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The wingtips of the pterosaurs: Anatomy, aeronautical function and ecological implications

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Highlights

The wingtips of the pterosaurs: Anatomy, aeronautical function and ecological implications

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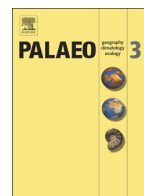
- Many pterosaurs possessed curved distal wing phalanges.
- Curvature will affect the flight performance of the wing.
- High curvature is linked to flight in cluttered environments or over open oceans.
- Potential taphonomic distortion limits interpretation.

Q1 # The wingtips of the pterosaurs: Anatomy, aeronautical function and ecological implications

Q2 D.W.E. Hone [a,*], M.K. Van Rooijen [b], M.B. Habib [c]

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ABSTRACT

The leading edge and shape of the pterosaur wing is constrained by the skeleton. Although it has long been known that at least some pterosaurs had posteriorly curved distal wing phalanges, affecting the shape of the wingtip, this has been little studied despite that this may have profound effects on flight performance. Here we examine the evidence for curved wingtips in pterosaurs and evaluate the possible aerodynamic and aeronautical effects. Curved wingtips are shown to be common in both pterosaurs likely to have inhabited terrestrial environments, and those which were strongly pelagic. The recently described genus *Bellubrunnus* provides new anatomical novelty for pterosaurs having anteriorly directed wingtips and thus likely had a different flight profile to all previously known pterosaurs.

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1. Introduction

From almost the very start of scientific research into pterosaurs, they were recognized as volant animals where the main wing was formed of a membrane that was anchored onto the massively enlarged fourth finger of the hand (Wellnhofer, 2008). Although the function of the pterosaur wing as a flight apparatus have long been apparent, the exact structure of the wing and how it may have performed has been the subject of much research and scientific debate. Despite recent advances in pterosaur research (Hone, 2012), the work to date on pterosaur flight remains relatively limited in scope. Our understanding of, and research into, pterosaur flight has been limited by a lack of clear understanding of their flight apparatus (Middleton and English, 2014).

Numerous studies have examined the possible flight characteristics and ecology of the pterosaurs with regards to wing shape (e.g. Hazelhurst and Rayner, 1992; McGowan and Dyke, 2007) and performance (e.g. Pennycuick, 1988; Chatterjee and Templin, 2004; Habib, 2008; Witton and Habib, 2010; Palmer, 2011) but only in relatively recent years have new specimens and new reviews established a better understanding of the detailed soft tissue structure of the wing (e.g. Frey et al., 2003) and its integration with the body (Elgin et al., 2011). Although there were likely some differences between various pterosaur wing constructions, the evidence suggests that overall they were conservative in shape and structure (Dyke et al., 2006; Elgin et al., 2011).

Thus, unlike fossil birds, for example (where feathers of different shapes, sizes and distributions could potentially produce profoundly different wing planforms from the same, or at least a very similar, skeleton), the extent and shape of the pterosaur wing can be largely determined by the preserved skeletal elements and the absence of preserved soft tissues are less critical.

One aspect of the pterosaur wing has, however, been almost entirely overlooked in assessments of their flight capabilities — the shape of the wingtip. This aspect of the wing has important implications for how the wing will function. Different wingtip shapes will affect stall thresholds, vortex shedding efficiency, and gust load alleviation, among other factors (Vogel, 2003; Pennycuick, 2008). That pterosaurs present a variety of different morphological shapes to their wingtips as seen in the different levels of curvature to the distal phalanx, attests to potential differences in flight performance and differing morphological adaptations to optimize their flight apparatus to an ecological role.

Here we survey the available information on the variety of shapes for pterosaur wingtips. Using aeronautical theory and comparisons to extant vertebrate fliers, we hypothesize the likely effects of these differing shapes on performance and therefore ecology. Special consideration is given to the unusual pterosaur *Bellubrunnus* and its anteriorly directed wingtips — a feature apparently unique among volant vertebrates.

Institutional abbreviations

BSPG, (formerly BSP) Bayerische Staatssamlung für Paläontologie, Munich, Germany; CM, Carnegie Museum, Pittsburgh, Pennsylvania,

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USA; GMV, Geological Museum of China, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; OXFUM, (formerly J) Oxford University Museum of Natural History, Oxford, UK; LACM, Los Angeles County Museum of Natural History, Los Angeles, California, USA; MBR, Museum für Naturkunde, Humboldt Universität, Berlin, Germany; NHMUK (formerly BMMS, BMNH), Natural History Museum, London, UK; NSM, National Science Museum, Tokyo, Japan; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; YH, Yizhou Museum, Yixian, China.

Anatomy of the pterosaurian wingtip

Osteology

The wingfinger of pterosaurs is traditionally described as being 'straight'. Although the wing metacarpal and phalanges 1–3 of the wing are indeed straight elements, the fourth phalanx is not infrequently seen to have a degree of posteriorly directed curvature along its length. (Note: The pteranodontid pterosaur *Nyctosaurus* has only three wing finger phalanges (Williston, 1911), and this is also likely true of the anurognathid *Anurognathus* (Bennett, 2007) — here we consider the 3rd wing phalanges of *Nyctosaurus* and *Anurognathus* functionally analogous to the 4th of other pterosaurs). Rarely is this curvature strong, but it is quite evident in contrast to the more proximal phalanges in numerous specimens of pterosaurs that represent much of the familial diversity of Pterosauria.

Only a limited amount of information on the shape of the pterosaur distal wing phalanx is available as a many pterosaur specimens are preserved in only two dimensions. The fourth wing phalanx tapers along its length and generally terminates in a sharp point. Proximally there is a posteriorly directed expansion to articulate with the third phalanx,

but other information is rarely available (Fig. 1). Although a good number of pterosaur specimens are well preserved in three dimensions, distal phalanges are rarely preserved and descriptions are uncommon. As such, our knowledge of the three dimensional anatomy of the distal wing phalanx is largely limited to a few derived pterodactyloids.

Kellner and Tomida (2000) provide a description of a well-preserved specimen of the pterodactyloid *Anhanguera* noting that the distal phalanx was close to triangular in cross-section at the point of articulation and became more oval along its length. Bennett (2001) presented a synthesis description of multiple specimens of *Pteranodon* and observed that the fourth phalanx tended to be strongly curved. Bennett (2001) also described the 3-D structure as being sub-circular at the articular end and with a circular or oval cross-section in the middle part, and tear-dropped shape at the very end of the bone, producing a sort of shelf on the posterior face. This distalmost section of the bone was roughened on the posterior face, presumably for the attachment of the patagium (Bennett, 2001). However, the bone was described as tapering initially, before remaining constant in diameter for much of its length. Young (1964) described two incomplete distal phalanges in *Dsungaripterus* and these are illustrated with having a narrow oval cross-section. However, Young (1964) noted the presence of a 'shelf' on the posterior face of the bone which would be analogous to that noted in *Pteranodon* above, though here Young noted that this decreased in size towards the distal end of the bone, rather than increasing as in *Pteranodon* (Bennett, 2001).

At least some pterosaurs have a groove along the posterior midline of the bone (e.g. *Rhamphorhynchus*, Padian and Rayner, 1993). This would modify the cross-sectional shape of the element and give it something of a C-shape. Furthermore, Martill and Frey (1999) described a T-shape to Y-shape cross-section of the distal phalanges in some azhdarchids, particularly *Quetzalcoatlus*, which is probably the result of having two grooves along the long axis of the bone rather than one. The location of the groove(s) is proposed to occur in areas of tensile strain in the same manner as the ventral grooves of the rachis in avian primary feathers. These grooves would help the bone resist bending (Padian and Rayner, 1993), which could promote spanwise twisting of the wing finger (especially near the tip of the wing), while still providing strong resistance to bending (Habib, 2010).

The length of the distal wing phalanx varies greatly between various specimens. In very young or smaller pterosaurs it may be very short, for example being as little as 17 mm in the adult holotype of *Jeholopterus* (IVPP V 12705 — data from Elgin, 2014), and as little as 10 mm for a juvenile of *Pterodactylus antiquus* BSPG 1924 V 1 — (Elgin, 2014). The longest we were able to find in the literature is 330 mm in *Coloborhynchus piscator* SMNK 1133 PAL though this is estimated from an incomplete element (data from Elgin, 2014). The proportional length also varies — in derived azhdarchids, it may be as little as 1.4% of the total length of the wingfinger as seen in *Quetzalcoatlus* TMM 14961 (Elgin, 2014), through to 27.5% in *Campylognathoides* (Wellnhofer, 1974 in Elgin, 2014).

Although most pterosaur specimens have the 4th wing phalanx terminating at a point, this is not the case for all. There is a slight expansion or possible 'ball' of bone at the very distal tip of the phalanx in several specimens. This is seen in the large *Rhamphorhynchus* specimen in Eichstätt (figured in Wellnhofer, 1974, Plate 28.1), a specimen of *Dorygnathus* (SMNS 50914), one of *Austriadactylus* (SMNS 56342), *Scaphognathus* (SMNS 59395), and of *Sinopterus* (IVPP V 13363). A similar expansion is seen in the distal 3rd phalanx of the juvenile specimen of *Anurognathus* (Bennett, 2007) on one wing but not the other, which terminates in a point (other anurognathid taxa show four phalanges on the wing finger). However, it is not clear whether or not this specimen has the 4th phalanx missing (in which case this is merely the expected expansion for articulation with that element) or only three (where this would be a distal expansion of the last phalanx). Notably, Bennett (2001) observed a similar ball-like structure in *Pteranodon* and suggested that its absence was likely due to the crushing nature of the preservation. Although not apparently present in the superbly
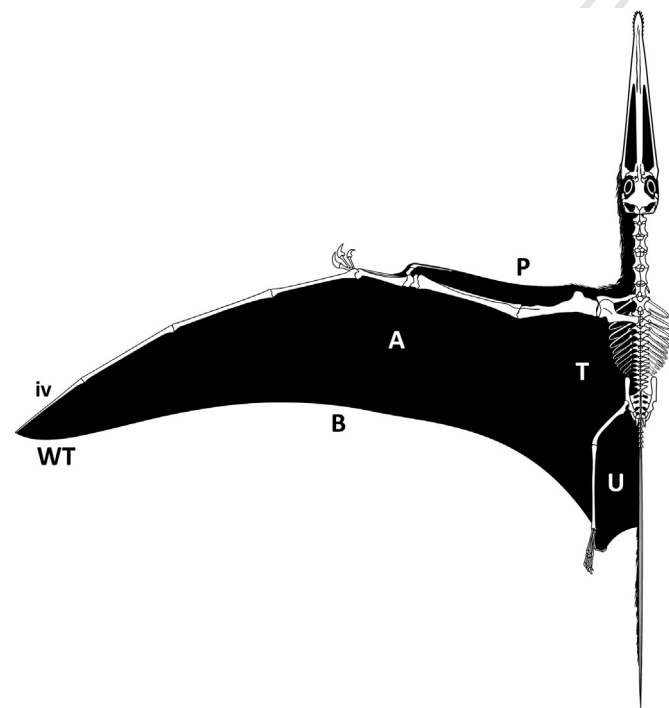

Fig. 1. Pterosaurian bauplan (*Darwinopterus*) showing key wing membranes and anatomical features in a flight posture but with the wings not loaded. Abbreviations as follows: A — actinopatagium, B — brachiopatagium, P — propatagium, T — tenopatagium, U — uropatagium, WT — wingtip, iv — fourth wing phalanx.

preserved *Anhanguera* specimen described by Kellner and Tomida (2000) it is certainly plausible that this feature is much more widespread in pterosaurs than noted here and is simply not apparent on many two dimensionally flattened specimens.

There is no evidence for pneumaticity in the distal phalanx in basal pterosaurs and the internal structure of the bone is uncertain. Various pterodactyloids however possess pneumatic distal wing phalanges, though the number identified to date is limited. *Pteranodon* exhibits this condition (Bennett, 2001), and a pneumatopore is also apparently present in the ventral side of an unidentified azhdarchid (SMNK PAL 6409). The number of taxa showing this condition is perhaps limited owing to a lack of specimens that preserve a pneumatopore and/or show clear evidence of internal invasions of the bone, though given the extensive pneumaticity of elements in clades such as the ornithocheirids (Kellner and Tomida, 2000) and the pneumatisation of even elements such as ribs, sterna and ilia in azhdarchoids (Elgin and Hone, 2013), then this is likely more extensive and may be present in a variety of pterodactyloid pterosaurs.

Notably, a large number of specimens of pterosaurs exhibit a degree of posteriorly directed curvature along the length of the terminal wing phalanx. In addition to specimens that may be pathological (see below) this is commonly seen as a general curve along the length of most of the bone, but may be more localized. The degree of curvature, distribution, and possible functional and/or systematic implications of this curvature has not to date been explored.

Soft tissues

Pterosaur wings are complex structures that consist of multiple tissue types arranged into layers. In addition to the two layers of epidermis, there are one (Frey et al., 2003) or more (Kellner et al., 2010) layers of stiffening actinofibrils, a layer of muscle tissue fascia, and one of blood vessels (Frey et al., 2003). Actinofibrils are noticeably more concentrated at the tip of the wings, resulting in densely packed fibers at this point (Bennett, 2000).

The soft-tissue tip of the pterosaur wing is rounded and expanded posteriorly (Padian and Rayner, 1993; Elgin et al., 2011) — Fig. 1. This arrangement can be seen in several pterosaur specimens including those of *Rhamphorhynchus* (BSPG 1880 II 8 and BSPG 1907 I 37), *Scaphognathus* (SMNS 59395) and *Sordes* (PIN 2585/3). While material is clearly limited, given the conservative nature of the pterosaur wing planform (Elgin et al., 2011) and the functional implications of a pointed wingtip (susceptibility to catastrophic stall and sensitivity to gust load damage; see below) it is reasonable to infer that this was normal for all pterosaurs. When not under load, the membrane does not terminate at a point at the end of the fourth phalanx as often incorrectly illustrated.

In addition, a trailing edge tendon (or similar soft tissue structure) has been suggested to be anchored at the tip of the distal phalanx in order to support the wing, and presumably reduce flutter of the trailing edge (e.g. Pennycuick, 1988). This structure has been controversial, since although it makes sense from a functional point of view, evidence for it has been largely lacking (Padian and Rayner, 1993). If present, it would presumably represent a thicker and potentially robust part of the wing and so should be preserved at least as often as the main wing membrane, rather than being apparently entirely absent. However, it may have been destroyed through improper preparation, and recently specimens have surfaced that show some difference between the wing membrane and the trailing edge (Tischlinger and Frey, 2002). A roughened area for the attachment of soft tissue is seen in at least some pterosaurs (as noted above) though whether this was critical for the attachment of the patagium generally, or a tendon specifically, is not known.

In life position

The life position and shape of the wingtip might not have been the same as seen in fossil specimens. In particular, both theory and anatomical observations predict that the wingtip would take on a noticeably different shape during flight. To be functionally tensioned for flight, the trailing edge of the wing membrane in pterosaurs must have been either straight (if there was a trailing edge tendon), or at least slightly concave (Palmer and Dyke, 2010). Because the distalmost phalanx of the pterosaur wing was often quite gracile, it is probable that it would flex when the wing was tensioned, adding to the concavity of the trailing edge and producing a lunate wingtip.

The degree to which the wingtip would deform depends on the material properties of the original bone, in addition to its shape. The degree of mineralization in the original bone is not immediately apparent from the fossil remains. Bennett (2001) referred to the distal wing in pterosaurs as a 'flexible spar', with Steel (2008) describing the histology as "Longitudinal section (Section 3) through the proximal end of UP 2000.9 (wing phalanx 4), showing calcified cartilage supported by columns of bone". These observations, while inconclusive, support the possibility of the distal wing in pterosaurs having been composed, in part, of bone with low mineral content (and therefore potentially a low elastic modulus). Thus may have been curved in flight, but would appear straight 'at rest' and thus as preserved.

2. Methods

In Table 1 we catalog all specimens we are aware of with curved wingtips on one or both sides of the individual. Data were collected through searching museum collections and a search of the pterosaur literature. A variety of specimens (Fig. 2) show the different degrees of curvature seen and the variation between the left and right sides of the animal, or between straight and curved examples in different specimens of a single species. More than 50 specimens have been recorded representing more than 25 genera and these represent a wide diversity of pterosaur clades that include both basal and derived forms, and in some cases numerous examples from a single species.

Curvature was measured by marking a straight line between the tip of the phalanx and posterior edge of the proximal face. This was then bisected by a perpendicular line until it reached the phalanx. From this point, lines were drawn out to the two original points and the angle of the crux measured (see Fig. 3) to give a value. Note that this value will likely never reach 180° because the proximal part of the phalanx extends slightly posteriorly in its articulation with the preceding element. Thus, even a totally straight phalanx will have a value of a few degrees below 180°. While this method provides a highly simplified measure of curvature, it is sufficient in this case since we are testing against a null model of a straight phalanx. The simple curve measure used here is sufficient, even for our sample sizes, to differentiate even a relatively weakly curved phalanx from a straight one (see Fig. 2). It is also sufficient to differentiate overall strength of curvature (i.e. strongly curved vs weakly curved). More specific details of curvature (such as those sometimes employed to look at claws — e.g. Feduccia, 1993; Birn-Jeffrey et al., 2012) are not elucidated by our simplified metric, and we therefore do not make fine scale differentiations in phalanx curvature or shape in this analysis. Because the primary interest is the potential response of the phalanx to total-element bending under wing tension loads, the more specific details of curvature would effectively constitute noise in our analysis. Construction of the lines and measurements of the angles were completed in Photoshop.

3. Results

Not all pterosaurs exhibit curved distal phalanges. Measurements of *Pterodactylus* (BSPG 1937.I.18X) for example show minimal curvature (i.e. almost 180°) with values of 177.0° and 170.6° recorded and a specimen of *Darwinopterus* (YH 2000) was 170.4°. These are extremely straight, although other pterosaurs do exhibit distal phalanges with only very moderate curvature. Here we define a straight phalanx as being between 180 and 170°. In Table 1 we record all pterosaur

Table 1

Specimens of pterosaurs with curved wingtips (wing phalanx 4, except in *Nyctosaurus*). Curvature is always posteriorly directed unless noted. The descriptions of degrees of curvature are subjective, but all deviate from 'straight' as described in the main text. Specimen numbers are used where the material was measured from photographs taken by the authors, references are used when these were the source of the information (in literature figures, either photographs or drawings). Values close to 180° would indicate minimal curvature, lower numbers would indicate higher curvature and the anteriorly curved wingtips of *Bellubrunnus* lead to values greater than 180°. *Fig. 2b of Wang et al., 2009 suggests that the right wingtip of the holotype of *Wukongopterus* is anteriorly curved based on the shape of the proximal end of the phalanx, however examination of photos suggests that this is merely a slight error in the drawing and the expanded side of the phalanx means that the curvature is posteriorly directed. Specimens too poorly preserved or illustrated to be measured are recorded with a description of the curvature.

Clade	Genus	Source	Degree of curvature/notes
Triassic Pterosauria Indet.	–	Dalla Vecchia, 2003 p.20	166.8
Triassic Pterosauria Indet.	–	Dalla Vecchia, 2003 p.25	170.3
Anurognathidae	*Jeholopterus*	IVPP V 12705	161.7, 168.6
Anurognathidae	*Dendrorhynchoides*	GMV 2128	160.4
Dimorphodontidae	*Peteinosaurus*	Wellnhofer, 1991 p.66	165.2
Scaphognathinae	*Scaphognathus*	SMNS 59395	170.7, 169.7
Scaphognathinae	*Sordes*	PIN 2585/3	Moderate curvature to both phalanges.
Scaphognathinae	*Jianchangopterus*	Lü and Bo, 2011	161.5
?	*Austriadactylus*	SMNS 56342	168.3
Campylognathoidea	*Campylognathoides*	Padian, 2008b Plate 4	164.2, 163.8
Campylognathoidea	*Campylognathoides*	Padian, 2008b p90	Phalanx incomplete but curvature is visible.
?Rhamphorhynchinae	–	OXFUM 23047	170.7
Rhamphorhynchinae	*Dorygnathus*	SMNS 51827	170.2
Rhamphorhynchinae	*Dorygnathus*	SMNS 50164	168.2
Rhamphorhynchinae	*Dorygnathus*	SMNS 81205	168.3, 167.3
Rhamphorhynchinae	*Dorygnathus*	MBR 3665.1	171.7
Rhamphorhynchinae	*Dorygnathus*	BSPG 1938 I 49	170.7, 169.0
Rhamphorhynchinae	*Dorygnathus*	Padian, 2008a p15 MB. R 1920.16	163.8, 166.3
Rhamphorhynchinae	*Rhamphorhynchus*	Eichstätt collection. Figured in Wellnhofer, 1975 Plate 28.1	158.5, 168.3
Rhamphorhynchinae	*Rhamphorhynchus*	Wellnhofer, 1975 Plate 28.2	166.1
Rhamphorhynchinae	*Rhamphorhynchus*	TMP 2008.041.0001	165.7, 171.3
Rhamphorhynchinae	*Rhamphorhynchus*	RAM 14522	170.5
Rhamphorhynchinae	*Rhamphorhynchus*	SMNS 80429	155.9 (Near 90° turn in distal part of phalanx).
Rhamphorhynchinae	*Rhamphorhynchus*	BMMS 3	168.9, 172.5
Rhamphorhynchinae	*Rhamphorhynchus*	BMMS 6 AS 7	166.5, 170.7
Rhamphorhynchinae	*Bellubrunnus*	BSPG 1993 XVIII 2	198.2, 206.6
Wukongopteridae	*Kunpengopterus*	IVPP V 16047	168.7, 166.8 (second tip broken?)
Wukongopteridae	*Wukongopterus*	Wang et al., 2009	175., 163.9 *
Monofenestrata Indet.	Unnamed 'Pro-pterodactyloid'	Tischlinger and Frey, 2014	169.3
Pterodactyloidea Indet.	–	MBR 5591.1	162.7
Ctenochasmatoidea	*Ctenochasma*	CM 11425	166.9 (Juvenile specimen).
Ctenochasmatoidea	*Pterodactylus*	BSPG AS V 29	165.6
Ctenochasmatoidea	*Elanodactylus*	Zhou, 2010a	156.4
Ornithocheiridae	*Anhanguera*	NSM-PV 19892	175.5
Boreopteridae	*Zhenyuanopterus*	Lü, 2010	170.9, 171.7
Pteranodontidae	*Nyctosaurus*	NHMUK R4810	151.1
Pteranodontidae	*Nyctosaurus*	Bennett, 2003 p.67	148.5
Pteranodontidae	*Pteranodon*	NHMUK 4538	163.0
Pteranodontidae	*Pteranodon*	LACM 50921	163.3
Pteranodontidae	*Pteranodon*	LACM 51132	159.4
Pteranodontidae	*Pteranodon*	Bennett, 2001 p.95	163.0
Pteranodontidae	*Pteranodon*	Bennett, 2001 p.95	140.4
Dsungaripteridae	*Germanodactylus*	BSPG 1892 IV 1	170, 167
Azhdarchoid Indet.	–	Unwin and Martill, 2007 Fig. 17.1e	Slight curvature on the one preserved phalanx.
Azhdarchoid Indet.	–	SMNK PAL 6409	156.0
Chaoyangopteridae	*Eopteranodon*	Lü et al., 2006 p.74	159.9
Chaoyangopteridae	*Chaoyangopterus*	Zhou, 2010b	166.4
Thalassodromidae	'Tupuxuarid'	Unwin and Martill, 2007 Fig. 17.14	Slight curvature to one preserved wingtip.
Thalassodromidae	'Tupuxuarid'	Undescribed specimen: Unwin and Martill, 2007 Fig. 17.15	159.5 Slight curvature to one and moderate curvature to the other wingtip, though notably these also appear to be very different lengths.
?Tapejaridae	*Nemicolopterus*	IVPP V 14371	165.6, 166.3
Tapejaridae	*Sinopterus*	IVPP V 13363	157.8, 162.4
Tapejaridae	*Sinopterus*	Lü et al., 2006 p.54	Strong curvature to the one preserved phalanx.
Tapejaridae	*Huaxiapterus*	Lü et al., 2006 p.60	Moderate curvature to both phalanges.
Tapejaridae	*Tapejara*	Eck et al., 2011 p.2	158.2
Azhdarchidae	*Eoazhdarcho*	Lü et al., 2006 p.62	153.3, 166.3

specimens that we could identify with phalanx curvature greater than this range.

Although clearly the total number of specimens recorded here is low compared to the vast numbers of pterosaur specimens known (though obviously not all of those are preserved with either or both of the 4th phalanges intact) we would suggest that based on the observations, curved distal phalanges cannot be considered especially rare or unusual in pterosaurs. As noted by Bennett (2001) the plane of crushing of pterosaur specimens preserved in 2D may reduce the curvature of a 4th phalanx, but not increase it. However, other effects might also potentially increase the curvature — for example post mortem shrinkage of tendons might lead to tension on the fourth phalanx increasing its curvature. However, we consider it unlikely that these would exceed the forces during flight and therefore the values recorded would still

Fig. 2. Multiple pterosaur wingtips demonstrating the variation seen within and between specimens (not to scale). These include left and right distal phalanges, but have been reflected as appropriate so that they all appear to be the right distal phalanx. a. The so-called 'pro-pterodactyloid' (Tischlinger and Frey, 2014), b. *Darwinopterus* (YH-2000) c., d. right and left wings of *Rhamphorhynchus* (JME-SOS4009) respectively, e. *Anhanguera* (NSM-PV 19892 — preserved in 3D), f. Rhamphorhynchine (J 23047).
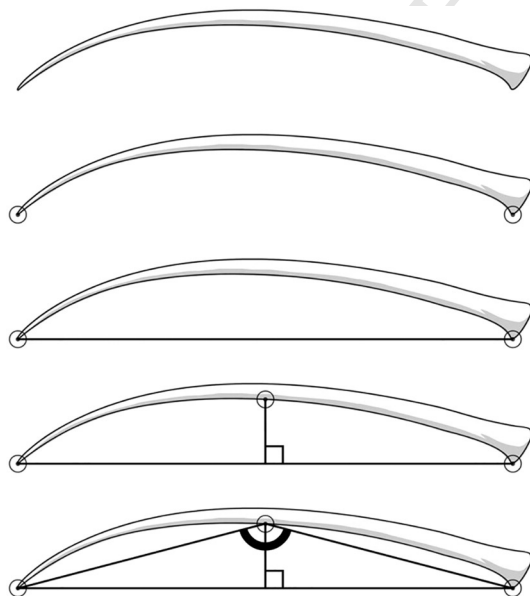

Fig. 3. Diagram to demonstrate measurement of the angles of the wingtips. Points are taken from the distal tip and the posterior most part of the proximal articulation, a line is drawn between them, this is then bisected by a perpendicular line until it contacts the ventral margin of the bone, from this point lines are drawn back to the original starting points and the internal angle measured.

be an appropriate minimum value for the curvature of the wingtip when flying. As such, some apparently straight wingtips may not have been straight in life, but those that are curved may be considered genuine and should therefore represent a *minimum* amount of curvature for the element.

However, this uncertainty means that any interpretation of the available data should be tentative and it is possible that there are outliers, especially where curvature is markedly less than might be expected as this is likely to be a result of crushing.

Furthermore, there are potential sources of error here that may alter the results. Firstly, an expanded posterior part of the proximal wingtip articulation would exaggerate the value and make the phalanx appear more curved than it truly is. As all pterosaurs have at least some expansion to this element however, the changes are likely to be largely limited. Similarly, a slight bulb on the distal tip of the phalanx might reduce the apparent curvature, though given how tiny this feature is when present, it is likely to have only a limited effect. Finally, the method used here does not discriminate between curvature along the whole length of a phalanx, and localized curvature. For example, in *Anhanguera* the curvature is largely limited to the distal part of the phalanx, and in a pathological specimen of *Rhamphorhynchus* (see Fig. 4) this is a sharp curve in an otherwise straight element. An odd shape to a phalanx such as the apparent S-curve in the holotype of *Zhenyuanopterus* might also distort the value depending on if the perpendicular line hits a convex or concave part of the wing.

The degree of curvature varies markedly between specimens with a range of nearly 30°, with a *Pteranodon* specimen at 148.5° being the lowest value and (aside from the unusual *Bellubrunnus*) the highest value is *Anhanguera* showing the least curvature at 175.5°. Ranges within a single genus may also be high, with a range of greater than 20° recoded in *Pteranodon*. Despite the potential errors noted above, there is some strong consistency in places. For example, there are less than 3° difference between six of the seven specimens of *Dorygnathus*, and values for the respective specimens of *Pteranodon* and *Nyctosaurus* are similarly close. This suggests that some genuine signal is in the available data and that phalanx curvature may have genuine phylogenetic and/or functional signal despite the limits of compression or distortion.

4. Discussion

Pathology vs function

At least some of the wingtips described and figured above can be attributed to pathologies or developmental deformities. Sudden and dramatic shifts in curvature, especially when these are asymmetric between the wings are unlikely to be the normal shapes and can be considered anomalies (e.g. Fig. 4) and need not be considered further in terms of possible phylogenetic or functional signal.

The distal wing phalanx would have been strongly loaded during flight (Palmer, 2011) and it is perhaps not unexpected that this would be more vulnerable to microfractures and stresses than more proximal phalanges. Pterosaurs may be more vulnerable to such damage than other vertebrate fliers since the tips of bird wings are composed of

Fig. 4. Wing phalanx of a specimen of *Rhamphorhynchus* (SMNS 80429) inferred to be pathological based on the extreme but localized curvature of the element (compare to Fig. 2.). Scale bar is 20 mm.

367 feathers that may be somewhat flexible (or at least may be shed and re-
368 placed) and the bones of bats are typically highly pliant (though as
369 noted above, the fourth phalanx of pterosaurs may also be compliant).
370 If the distal phalanx in pterosaurs was indeed compliant (i.e. relatively
371 low mineral, low stiffness bone) and under high strains, as we predict,
372 then it may explain why the fourth phalanx appears to be apneumatic
373 in all known taxa (at least all that have been examined for pneumatic
374 wing elements). Such compliant bones might not maintain a consistent
375 internal chamber size, making pneumatic passageways inconsistently
376 open and/or difficult to grow.

377   It is worth noting that presumably these pathological features as
378 seen in pterosaur phalanges took some time to develop into the shapes
379 seen through healing, and thus although they may well have had a det-
380 rimental effect on the performance of the animals bearing them, never-
381 theless they presumably survived for some considerable time with
382 these 'distorted' wingtips. Wingtip damage may have been common
383 in pterosaurs through ground strike during take-offs, or as the most
384 likely part of a wing to hit an object when flying in a cluttered environ-
385 ment or close to the ground.

386   On the other hand, at least some of the above described curved
387 wingtips must be considered genuine anatomical features on the ani-
388 mals in question. When the curvature is uniform to both wingtips (es-
389 pecially when these lie in different orientations to one another and
390 thus confounding crushing effects) and indeed across multiple speci-
391 mens of a species, it would be more parsimonious to interpret these as
392 being genuine. In at least some cases (e.g. *Sinopterus*, *Dorygnathus*) mul-
393 tiple specimens are seen with similar curvature both within and be-
394 tween specimens, further supporting the inference that these features
395 are genuine and that in life these animals bore curved distal phalanges.
396 This may still be a polymorphic characteristic with perhaps some indi-
397 viduals bearing curved tips and others not (or varying degrees of curva-
398 ture), but the repeated presence suggests it was at least common.

399   Other taxa and specimens are harder to classify. Curvature may be
400 very minor, or subtly different between the left and right sides, or rather
401 different between various specimens of a given taxon. Here, in addition
402 to the possible effects of crushing, the differences may be linked to slight
403 differences as a result of taphonomic distortion, or intraspecific varia-
404 tion or as the result of minor injuries and stress to the wingtip having
405 affected one side more than the other.

Effect of wingtip shapes

407   There are three functions related to wingtips that we consider here:
408 stall, wing shape, and wingtip mechanical loading. The potential of a
409 strongly pointed tip on a lifting surface to stall is a general parameter
410 that affects all such surfaces, from sails (Fossati, 2010) to mechanical
411 and biological wings (Pennycuick, 2008; Palmer and Dyke, 2011). To
412 this end, all pterosaurs could benefit from some wingtip phalanx curva-
413 ture, since this will tend to round out the wingtip (as will the apparently
414 expanded tip of the patagium – see Elgin et al., 2011 – although the tip
415 might still be straight or concave under loading during flight — Fig. 5)
416 and therefore fits with the above suggestion of wingtips bending
417 under loading in flight.

418   The issues of wing shape and mechanical loading are more complex,
419 but also interesting in terms of examining potential ecological corre-
420 lates. More strongly curved phalanges (and those with grooves) will
421 have a greater tendency to twist under load (assuming all else is equal
422 in terms of membrane material properties) because the curvature pro-
423 vides a more effective moment arm for twisting under aerodynamic
424 load from the wing. A high degree of twist in the wing will tend to pro-
425 mote washout along the wing, particularly at high lift coefficients.
426 Washout entails a twisting of the wing such that the distal portion of
427 the wing acts at a lower angle of attack than the proximal portion of
428 the wing (Thomas, 1996; Palmer and Dyke, 2011). This reduces induced
429 drag at the wing tip and helps to prevent stall of the distal wing. These
430 effects are particularly important for flapping flyers, since their distal
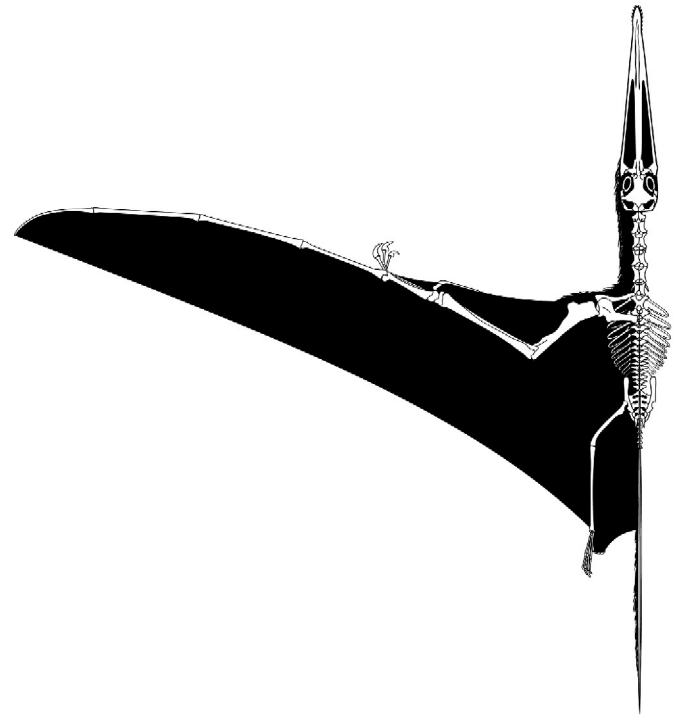

Fig. 5. Hypothetical alteration to the wingtip under loading in flight (cf Fig. 1).

wing moves faster than the proximal wing during propulsion, and 431
therefore acts at a higher total lift and drag per unit area for a given 432
angle of attack than the proximal wing. Spanwise twist is also critical 433
for generating high proportions of thrust to weight support in slow flap- 434
ping flight (Alexander, 2002; Vogel, 2003). 435

A strongly curved distal phalanx is also potentially more resistant to 436
impact and may more effectively offload sudden gusts, particularly if the 437
distal phalanx is comprised of relatively low modulus bone (some bats, 438
for example, can actually launch off of the distal phalanges, e.g. see fig- 439
ures in Adams et al., 2012). Wings with a deeper chord may also provide 440
greater total load to the distal phalanx since the force required to ten- 441
sion the larger area of membrane can be greater than for a small mem- 442
brane area, assuming a similar degree of active camber control. A 443
phalanx with greater capacity to flex under these loads (i.e. greater 444
compliance) could help to offset the high forces produced within 445
broader tensile membranes. These considerations all indicate that in- 446
land flying species should be expected, on average, to possess distal 447
phalanges with greater curvature (assuming that inland flying ptero- 448
saurs, as in modern thermal soaring birds, tended to possess compara- 449
tively broad wings and spend long periods of time in slow flight at 450
high lift coefficients). 451

Ecology 452

It is beyond the scope of this study to assess every specimen and 453
taxon here, not least given the limited data and the variation seen in 454
at least some, as well as the complicating factors of taphonomy. Howev- 455
er, some taxa show some interesting and relatively consistent patterns 456
and are worthy of comment. 457

As noted above, inland flying species should be expected, on aver- 458
age, to possess distal phalanges with greater curvature. Therefore it is 459
of interest that multiple specimens of scaphognathids and the tapejarid 460
Sinopterus have highly curved distal-most phalanges which matches 461
with their presence in fossiliferous beds from inland settings and that 462
may feature cluttered environments. 463

Anurognathids: Based on our assessments, maneuverable taxa at 464
risk for wing tip strikes are expected to have relatively short, curved 465

distal phalanges. This is seen in anurognathids that show values of around 160–170° (see Table 1). Anurognathids are known from terrestrial deposits (e.g. Bakhurina and Unwin, 1995; Bennett, 2007) including those that were likely cluttered based on the presence of gliding taxa (Sullivan et al., 2014) indicating large numbers of trees. Impact resistance would be conferred by short, low modulus wing tips for two reasons — short phalanges would be less prone to bending, and low modulus bone should improve impact resistance (greater toughness, increased low alleviation). Since a low elastic modulus in the distal phalanx would also increase its tendency to bend under wing tension, impact resistance is likely to be correlated with wing tip curvature. We confirm that this is the case in anurognathids, which matches the predictions. We therefore suggest that this apparent absence may be a preservation bias resulting from the distal phalanx being exceptionally low modulus bone, possibly to the point of being primarily cartilaginous or comprised of collagen (to an even more extreme extent than in living bats, which have low modulus bone in the distal phalanges but do preserve them regularly in fossils). This hypothesis would also explain the apparent reduction of the wingfinger in a specimen of *Anurognathus* that is both very young and lacks a fourth phalanx (Bennett, 2007). The high degree of wing tip curvature seen is expected to help prevent tip stall during slow speed, high maneuverability flight while simultaneously being related to wing tip fracture resistance in cluttered environments.

Azhdarchoids: We have a small sample of azhdarchoids that show high degrees of wingtip curvature. While a larger sample will be needed to confirm this tendency, strong curvature in the wing tip of azhdarchoids is consistent with their suspected terrestrial habits (e.g. Witton and Naish, 2008; Witton, 2013p 227, 242) and potential risk of wing tip strikes during low flight and launch (see section above on anurognathids). This is particularly true of tapejarids, which possess some of the most strongly curved wingtips in our dataset. Tapejarids, particularly *Sinopterus*, may also have frequented cluttered environments (or at least those with tall trees — Wu, 2003), which would increase the risk of wingtip strikes and increase the need for slow, maneuverable flight. Both factors would, we predict, increase the advantage of strong wingtip curvature.

We expected that azhdarchids would have somewhat straighter wing tips than tapejarids, working under the assumption that azhdarchids would prefer more open habitats. The single azhdarchid we recorded does not match this pattern, possessing a relatively strongly curved wingtip. However, it is likely that azhdarchids utilized thermal soaring and therefore would have benefited from adaptations to slow, maneuverable, flight. Since curved wingtips can reduce induced drag, curved wingtips might have been important for azhdarchids even if they lived in open habitats. The situation in the azhdarchids may also be complicated by the fact that the distal phalanx is proportionally very short (typically circa 10% of the length of the wing phalanges — based on data in Elgin, 2014). We originally suspected that this would make the wingtips relatively robust and might mediate the risk of damage through wingtip strikes. However, this might also simply reduce the importance of impact adaptations for the wingtips in azhdarchids, living the distal phalanx under selection primarily related to flight gait and speed. Additional data should resolve this issue; it is possible that curvature is generally reduced in the azhdarchids despite the curved condition in the only measured specimen.

Pteranodontids: Although a curved wingtip would be predicted for pterosaurs living primarily in terrestrial environments, there are some taxa interpreted primarily as pelagic animals that also show some strong curvature (e.g. *Pteranodon* — Bennett, 2001). We note that wingtip strikes might be a constraint when launching from water (Habib and Cunningham, 2010). *Nyctosaurus* was likely a pelagic animal that rarely came to shore given its limited terrestrial abilities (Witton, 2013), and it therefore may have water launched with more regularity than other taxa. Palmer and Dyke (2010) predicted that a lunate tip would be highly advantageous with forward swept wings in particular.

As a result, taxa with especially large heads or long necks which is true of pteranodontids (that would therefore have an anteriorly positioned center of mass), might have a tendency to possess curved wing tips, regardless of their habitat as the wings would be more forwards swept.

Bellubrunnus Q3

The holotype and only known specimen of *Bellubrunnus rothgaengeri* is that of a young juvenile rhamphorhynchine pterosaur with a wingspan of around 30 cm (Hone et al., 2012) Fig. 6. This individual displays a feature apparently unique among pterosaurs in having both wingtips strongly curved anteriorly along their length (Hone et al., 2012). As with other examples detailed above, we consider these features genuine and not pathological given how similar each is to the other. Although both young and small, and despite having a unique wingtip shape, *Bellubrunnus* was volant. As with many other young pterosaurs (Bennett, 1995; Unwin, 2003), and unlike many other young amniotes, the bones of the holotype are well ossified and thus presumably both capable of taking locomotory loads, but also having evolved to do so at a young age (though see Prondvai et al., 2012 for an alternative view on flight in very young pterosaurs). Moreover, *Bellubrunnus* was recovered from a sedimentary layer considered not part of the direct paleocoastline (Hone et al., 2012). Although carcasses may float and travel some distance after death, the minimal degree of damage and disarticulation to the holotype suggests that it was buried soon after death and as such was unlikely to have drifted from a terrestrial or fluvial environment. This inference also implies that the anteriorly directed wingtips of *Bellubrunnus* were functional and were, at the very least, not a major impediment to powered flight.

If the wingtip of *Bellubrunnus* was deflected anteriorly in flight, the wing membrane would be forced to take on a convex shape at the trailing edge (Fig. 7). As demonstrated by Palmer and Dyke (2010),

Fig. 6. Holotype of *Bellubrunnus* under U.V. light seen in ventral view. Scale bar is 10 mm.

such a shape would not tension effectively and can be therefore rejected as a functional wing shape for pterosaurs. As a result, the wing tips must either have preserved in an extremely unusual manner (which we consider unlikely — see above), or else they must have taken on a straight to recurved shape in flight under wing tension.

This has notable implications for our understanding of material properties in the distal wing of pterosaurs (or at least for *Bellubrunnus*). For a given strain, deflection angle is a simple function of slenderness (length divided by element diameter: L/y). Specifically, the angle of deflection is related to the elastic modulus and slenderness of the beam as:

$$\theta = 2E(L/y)$$

(Currey, 2004; Palmer and Dyke, 2010).

The curvature of the distal phalanx in *Bellubrunnus* is approximately 25°. Straightening the bone would require 3750 microstrain, which
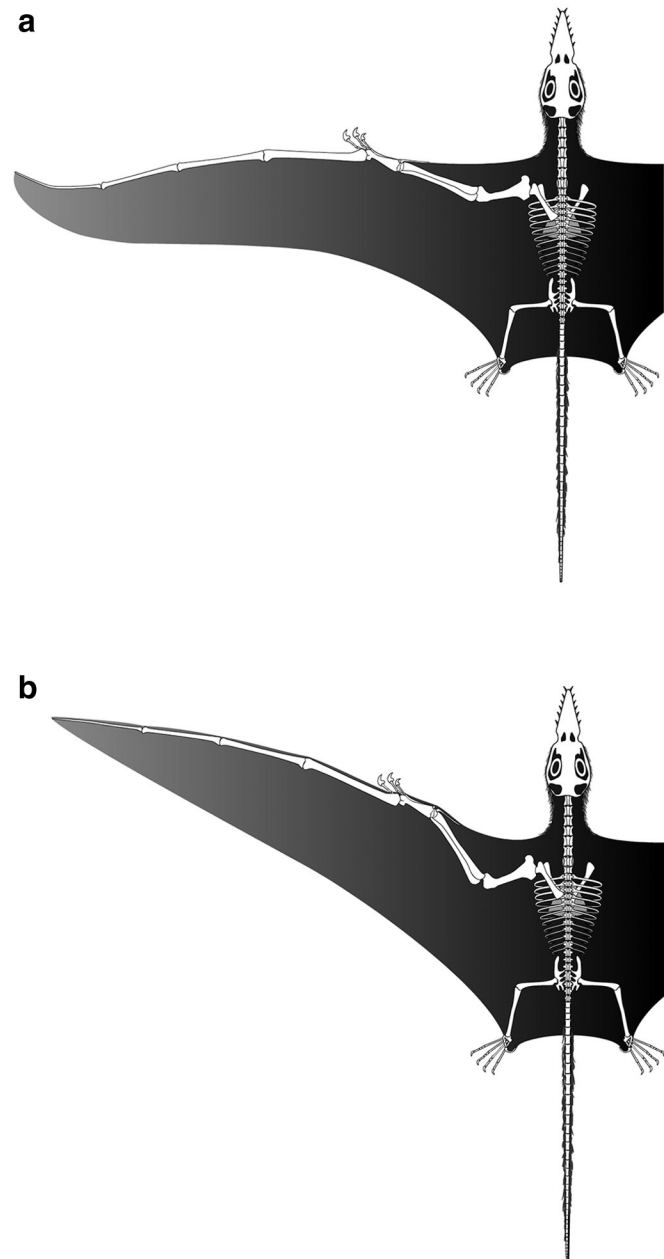
provides an exceptionally low safety factor (less than 2.0) if the phalanx was composed of high modulus bone. This would fit the idea of a low modulus distal phalanx as suggested above and is exactly what is seen in bats — which have stiff inboard wing elements but extremely compliant wing phalanges (Swartz and Middleton, 2008). Fossil bats preserve the distal phalanx readily, even some of the oldest specimens (e.g. *Icaronycteris index*, and numerous specimens from the Messel deposits), and so there is no indication that low modulus bone in the distal wing of a vertebrate flyer must necessarily preserve with any qualitative indication of its original material properties.

This raises the possibility that the wing phalanges of other pterosaurs were also comprised of lower modulus bone than the rest of the wing, which could be an adaptive response to improving gust response and/or tensioning of the distal membrane (Palmer, pers com.). Compliant distal phalanges would also provide a mechanism for generating a lunate wing tip, which has advantages for drag and stall reduction at the distal wing (Palmer and Dyke, 2010) — Fig. 7. If low modulus bone was typical of pterosaur terminal wing phalanges, then the distal wing of most species would have presumably taken on a lunate shape in flight (since the "resting state" of their phalanges is straight to recurved). The wing phalanges of *Bellubrunnus*, owing to their tendency to curve anteriorly when not tensioned by the wing, may have produced a straighter leading edge along the distal wing.

A straighter, less lunate shape to the wing tip could have been related to a difference in the overall wing shape (perhaps a broader chord on the approach to the hind limb), or perhaps a difference in average wing position in *Bellubrunnus* compared to other pterosaur taxa. It is interesting to note that the tail in *Bellubrunnus* possesses morphology indicative of greater flexibility than in close relatives such as *Rhamphorhynchus* (Hone et al., 2012) as it lacks the long zygapophyses and chevrons seen in the latter. A change in the sweep of the wing relative to related taxa, along with a more flexible tail, could be indicators of a greater emphasis on pitch stability and a lower emphasis on yaw stability

5. Conclusions

Overall, both the general morphology, and especially the curvature of the distal wing phalanx of pterosaurs, has been little studied to date. However the data available, despite the possible issues of taphonomic distortion, suggests that there is likely to be a genuine phylogenetic and taxonomic signal present in the curvature of distal phalanges. We suggest that the cautious integration of this data into taxonomic definitions and phylogenetic studies is likely warranted and in worthy of further investigation.

From a functional perspective, the importance of the wingtip in an animal that flies with a single spar for the leading edge of the wing, may be greater than for other vertebrate fliers. There are also functional and ecological implications to wingtip curvature. In flight, it was likely loaded increasing curvature to a greater degree than seen in the fossil record, and curvature would affect wingtip shape and flight issues such as stall. The distribution of curved wingtips in the pterosaurs suggests that curvature may especially correlate with animals operating in terrestrial settings although a function in pelagic settings should not be overlooked.

6. Uncited reference

Habib and Witton, 2011

Acknowledgments

Fig. 7. Differing wing profiles for *Bellubrunnus* with A) laterally directed wings and B) anteriorly directed wings also showing straightening of the curved tip under stress in flight.

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