cervical VII (OCP DEK/GE 111), left lateral aspect; K, *A. lancicollis* cervical VIII (ZIN PH 137/44), dorsal aspect. Abbreviations as for Figure 2, also with con; condyle; ex, exapophysis; ns, neural spine. A, D, G-H, and K after Averianov (2010); F, after Frey and Martill (1996); J, after Pereda-Suberbiola et al. 2003.

Figure 3. Relationships between azhdarchid cervical vertebrae to cervical III-VII length.

Figure 4. Metrics and cross sections used in estimates of bending strength analysis. A, EME 315 in dorsal view showing line of modelled section (dotted line) and projected 300 mm length; B, UJA VF1 in dorsal view showing line of section and projected 770 mm length (Frey and Martill 1996); C, cross section and dimensions of EME 315; D, cross section of UJA VF1. Note difference in shape and bone wall thicknesses in C and D.

Figure 5. Measured and estimated azhdarchid pterosaur neck lengths against approximate wingspans.

Figure 6. Speculative skeletal reconstructions of *Hatzegopteryx* sp. and *Arambourgiania philadelphiae* (estimated wingspans ≥ 10 m – Martill and Frey 1996; Buffetaut et al. 2003) to show discrepancy in neck length alongside a 'typical' azhdarchid body plan. A, *Hatzegopteryx* skeleton in lateral aspect; B, dorsal view of EME 315 and FGGUB R1083 jaw elements, proportionate to actual size, suggesting *Hatzegopteryx* bore a wide, as well as relatively short,

neck construction (soft-tissue outline in black). Jaw width after Buffetaut et al. (2003); C, reconstructed *Arambourgiania philadelphiae* cervicals III-VII in lateral aspect; D, 4.6 m wingspan *Q.* sp. skeleton in lateral aspect; E, *Q.* sp. cervical vertebrae III-V and skull in dorsal view; Note how the neck length of *Hatzegopteryx* is similar to this much smaller pterosaur. *H. thambema* holotype (FGGUB R1083) and undescribed referred elements are shown in A; known elements of *A. philadelphiae* (UJA JF1) indicated in white shading in C. Scale bar represents 1 m.

Figure 7. Azhdarchid craniocervical skeleton compared to those of some other tetrapods. A, *Tanystropheus* cf. *longobardicus*; B, reconstruction of *Zhejiangopterus linhaiensis* cervical skeleton, vertebral morphology adapted from Averianov (2010); C, *Giraffa camelopardalis*; D, *Camelus dromedarius*; E, *Odocoileus virginianus*. Note that the mid-series vertebrae of all taxa – even those with highly complex, strongly-muscled neck skeletons – have reduced features compared to those at the posterior and anterior: the fact that azhdarchid mid-series cervicals have reduced features does not necessarily reflect underdeveloped cervical soft-tissues. A, reconstructed from fossils illustrated by Rieppel et al. (2010); B, reconstructed from Cai and Wei (1994) and Averianov (2010); C-E after Goldfinger (2004). Images not to scale.

Figure 8. Azhdarchid disparity in cranial and limb anatomy. A, ZIN PH 112/44, rostral fragment of *Azhdarcho lancicollis* showing concave dorsal skull margin (after Averianov 2010); B, anterior skull and mandible of TMM 42489-2, unnamed azhdarchid from the Javelina Formation, USA; C, restored skull of *Quetzalcoatlus* sp. (based on Kellner and Langston 1996); D, skull of *Zhejiangopterus linhaiensis* (based on Cai and Wei 1994); E, MOR 69I, *Montanazhdarcho minor* holotype pectoral girdle and left forelimb (note stunted metacarpal IV); F, M1323 postcrania of *Z. linhaiensis*. Abbreviations: car, carpals; cer, cervical vertebrae; cor, coracoid; fem, femur; hum, humerus; mcIV, metacarpal IV; pt, pteroid; rad, radius; tib, tibia; ul, ulna; wpI, wing phalanx I. Scale bars represent 100 mm, except for A (10 mm).

Figure 9. Diversity in predicted life appearance and ecologies for giant azhdarchid pterosaurs. A, two giant, long-necked azhdarchids – the Maastrichtian species *Arambourgiania philadelphiae* - argue over a small theropod; B, the similarly sized but more powerful Maastrichtian, Transylvanian giant azhdarchid pterosaur *Hatzegopteryx* sp. preys on the rhabdodontid iguanodontian *Zalmoxes*. Because large predatory theropods are unknown on Late Cretaceous Haţeg Island, giant azhdarchids may have played a key role as terrestrial predators in this community.

Figure 1

Giant azhdarchid cervical vertebra referred to *Hatzegopteryx* sp.

Figure 1. Giant azhdarchid cervical vertebra referred to *Hatzegopteryx* sp. A-D, line drawings of EME 315 in anterior (A), right lateral (B), ventral (C) and dorsal (D) views; E, proportions of EME 315 compared to other azhdarchid cervicals: note atypical combination of length/width ratio (l:w) and length compared to other azhdarchid cervicals, and especially against the only other known giant cervical, *Arambourgiania* (UJA RF1). Light shading indicates damage; dark shading indicates filler. Abbreviations: co, cotyle; hy, hypapophysis; nc, neural canal; nsa; neural spine (anterior region); nsp, neural spine (posterior region); pnf, pneumatic foramen; prz, prezygapophysis; poz, postzygapophysis; vprzt, ventral prezygapophyseal tubercle (fused cervical rib). Scale bar is 100 mm.

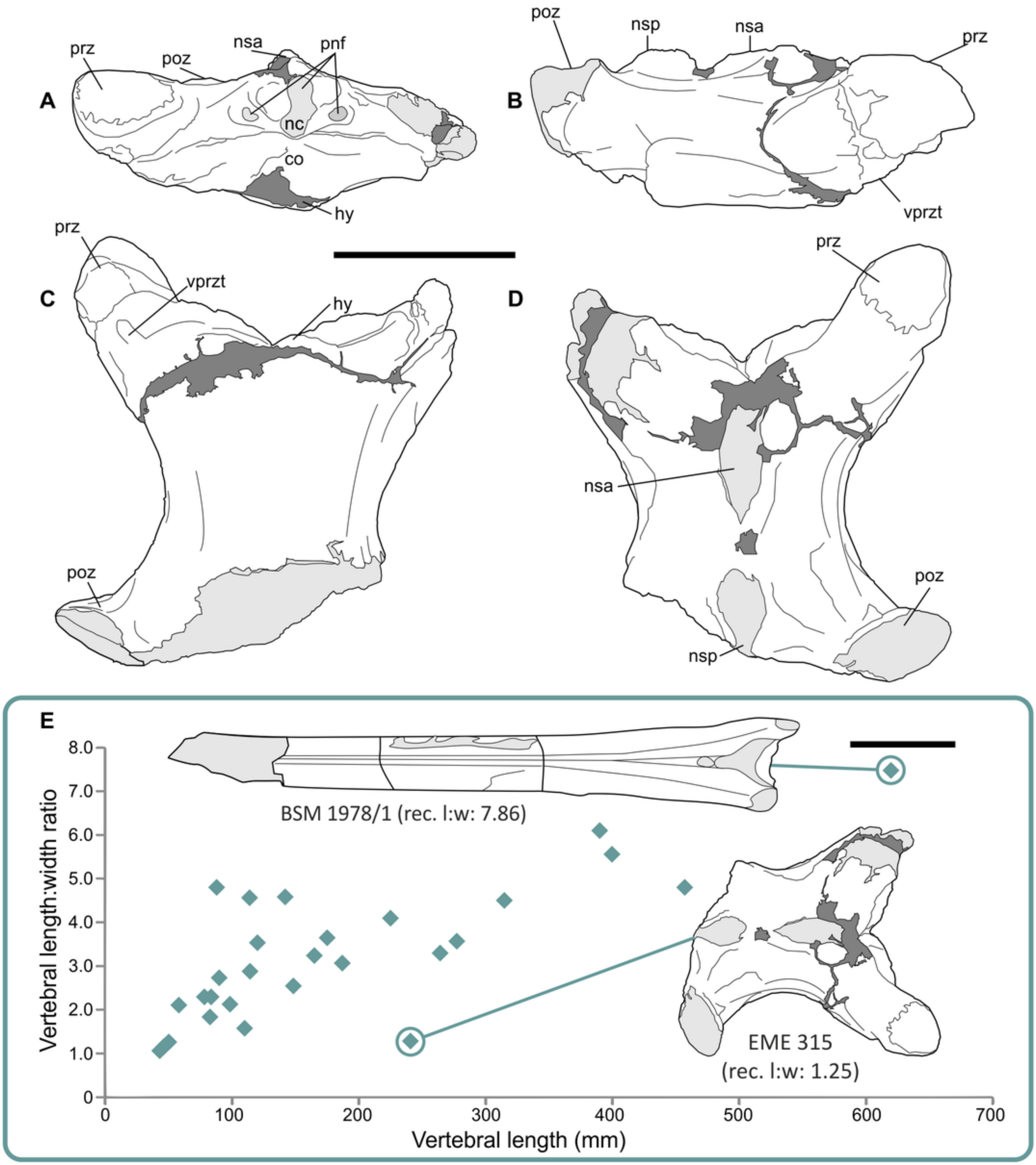
A
prz
poz
nsa
pnf
nc
co
hy
B
poz
nsp
nsa
prz
vprzt
C
prz
vprzt
hy
poz
D
prz
nsa
poz
nsp
E
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
Vertebral length:width ratio
0
100
200
300
400
500
600
700
Vertebral length (mm)
BSM 1978/1 (rec. l:w: 7.86)
EME 315
(rec. l:w: 1.25)

Figure 2

Characteristics of azhdarchid vertebrae across their cervical series, demonstrated by several azhdarchid taxa.

Figure 2. Characteristics of azhdarchid vertebrae across their cervical series, demonstrated by several azhdarchid taxa. A, *Azhdarcho lancicollis* cervical III (ZIN PH 131/44), left lateral aspect; B-C, *Quetzalcoatlus* sp. cervical III (TMM 41544.16) in dorsal (B) and left lateral (C) aspect; D, *A. lancicollis* cervical IV (ZIN PH 144/44), left lateral aspect; E, *Q.* sp. cervical V (TMM 41455.15), left lateral aspect; F, *Arambourgiania philadelphiae* cervical V (UJA VF1), dorsal aspect; G-H, *A. lancicollis* cervical VI (ZIN PH 147/44) in left lateral (G) and posterior (H) aspect (note especially large neural spine); I, *A. lancicollis* cervical VII (ZIN PH 138/44), dorsal aspect; J, *Phosphatodraco* cervical VII (OCP DEK/GE 111), left lateral aspect; K, *A. lancicollis* cervical VIII (ZIN PH 137/44), dorsal aspect. Abbreviations as for Figure 2, also with con; condyle; ex, exapophysis; ns, neural spine. A, D, G-H, and K after Averianov (2010); F, after Frey and Martill (1996); J, after Pereda-Suberbiola et al. 2003.

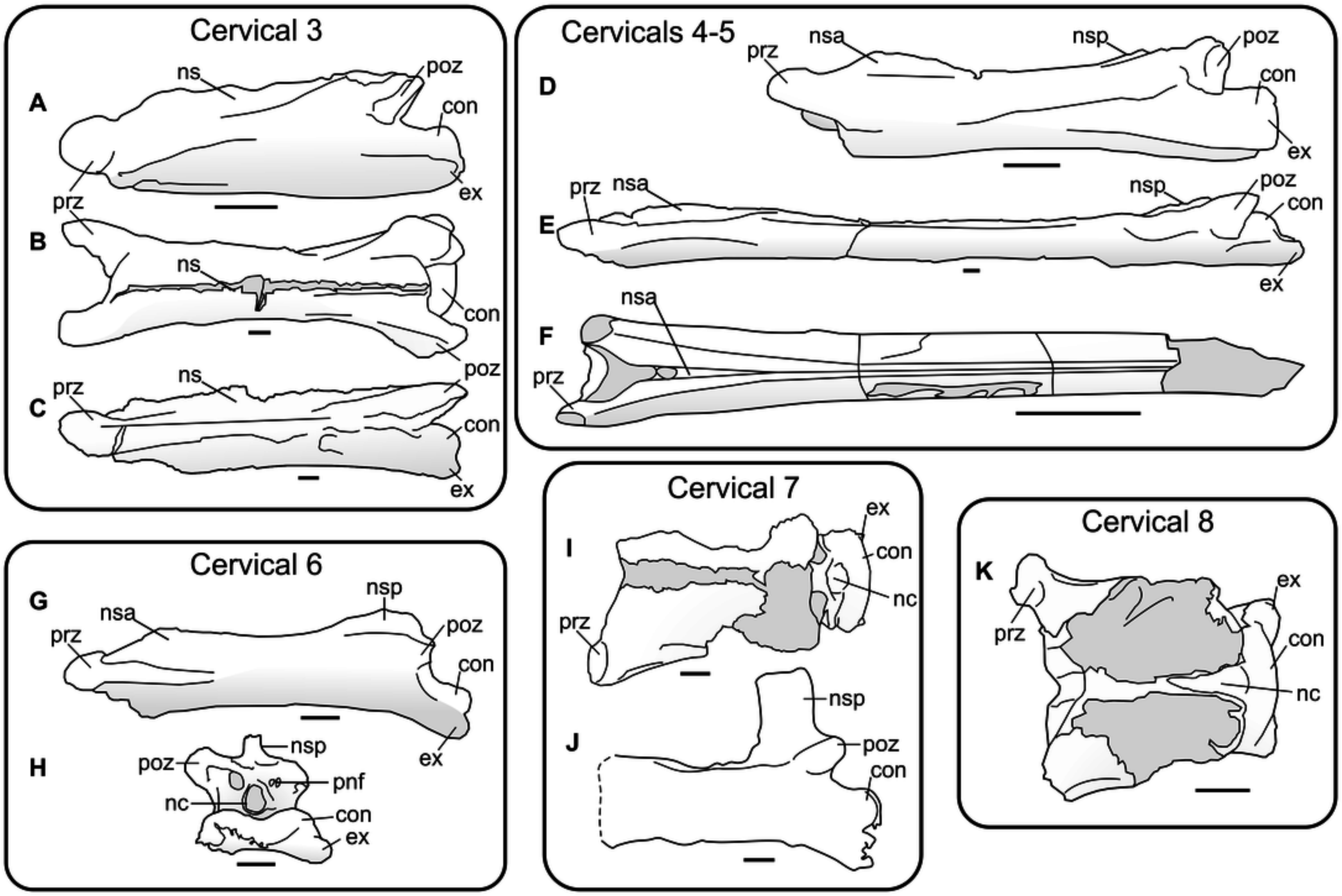
Cervical 3
A
ns
poz
con
ex
prz
B
ns
con
poz
C
prz
ns
con
ex
Cervicals 4-5
D
prz
nsa
nsp
poz
con
ex
E
prz
nsa
nsp
poz
con
ex
F
nsa
prz
Cervical 6
G
nsa
prz
nsp
poz
con
ex
H
poz
nsp
pnf
nc
con
ex
Cervical 7
I
ex
con
nc
prz
J
nsp
poz
con
Cervical 8
K
prz
ex
con
nc

Figure 3

Relationships between azhdarchid cervical vertebrae to cervical III-VII length.

Figure 3. Relationships between azhdarchid cervical vertebrae to cervical III-VII length.

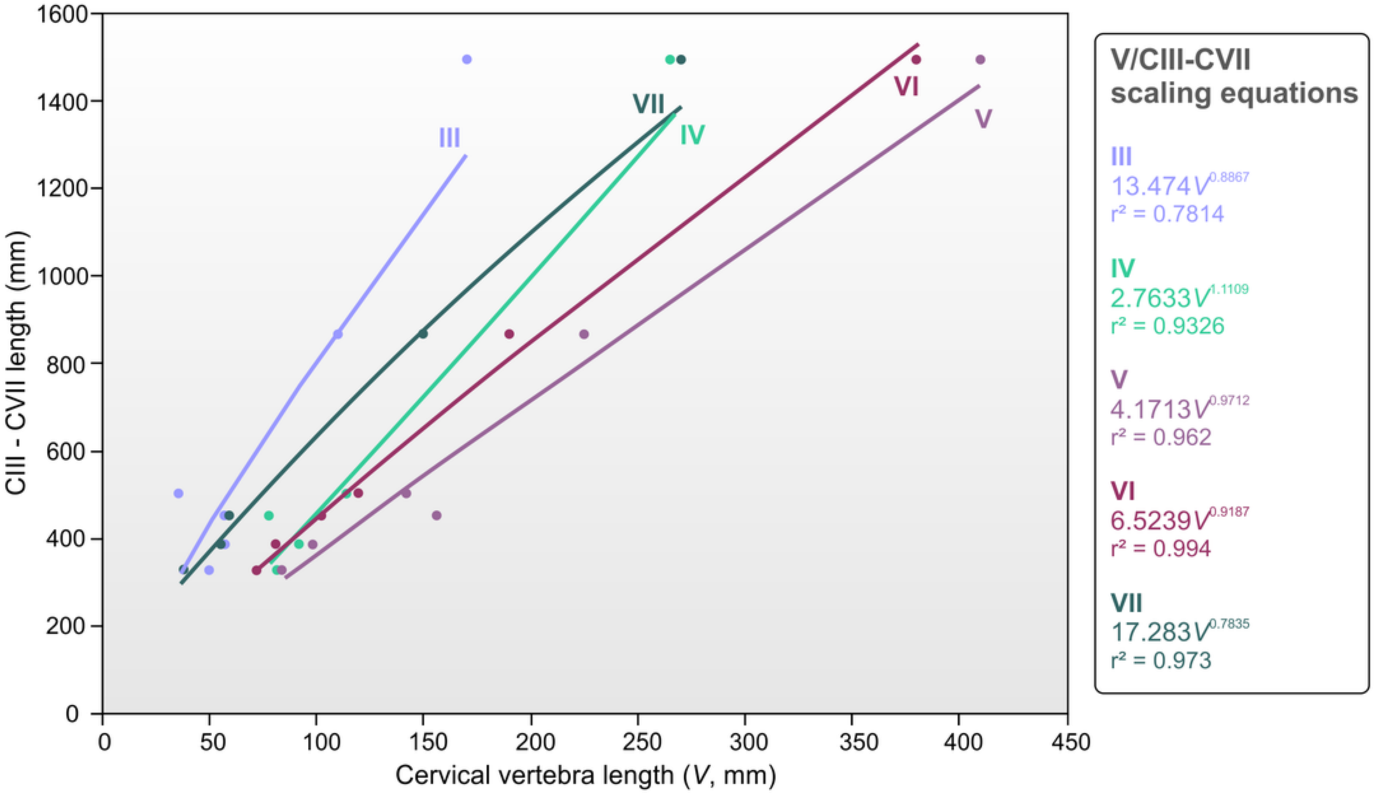

Figure 4

Metrics and cross sections used in estimates of bending strength analysis.

Figure 4. Metrics and cross sections used in estimates of bending strength analysis. A, EME 315 in dorsal view showing line of modelled section (dotted line) and projected 300 mm length; B, UJA VF1 in dorsal view showing line of section and projected 770 mm length (Frey and Martill 1996); C, cross section and dimensions of EME 315; D, cross section of UJA VF1. Note difference in shape and bone wall thicknesses in C and D.

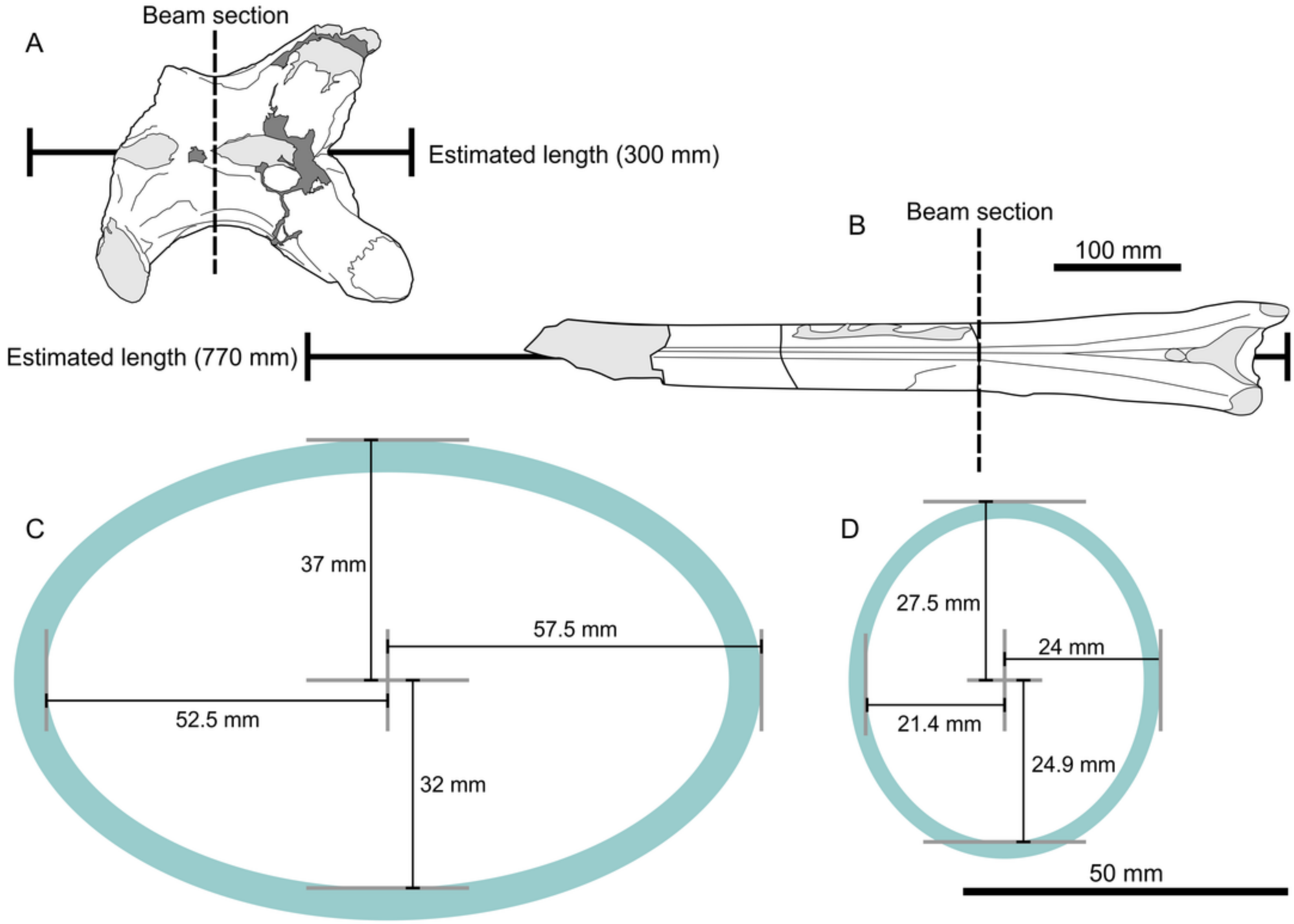

Figure 5

Measured and estimated azhdarchid pterosaur neck lengths against approximate wingspans.

Figure 5. Measured and estimated azhdarchid pterosaur neck lengths against approximate wingspans.

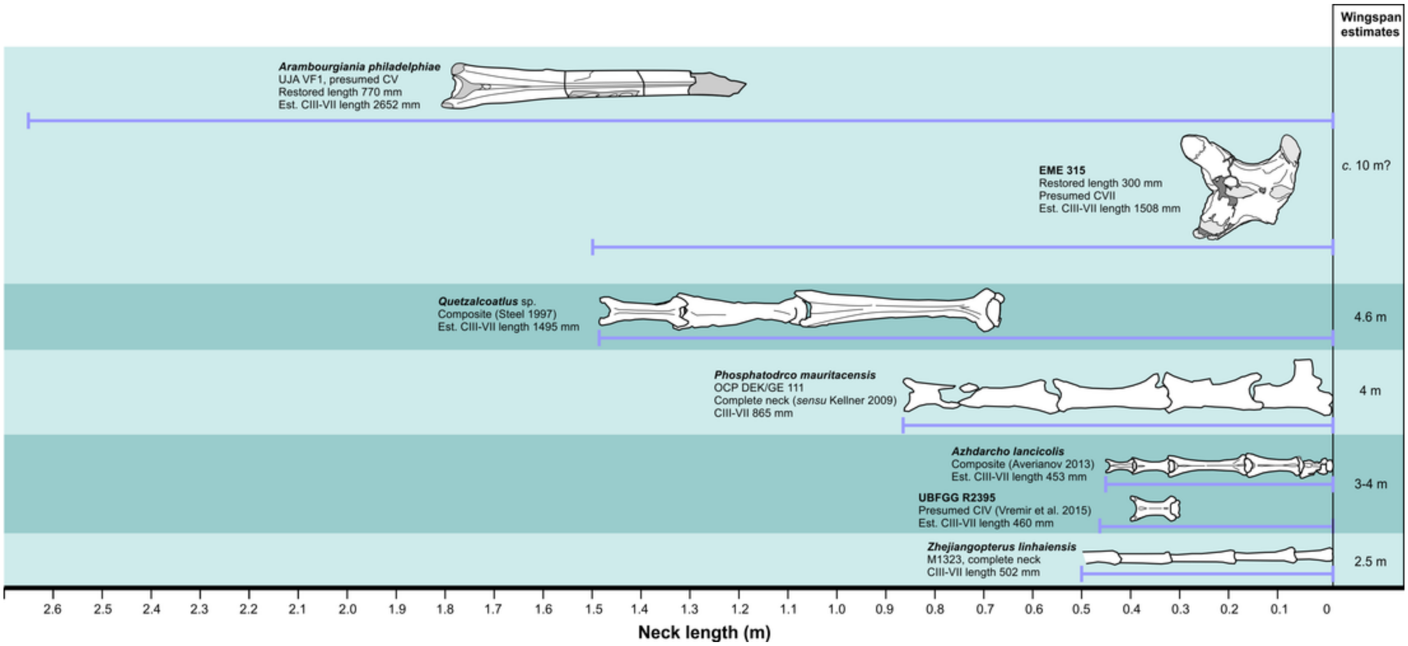

Figure 6

Speculative skeletal reconstructions of *Hatzegopteryx* sp. and *Arambourgiania philadelphiae* to show discrepancy in neck length alongside a ‘typical’ azhdarchid body plan.

Figure 6. Speculative skeletal reconstructions of *Hatzegopteryx* sp. and *Arambourgiania philadelphiae* (estimated wingspans ≥ 10 m – Martill and Frey 1996; Buffetaut et al. 2003) to show discrepancy in neck length alongside a ‘typical’ azhdarchid body plan. A, *Hatzegopteryx* skeleton in lateral aspect; B, dorsal view of EME 315 and FGGUB R1083 jaw elements, proportionate to actual size, suggesting *Hatzegopteryx* bore a wide, as well as relatively short, neck construction (soft-tissue outline in black). Jaw width after Buffetaut et al. (2003); C, reconstructed *Arambourgiania philadelphiae* cervicals III-VII in lateral aspect; D, 4.6 m wingspan *Q.* sp. skeleton in lateral aspect; E, *Q*. sp. cervical vertebrae III-V and skull in dorsal view; Note how the neck length of *Hatzegopteryx* is similar to this much smaller pterosaur. *H. thambema* holotype (FGGUB R1083) and undescribed referred elements are shown in A; known elements of *A. philadelphiae* (UJA JF1) indicated in white shading in C. Scale bar represents 1 m.

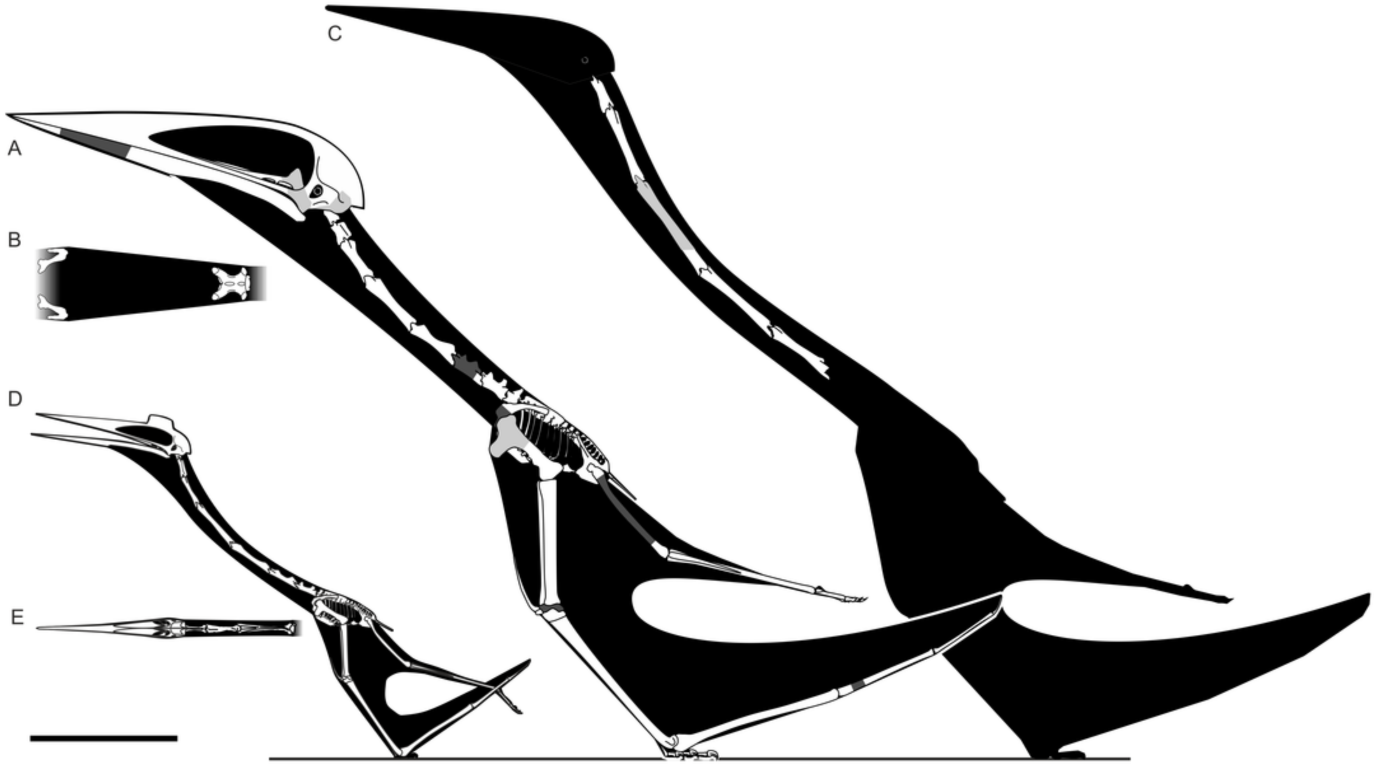
C
A
B
D
E

Figure 7

Azhdarchid craniocervical skeleton compared to those of some other tetrapods.

Figure 7. Azhdarchid craniocervical skeleton compared to those of some other tetrapods. A, *Tanystropheus* cf. *longobardicus*; B, reconstruction of *Zhejiangopterus linhaiensis* cervical skeleton, vertebral morphology adapted from Averianov (2010); C, *Giraffa camelopardalis*; D, *Camelus dromedarius*; E, *Odocoileus virginianus*. Note that the mid-series vertebrae of all taxa – even those with highly complex, strongly-muscled neck skeletons – have reduced features compared to those at the posterior and anterior: the fact that azhdarchid mid-series cervicals have reduced features does not necessarily reflect underdeveloped cervical soft-tissues. A, reconstructed from fossils illustrated by Rieppel et al. (2010); B, reconstructed from Cai and Wei (1994) and Averianov (2010); C-E after Goldfinger (2004). Images not to scale.

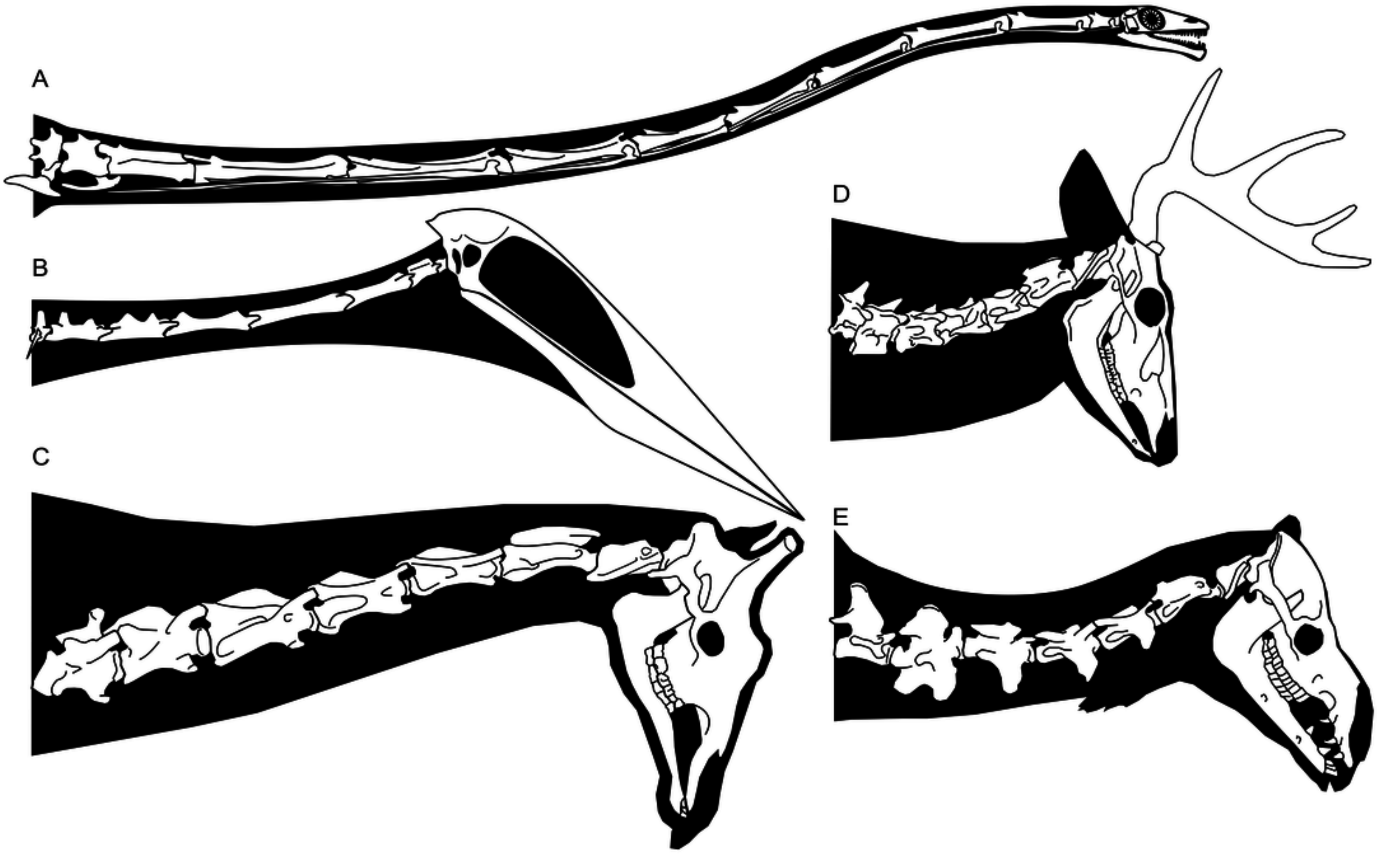

Figure 8

Azhdarchid disparity in cranial and limb anatomy.

Figure 8. Azhdarchid disparity in cranial and limb anatomy. A, ZIN PH 112/44, rostral fragment of *Azhdarcho lancicollis* showing concave dorsal skull margin (after Averianov 2010); B, anterior skull and mandible of TMM 42489-2, unnamed azhdarchid from the Javelina Formation, USA; C, restored skull of *Quetzalcoatlus* sp. (based on Kellner and Langston 1996); D, skull of *Zhejiangopterus linhaiensis* (based on Cai and Wei 1994); E, MOR 69I, *Montanazhdarcho minor* holotype pectoral girdle and left forelimb (note stunted metacarpal IV); F, M1323 postcrania of *Z. linhaiensis*. Abbreviations: car, carpals; cer, cervical vertebrae; cor, coracoid; fem, femur; hum, humerus; mcIV, metacarpal IV; pt, pteroid; rad, radius; tib, tibia; ul, ulna; wpI, wing phalanx I. Scale bars represent 100 mm, except for A (10 mm).

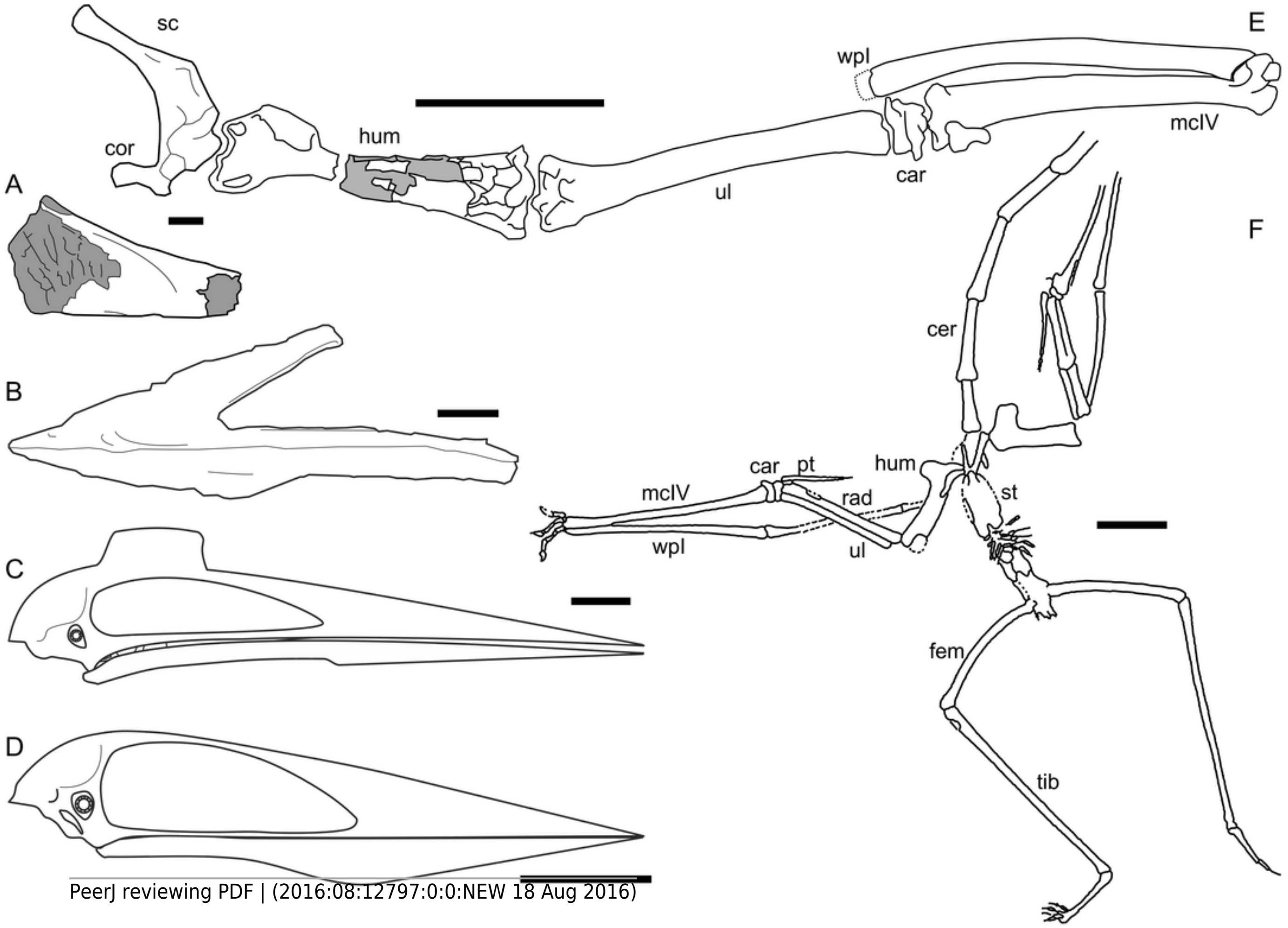

Figure 9

Diversity in predicted life appearance and ecologies for giant azhdarchid pterosaurs.

Figure 9. Diversity in predicted life appearance and ecologies for giant azhdarchid pterosaurs. A, two giant, long-necked azhdarchids – the Maastrichtian species *Arambourgiania philadelphiae* - argue over a small theropod; B, the similarly sized but more powerful Maastrichtian, Transylvanian giant azhdarchid pterosaur *Hatzegopteryx* sp. preys on the rhabdodontid iguanodontian *Zalmoxes*. Because large predatory theropods are unknown on Late Cretaceous Haţeg Island, giant azhdarchids may have played a key role as terrestrial predators in this community.


A
B