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Source: *Acta Palaeontologica Polonica*, 60(3) : 651-660

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.00005.2013>

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Azhdarchid pterosaurs: water-trawling pelican mimics or “terrestrial stalkers”?

MARK P. WITTON and DARREN NAISH



Witton, M.P. and Naish, D. 2015. Azhdarchid pterosaurs: water-trawling pelican mimics or “terrestrial stalkers”? *Acta Palaeontologica Polonica* 60 (3): 651–660.

The lifestyles of all pterosaurs are contentious, but those of the pterodactyloid clade Azhdarchidae are particularly debated. A 2008 review of the functional morphology of azhdarchid pterosaurs concluded that they were probably terrestrial foragers, as evidenced by their long limbs, generalised skull construction, the arthrological limitations of their cervical series, trackway data indicating terrestrial proficiency, a strong continental skew in the depositional context of their fossils, and several additional lines of corroborating evidence. This hypothesis was recently challenged on three counts: (i) azhdarchid fossils routinely occur in aquatic deposits; (ii) terrestrially-foraging pterosaurs were highly vulnerable to predation and (iii), aerial “water trawling”, where the mandible is pulled through water to catch food in a distended throat pouch, is a more likely foraging strategy. Pelican-like jaw mechanics were suggested for azhdarchids because of the asymmetrical jaw joints in these pterosaurs, which permit lateral deflection of the mandibular rami during jaw extension. We evaluate these three claims and conclude that all are flawed. The frequent occurrence of azhdarchid fossils in aquatic sedimentary systems is not significant with regard to ecology or behaviour, since these provide the overwhelming mechanism for the preservation of all fossil terrestrial animals. Likely pterosaur takeoff abilities and the ubiquitous nature of modern, terrestrially-foraging birds indicate that predation risks on ground-foraging pterosaurs are probably overstated. The kinematics of pterosaur jaws are entirely different to those of pelicans, which are highly specialised compared to those of all other tetrapods, and there are no indications from azhdarchid jaw anatomy that azhdarchids indulged in pelican-like foraging behaviour. The estimated amount of jaw expansion present in azhdarchids was minimal compared to that of pelicans, even when the asymmetrical jaw joints of azhdarchids are taken into account. Moreover, the widespread occurrence of asymmetrical jaw joints in other reptiles demonstrates that they are not related to any specific feeding habits. We conclude that terrestrial foraging remains the most parsimonious habit for azhdarchid pterosaurs.

Key words: Pterosauria, Azhdarchidae, pelican, foraging methods, palaeoecology.

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Received 3 July 2013, accepted 25 October 2013, available online 28 October 2013.

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Introduction

Azhdarchids are among the most aberrant and remarkable of pterodactyloid pterosaurs. Represented by Cretaceous fossils discovered virtually worldwide, they are remarkable for their highly elongate necks and skulls, cylindrical cervical vertebrae, robust, powerfully muscled proximal forelimb elements and frequent occurrence in continental sediments (Barrett et al. 2008; Witton and Naish 2008). The ecology, lifestyle, and behaviour of this group has been controversial and numerous palaeobehavioural hypotheses have been proposed since the distinctive nature of azhdarchid anatomy became apparent in the 1970s. Suggested lifestyles include

obligate scavenging, sediment probing, pursuit swimming, aerial hawking, and dip- or skim-feeding (e.g., Lawson 1975; Nesov 1984; Kellner and Langston 1996; Lehman and Langston 1996; see Witton and Naish 2008 for a recent review). In 2008, we argued that none of these hypotheses were consistent with azhdarchid anatomy or functional morphology, largely because the elongate and relatively inflexible mid-section of the azhdarchid neck precluded feeding in the manners proposed by previous authors (Witton and Naish 2008). We interpreted the elongate necks, hypertrophied, stork-like rostra, and distinctive limbs of azhdarchids as adaptations to “terrestrial stalking”, a lifestyle akin to that of modern ground hornbills and large stork species in which small foodstuffs (e.g., fruit, carrion, invertebrates, and

small vertebrates) are procured during sustained periods of terrestrial foraging. Corroborating evidence for this hypothesis is provided by (i) *Haenamichnus* trace fossils, tracks referred to azhdarchid pterosaurs which record an efficient, parasagittal gait, presumably typical for the group (Hwang et al. 2002); (ii) azhdarchid wing planform, which is probably better suited for flight in terrestrial settings than aquatic ones (assuming that azhdarchid planforms corroborate with fore- and hindlimb proportions, as is indicated by analyses of wing membrane distribution: see Witton 2008 and Elgin et al. 2011); and (iii) a strong bias linking azhdarchid fossils to continental depositional settings (Witton and Naish 2008). Other workers have since reported anatomical details of the azhdarchid skeleton that add further support to the terrestrial stalking hypothesis (Carroll et al. 2013).

Averianov (2013) recently published a short review of azhdarchid palaeoecology within the context of an examination of neck flexibility in *Azhdarcho lancicollis* from the Turonian of Uzbekistan. Many of Averianov's (2013) conclusions and observations match ours (Witton and Naish 2008), and parts of his discussion support our proposals that azhdarchid planform and hindlimb morphology appear suited for a terrestrial stalking lifestyle (Averianov 2013: 207). Confusingly, inconsistency is provided by the fact that he also referred favourably to the *Rynchops*-like skim-feeding technique promoted by Prieto (1998) and pointed to three perceived flaws with the terrestrial stalking hypothesis.

The first of these "flaws" concerns an alleged "confinement" of azhdarchid fossils to lacustrine or fluvial deposits that supposedly demonstrate a "wetland mode of life" (Averianov 2013: 207); the second is the idea that terrestrial stalking azhdarchids were highly vulnerable to predators "...because their terrestrial locomotion ... remained insufficient to escape rapidly running predatory dinosaurs. It is hardly probable that huge azhdarchids could take wing in one go and running for acceleration is difficult in marshland conditions" (Averianov 2013: 207); and the third proposes that the asymmetrical jaw joint of azhdarchids "is probably evidence of the presence of a throat sac. Perhaps, jaw tips of azhdarchids did not touch food objects and caught them using a 'scoop net' formed by the lower jaw rami and throat sac" (Averianov 2013: 208). Averianov specifically likened azhdarchid mandibular kinematics to those of pelicans, suggesting that the "helical" jaw joint of pterosaurs allowed lateral bowing of their mandibular rami when the mouth is opened, thereby expanding the size of the oral cavity. Averianov (2013) is not the first author to compare pterosaur and pelican jaw anatomy (e.g., Wellnhofer 1980, 1991; Unwin 2005), a comparison that appears superficial in ignoring the complex, specialised nature of the pelican mandible (Myers and Myers 2005; Field et al. 2011). In his concluding summary, Averianov stated "azhdarchids flew [sic!] slowly above the water surface of large inland water bodies ... looking out for fish or small fish shoals. As prey is detected, they opened the mouth, expanding the throat sac due to the spiral jaw joint, and captured fish in this scoop net, formed by the

jaw rami and throat sac. Then, the head was thrown abruptly back by extension of the neck in the posterior region and prey was swallowed." (2013: 209). Here, we evaluate each of Averianov's (2013) three points: do they really represent problems for the "terrestrial stalker" hypothesis, and is the proposed "scoop net" foraging method a viable alternative to terrestrial feeding?

Institutional abbreviations.—MTM, Magyar Természettudományi Múzeum, Budapest, Hungary; TMM, Texas Memorial Museum, Austin, USA.

The bias of azhdarchid remains to aquatic settings

The assertion that a terrestrial stalking lifestyle for azhdarchids can be dismissed due to discovery of the group's remains in lacustrine and fluvial settings (Averianov 2013: 207) is naïve and problematic, at best. It is universally well known that the remains of continental, terrestrial organisms—examples include fossil cattle, giraffes, primates, and perching birds—are virtually always discovered in sediments that were deposited in aquatic settings such as rivers, lakes, and ponds. After all, aquatic habitats represent the most important places in which animal remains become incorporated into the sedimentary record. As may be expected, the river and lake sediments that yield azhdarchid fossils frequently include animals from both terrestrial as well as aquatic settings, including sauropods, ornithopods, theropods (including birds), lizards, small mammals, crocodyliforms, turtles, and fish (e.g., Company et al. 1999; Wellnhofer and Buffetaut 1999; Ősi 2005; Averianov 2010; Vremir 2010; see Witton and Naish 2008: table 1). In some instances, azhdarchid remains are found directly alongside the remains of diverse dinosaur taxa in bone beds deposited in fluvial channel and overbank sediments (e.g., Ősi 2005; Vremir 2010; Vremir et al. 2013).

Averianov (2013) qualified the notion of a strong terrestrial signal in the azhdarchid fossil record by noting that evidence for rivers and/or lakes are present at "almost each locality" (Averianov 2013: 207) that yields azhdarchid fossils. As per the discussion above, this may not be informative with respect to the palaeoecology of these animals. Furthermore, it is misleading to downplay the arid nature of many azhdarchid-bearing sediments. Evaporite pseudomorphs and gypsum crystals are known from the Javelina and Sebeş formations, both of which have yielded relatively large amounts of azhdarchid material (Coulson 1998; Lawson 1975; Vremir et al. 2013) and the Kem Kem beds of Morocco (Cavin et al. 2010; Ibrahim et al. 2010); several skeletons of the small azhdarchid *Zhejiangopterus linhaiensis* are known from volcanically-derived ignimbrites in the Tangshang Formation of China (Cai and Wei 1994), and fragments of probable azhdarchids have been recovered from aeolian sands at Tugrikin

Shireh, Mongolia (Hone et al. 2012). Azhdarchid remains are not, therefore, exclusive to deposits that formed in wet or aquatic settings and, by contrast, several formations which present particularly large amounts of azhdarchid material, or high quality azhdarchid remains, represent dry, terrestrially exposed environments. There is no more palaeoecological significance to their frequent recovery from lake, stream and floodplain deposits than there is for the fossils of undoubted terrestrial species.

Terrestrially-foraging azhdarchids were particularly vulnerable to predators

Discussions of predator-prey interactions in fossil species are frequently little more than speculative, intuitive inferences and we are wary of that fact here. However, recent research on pterosaur biomechanics, the composition of the Late Cretaceous faunas that include azhdarchids, and the behaviour of modern animals permit some comment on the perceived vulnerability of ground-foraging azhdarchids to predators.

Firstly, the suggestion that azhdarchids would struggle to take off when escaping predators and that they could not take off from standing starts (Averianov 2013) ignores recent work on pterosaur takeoff biomechanics (Habib 2008; Witton and Habib 2010). Bipedally launching pterosaurs may have struggled to take off rapidly (e.g., Chatterjee and Templin 2004), but pterosaur quadrupedality, limb scaling, proximal limb bone strength and, to a lesser extent, body size all indicate that pterosaurs were proficient quadrupedal launchers (Habib 2008, 2013; Witton and Habib 2010), perhaps even when alighted on water (Habib and Cunningham 2010). All indications are that quadrupedal launches were powerful, rapid events which enabled even the largest pterosaurs to take off from standing starts and attain high speed early in the flight cycle (Habib 2008). In terms of predator evasion, quadrupedal launches may be superior to bipedal ones, particularly for large, heavy fliers such as azhdarchids. We note in addition that the long necks and limbs of azhdarchids would have increased their stature substantially, granting them elevated fields of vision which may have been useful in predator detection. A number of pterosaur trackways (e.g., Mazin et al. 2003) indicate that pterosaurs were indeed capable of running as well as flying, meaning that azhdarchids may not have been easy to catch even if they did not launch immediately.

Secondly, the notion that azhdarchids were “easy targets” for predators is questionable. It is well known that many azhdarchid species were the largest animal fliers of all time, attaining wingspans of at least 10–11 m (Langston 1981; Buffetaut et al. 2002; Witton and Habib 2010) and body masses likely exceeding 200 kg (Paul 2002; Witton 2008). Such gigantic proportions equate to shoulder heights of 2.5 m (assuming parasagittal limbs, as indicated by probable azhdarchid

tracks—see Hwang et al. 2002) and, with necks likely reaching 2.5–3 m in length (Frey and Martill 1996), overall standing heights that easily surpassed 4 m (Witton 2008). In some cases, these giants represent the largest carnivorous animals known, by far, from their respective faunal assemblages. The largest dinosaurian predator known from the Romanian Hăţeg Basin, for instance, is the 2 m long maniraptoran theropod *Balaur bondoc* (Csiki et al. 2010), and this was probably ill equipped to attack even relatively small, young individuals of the stocky, contemporaneous giant pterosaur *Hatzegopteryx thambema* (Buffetaut et al. 2002, 2003; see Hone et al. 2012 for further discussions of maniraptoran predation on azhdarchids). Indeed, the stature of fully grown large azhdarchids is impressive even alongside contemporary North American tyrannosaurids (Fig. 1), the hip heights of which are between 2.3–2.9 m in even the largest species (Hutchinson and Garcia 2002). Perceived size alone may have deterred many potential predators of azhdarchids.

Observations of modern azhdarchid analogues suggest that azhdarchid offensive capabilities have likely been under-estimated. Large modern storks have been suggested to be good analogues for azhdarchids in at least rostrum form and function (Witton and Naish 2008): notably, the bills of large storks are, despite their primary use in procuring small prey items and other foodstuffs, highly effective weapons. Usually placid Marabou storks (*Leptoptilos crumeniferus*) use the bill to repeatedly stab human attackers when provoked and can inflict injuries capable of killing children (Mackay 1950). Captive Jabiru storks (*Jabiru mycteria*) are noted for their aggression and will attack other animals in their territories including much larger species, such as tapirs (Shannon 1987). Some Jabiru individuals are so aggressive that their handlers routinely expect attacks and are forced to use weapons to defend themselves (Shannon 1987). While the behaviours of these modern storks do not directly inform us about that of azhdarchids, they indicate that azhdarchid-like rostra are dangerous weapons in some instances. We speculate that both the unusually broad jugal common to azhdarchids (e.g., Cai and Wei 1994; Kellner and Langston 1996) and robust skull construction of some species (Buffetaut et al. 2002) are possible indications that azhdarchid skulls were atypically strong compared to those of other pterosaurs, perhaps permitting aggressive use of the rostrum, if required.

In addition, although ground feeding has historically been considered an unusual and controversial lifestyle for pterosaur species (see reviews of pterosaur palaeoecology in Witton 2013), various methods of ground-feeding are extremely common in modern birds. For instance, birds that we consider effective analogues of ground-feeding azhdarchids, large African storks, such as *Leptoptilos crumeniferus* and the ground hornbills, *Bucorvus* (Witton and Naish 2008), inhabit African savannahs populated by numerous predators: big cats, wild dogs, crocodiles, predatory lizards, and other dangerous animals such as hippos and buffalo. Despite co-existing with many dangerous species and practising terrestrial feeding for protracted periods, we are unaware of any

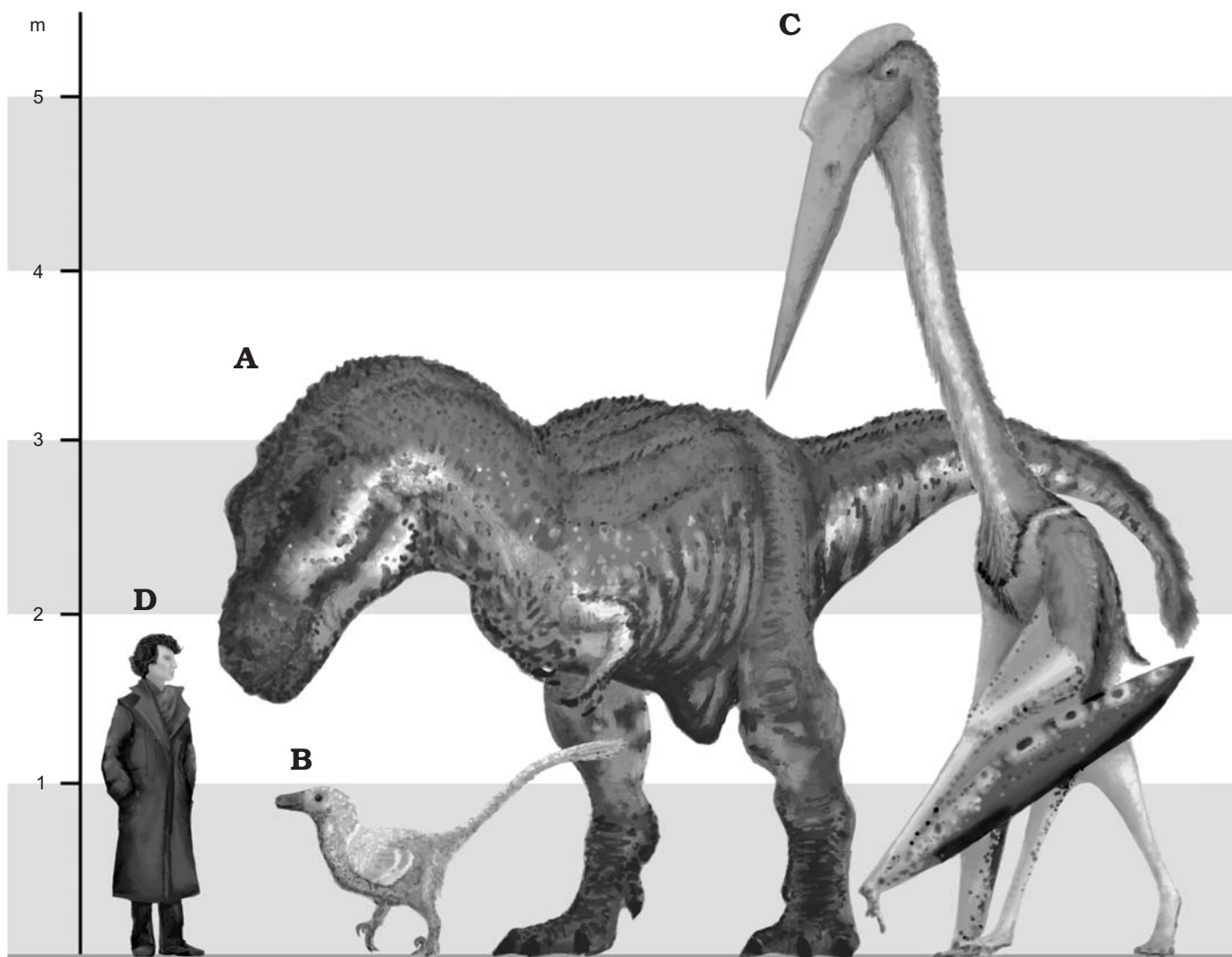


Fig. 1. Apex predators contemporaneous with giant azhdarchid taxa, shown to scale with a representative giant azhdarchid and a human. **A.** The largest known tyrannosaurid, *Tyrannosaurus rex* from North America, contemporary of *Quetzalcoatlus northropi* and other large azhdarchids. **B.** The Hateg paravian *Balaur bondoc*, contemporary of *Hatzegopteryx thambema*. **C.** The 10 m wingspan *Arambourgiania philadelphiae* (note that *H. thambema* was proportionally more robust than *Arambourgiania*). **D.** *Homo sapiens*, standing height of 1.83 m.

studies or even anecdotal reports suggesting that these birds are overtly vulnerable to attack. As with many other animal species, the eggs and juveniles of ground-foraging birds are vulnerable, but there are no indications of atypical predation risk to adults (Hancock et al. 1992).

In sum, the idea of azhdarchids as being highly vulnerable to terrestrial predation labours under several probably erroneous assumptions, including viewing theropods as unstoppable killing machines, immediately pouncing on and devouring any grounded pterosaur. In point of fact, the behaviour of living predators indicates that theropods large and small likely exploited easy prey (Hone and Rauhut 2010), ignored or avoided large or awkward prey, and were not a perpetual, 24-hour menace across all environments, worldwide. We are not suggesting that azhdarchids were immune to predation, but we do not agree that their lifestyles, flight abilities or anatomy make them unusually vulnerable to predatory acts. Quite the contrary may have been the case.

Azhdarchids possess “pelican-like” jaw mechanics

A number of pterodactyloids have so-called “helical jaw joints”: asymmetrical quadrate condyles and glenoid fossae with anteromedially orientated ridges that laterally deflect the mandibular rami when the mouth is opened (e.g., Wellnhofer 1978). As indicated by Averianov (2013), these are well known in at least four azhdarchid taxa: *Quetzalcoatlus* sp., *Hatzegopteryx thambema*, *Bakonydraco galaczi*, and *Azhdarcho lancicollis* (Kellner and Langston 1996; Buffetaut et al. 2002; Ősi et al. 2005; Averianov 2010). The effect of these structures in pterosaurs has been likened to the mandibular bowing of pelicans, which are famously capable of considerable lateral bowing to facilitate expansion of the enormous gular pouches that they use in capturing fish and other prey (Schreiber and Woelfenden 1975; Fig. 2). Averianov (2013)



Fig. 2. Foraging great white pelicans, *Pelecanus onocrotalus*, with partially distended mandibles. When completely filled with water and prey, the mandibular rami of these birds are capable of considerably greater lateral expansion. Photo by DN.

cited the structures in azhdarchids as evidence for a novel feeding hypothesis that, to our knowledge, is not practised by any modern animal. Specifically, he proposed that azhdarchids deployed their bowed mandibles (along with the gular pouches and associated tissues) as “scoop nets” to capture fish sighted when flying across lakes and rivers. Within this scenario, ventral depression of the head is allowed by motion at the neck base, since much of the azhdarchid neck permits little flexion (Martill 1997; Witton and Naish 2008; Averianov 2013). Averianov (2013) specifically stated that the elongate jaw tips of azhdarchids would have been redundant in terms of prey-catching behaviour.

We note considerable problems with this idea. Firstly, the assumption that azhdarchids bore an extensible throat sac is far from certain. Throat tissues are preserved in the ctenochasmatooid *Pterodactylus antiquus* and the rhamphorhynchid *Rhamphorhynchus muensteri* (e.g., Frey et al. 2003b), and are inferred for the ornithocheiroids *Ludodactylus sibbicki* and *Pteranodon* sp. from the preservation of ingested material between their mandibular rami (Frey et al. 2003a; Bennett 2001). The exact nature of these tissues (e.g., muscular component, elasticity) remains poorly understood, however, and even if throat pouches are common to all pterosaurs, their functional significance is not clear. It is also possible, perhaps likely, that the form and properties of pterosaur gular tissues varied considerably between species, just as they do in modern animals. With no evidence currently available on the nature of azhdarchid throat tissues, it is not at all certain that their gular regions were conducive

to pelican-like foraging, nor indeed that their throat tissues played any specific role in feeding at all.

Many or all azhdarchids possess very long mandibular symphyses which may account for as much as 60% of mandible length (Kellner and Langston 1996; Ősi et al. 2005). Thus, for even the anterior tip of the proposed throat sac to reach the water surface, most of the lower jaw has to be submerged. Recent work on the energetics of trawling pterosaur mandibles through water while flying suggests that submersion of even 40 mm of the jaw tip is energetically unsustainable, and perhaps entirely untenable, for any pterosaur exceeding a wingspan of 2 m (Humphries et al. 2007). We predict that submersion of over 60% of the lower jaw (equating to ca. 60 cm of the mandible in *Quetzalcoatlus* sp., and perhaps over 1 m in giant species) would cause tremendous drag-related problems, a condition exacerbated in azhdarchids since their mandibles have flat occlusal surfaces that widen posteriorly and are thus very different from the blade-like jaws present in modern water trawlers (Zusi 1962). Moreover, we note that azhdarchid jaw tips are much longer than those of virtually all other pterosaurs (Martill and Naish 2006), prompting critical questions over the development of this derived condition if it was so strongly detrimental to their foraging methods.

Furthermore, as noted by Humphries et al. (2007) and Witton and Naish (2008), azhdarchid jaw, skull and neck anatomy shows none of the bracing adaptations against drag forces required for water-trawling. This can be demonstrated quantitatively using a measure of azhdarchid jaw area, an

estimate of azhdarchid cervical vertebra bending strength, and a simple drag equation:

$$0.5V^2SdCD$$

where V is velocity, d is fluid density, S refers to profile area of the trawling jaw, and CD is the drag coefficient. We measured the mandible and throat area of *Quetzalcoatlus* sp. specimen TMM 42161-2 as 440 mm² using the freeware program ImageJ v1.37 and images provided by Kellner and Langston (1996) (see Fig. 3 and Table 1). Assuming a flight speed of 18.4 m/s, the minimal speed for level flight for a 22.4 kg, 4.7 m wingspan, *Quetzalcoatlus* sp. (MPW, unpublished data) and a drag coefficient of 0.9, the resultant drag force is 67644 N, compared to a bodyweight of 218.7 N (Witton and Habib 2010). Cervical V of *Quetzalcoatlus* sp. has been estimated as capable of withstanding approximately 2 bodyweights under cantilever bending (Witton and Habib 2010), suggesting the neck of *Quetzalcoatlus* would endure more than 300 times its biomechanical limit during the trawling behaviour proposed by Averianov (2013). This comparison, while not particularly sophisticated, reinforces suggestions that azhdarchid anatomy is maladapted for lifestyles that involve habitually pulling the mandible through the water. We refer readers to the exhaustive work by Zusi (1962) on modern skim-feeders (*Rynchops*) for further information on the tremendous adaptations seemingly required for habitual in-flight skimming and trawling to work.

Averianov's (2013) proposed "scooping" of fish into a throat pouch is also problematic because, in addition to prey items, any "scoop net" would almost certainly uptake significant volumes of water. Brown pelicans (*Pelecanus occidentalis*) are reported to capture at least 10 l of water in their gular pouches when foraging, increasing their weight by 250% (Field et al. 2011). This water must be shed before the bird can engage in any other activity, flying especially (Schreiber and Woelfenden 1975). We therefore question whether flying animals can "scoop" fish prey from water in the manner proposed by Averianov (2013) without the acquisition of litres of water to the detriment of flight ability. The uptake of water is even more counterintuitive when the long, stiff necks of azhdarchids are considered, as these seem poorly suited for dealing with considerable stresses and weights at their anterior extreme (as acknowledged by Averianov [2013]; also see above and Witton and Naish 2008).

Furthermore, we find no evidence that azhdarchid mandibles, or those of any pterosaurs for that matter, are functionally

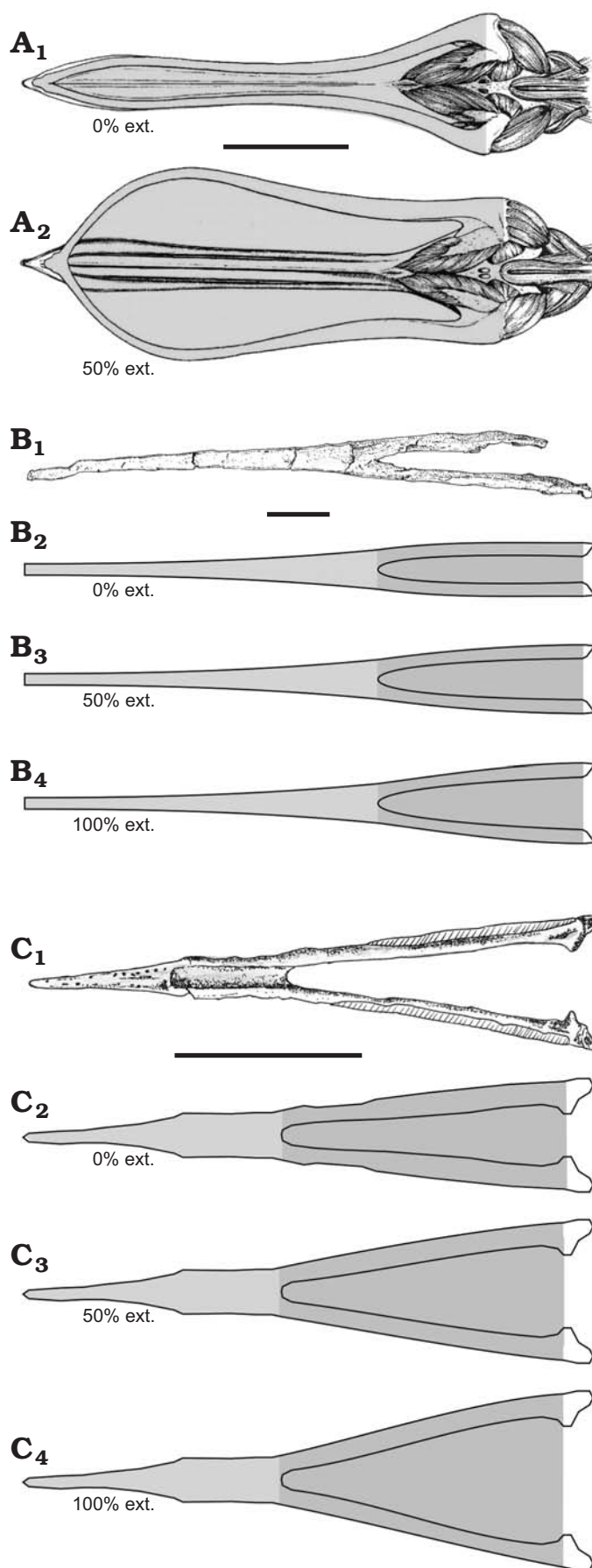


Fig. 3. Comparing mandibular bowing in pelican (A) and azhdarchids (B, C), showing areas measured for relaxed jaws (0% ext., A₁, B₂, C₂), jaws partially extended (50% ext., A₂, B₃, C₃), and fully extended (100% ext., B₄, C₄). Shaded regions denote areas measured for comparison; darker shading on azhdarchid jaws reflects regions measured for "gular alone" measurements. A. *Pelecanus occidentalis* skull and mandible in ventral view, modified from Meyers and Meyers (2005). B. *Quetzalcoatlus* sp. (TMM 42161-2) jaw in dorsal view (B₁), redrawn from Kellner and Langston (1996). C. *Bakonydraco galaczi* (MTMGyn/3) jaw in dorsal view (C₁), after Ősi et al. (2005). Scale bars 100 mm.

Table 1. Results of azhdarchid and pelican mandible area estimates and bowing analysis. Percentage values in area measurements denote degrees of lateral displacement of mandibular rami in the pterosaur jaws.

	Mandible extension	Jaw areas (entire) (mm ²)			Jaw areas (gular region) (mm ²)		
		0%	50%	100%	0%	50%	100%
<i>Pelecanus occidentalis</i> (Meyers and Meyers 2005: fig. 1)	jaw area	163.5	414.8				
	difference from 0% ext.		2.54				
<i>Quetzalcoatlus</i> sp. (TMM 42161-2)	jaw area	444.0	483.4	514.4	254.8	292.5	321.7
	difference from 0% ext.		1.09	1.16		1.15	1.26
<i>Bakonydraco galaczi</i> (MTM Gyn/3)	jaw area	88.4	102.4	116.4	65.9	79.6	93.2
	difference from 0% ext.		1.16	1.32		1.21	1.41

analogous to those of pelicans. We aimed to test hypothetical mandibular bowing in azhdarchid jaws since we were interested in assessing their ability to perform pelican-like feats of throat expansion (Fig. 3). We estimated the jaw and gular areas anterior to the glenoid fossae in *Quetzalcoatlus* sp. (reconstructed mostly TMM 42161-2, from Kellner and Langston 1996) and *Bakonydraco galaczi* (based on specimen MTM Gyn/3, from Ősi et al. 2005) in three guises: 1, a relaxed state; 2, with the mandibular rami laterally displaced at their posterior end by 50% of the widths of their glenoid fossae to simulate lateral bowing; and 3, at 100% of the same value (maximum displacement of 21 mm in *Quetzalcoatlus* sp., and 17 mm in *Bakonydraco*). The latter degree of displacement was almost certainly unobtainable for a live pterosaur, but we use this as a maximum estimate of jaw area increase during mandibular extension. Mandibular symphyses were unmodified in all three models. For comparison, we measured the jaw area in *P. occidentalis* using the figures of relaxed and distended jaws in Meyers and Meyers (2005: fig. 1). Note that the distended jaws in this figure are incompletely bowed compared to the distension actually possible in foraging *P. occidentalis* (e.g., Schreiber and Woelfenden 1975; MPW and DN personal observations), so our measurements of jaw area do not reflect the maximal condition. As above, jaw areas were measured using the freeware program ImageJ, v1.37.

The pterosaur jaws demonstrate considerably less area increase with mandibular bowing than the pelican (Table 1). At 50% lateral displacement, the gular regions of *Quetzalcoatlus* and *Bakonydraco* were increased in area by 15 and 21%, respectively, equating to only a 9 and 16% increase when the area of the mandibular symphysis is considered. The more broadly displaced models double these percentage increases, but even these are dwarfed by the 154% area increase of the bowed *P. occidentalis* jaws compared to their relaxed condition, despite only being partially flexed.

These results should not be considered surprising. Continued comparisons between pterosaur and pelican jaws are difficult to defend when the unusual and specialised nature of pelican mandibles are considered (e.g., Schreiber and Woelfenden 1975; Meyers and Meyers 2005; Field et al. 2011). Whereas pterosaur jaws simply bulged outwards at their joints, pelican mandibles are highly streptognathic, bowing laterally along the entire length of the rami (Meyers and Meyers 2005). Other birds, including anatids, larids,

and caprimulgids demonstrate streptognathy, but none have developed this specialisation as far as pelicans (Dawson et al. 2011; Meyers and Meyers 2005). *P. occidentalis* mandibles expand from 50 mm to 150 mm wide at maximum distension, creating wide arcs encompassing an estimated 50 000 mm² at the entrance to their pouches (Schreiber and Woelfenden 1975). Their mandibular symphyses are extremely short and their anterior rami contain low mineral concentrations of 20%, compared to 50% elsewhere in the jaw (Meyer and Meyers 2005). This permits greater flexion in the anterior part of the mandible, aided further by its solid cross-section and flexible, skin-like rhamphothecae. The lateral mandibular regions, in contrast, have higher (50%) mineral content and move via syndesmosis, where connective tissue between bones permits kinetic movement. In contrast with pterosaurs, the posterior mandibular region is relatively immobile. The entire jaw is extremely resistant to dorsoventral bending (Field et al. 2011). Further foraging adaptations are also seen in pelican jaw soft-tissues: they lack a tongue and possess reinforced but highly elastic gular tissues (McSweeney and Stoskopf 1988; Field et al. 2011).

To our knowledge, no azhdarchid or other pterosaur possesses jaws that are capable of pronounced streptognathy or any other clear adaptations for “scooping” prey, and they should not be favourably compared to pelicans in this manner. Such adaptations should be detectable in the azhdarchid fossil record because good mandibular material is known for several taxa (e.g., Wellnhofer 1991; Kellner and Langston 1996; Ősi et al. 2005) and none show, for instance, indications of reduced mineralisation or bones capable of syndesmosis. Indeed, few animals possess the remarkable mandibular architecture or soft-tissues present in pelicans, although some striking convergences are present between these birds and rorquals (Field et al. 2011). We further note that helical jaw joints occur commonly in other pterosaurs, ankylosaurs, ornithomimids and theropods (including birds) (e.g., Weishampel et al. 2004; Witton 2013); they are not uniquely shared by azhdarchids and pelicans and thus do not have a specific correlation with pelican-like throat sacs or “scooping” foraging methods. Gular pouches are also widespread across reptiles (including birds) and are variously involved in diverse feeding and foraging strategies, as well as visual and vocal communication. We assume that previous authors have favourably compared pterosaur jaws with those of pelicans

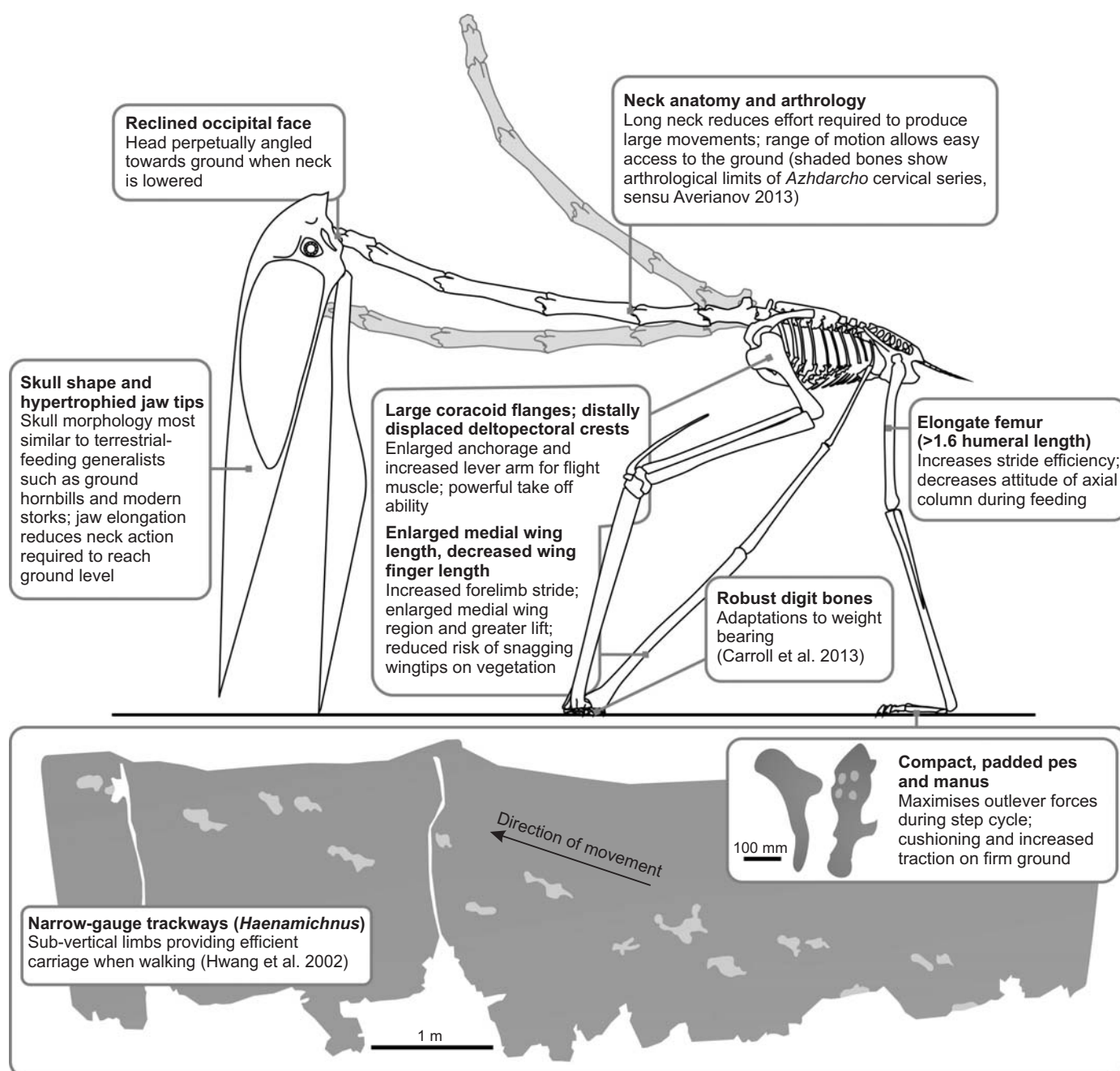


Fig. 4. Graphic summary of the terrestrial stalking azhdarchid hypothesis, demonstrated using the reconstructed skeleton of *Zhejiangopterus linhaiensis*. Skeletal reconstruction based on Cai and Wei (1994); annotations based on findings of Hwang et al. (2002); Witton and Naish (2008); Averianov (2013); and Carroll et al. (2013).

due to a biased assumption that volant waterbirds can be used as pterosaur analogues (Witton and Habib 2010).

Concluding remarks

In sum, we consider the hypothesis of “scoop” feeding in azhdarchids to be critically flawed for reasons outlined above. We note in closing that this notion does not, as with many other considerations of azhdarchid anatomy, explain attributes such as their long jaws, limbs, and necks and compact feet, whereas

the “terrestrial stalking” hypothesis rationalises most features of azhdarchid anatomy as adaptations for locomoting and foraging within terrestrial settings (Witton and Naish 2008; Fig. 4). Indeed, the quantification of azhdarchid neck arthrology presented by Averianov (2013) meets our prediction that azhdarchids were easily capable of foraging at ground level despite the unusually restricted joints between cervical vertebrae (Fig. 4; also see Witton and Naish 2008: fig. 8). We therefore maintain our view that azhdarchids did not forage while flying and consider their taphonomy, anatomy, and functional morphology fully consistent with terrestrial foraging.

Acknowledgements

We are grateful to David Hone (Queen Mary University of London, UK) and Michael Habib (University of Southern California, Los Angeles, USA) for informed reviews, which improved this manuscript. We thank Attila Ősi (MTA-ELTE Lendület Dinosaur Research Group, Budapest, Hungary) and Mátyás Vremir (Transylvanian Museum Society, Cluj-Napoca, Romania) for access to specimens relevant to this research. Finally, we have benefited from discussion with several colleagues who share our interests in azhdarchid palaeobiology, including Chris Bennett (Fort Hays State University, Hays, USA), Nathan Carroll (Montana State University, Bozeman, USA), Gareth Dyke (University of Southampton, Southampton, UK), David Martill (University of Portsmouth, UK), and David Unwin (University of Leicester, UK).

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