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Highlights

The wingtips of the pterosaurs: Anatomy, aeronautical function and ecological implications*Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2015) xxx–xxx*D.W.E. Hone^{a,*}, M.K. Van Rooijen^b, M.B. Habib^c^a School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK^b 210 Collins Street, Hobart, TAS, Australia.^c Cell and Neurobiology, Keck School of Medicine, University of Southern CA, Los Angeles, USA

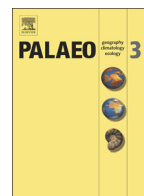
- Many pterosaurs possessed curved distal wing phalanges.
- Curvature will affect the flight performance of the wing.
- High curvature is linked to flight in cluttered environments or over open oceans.
- Potential taphonomic distortion limits interpretation.



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

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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. Pennycuik, 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; Pennycuik, 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 Staatssammlung für Paläontologie, 79 Munich, Germany; CM, Carnegie Museum, Pittsburgh, Pennsylvania, 80

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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.

94 Anatomy of the pterosaurian wingtip

95 Osteology

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

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

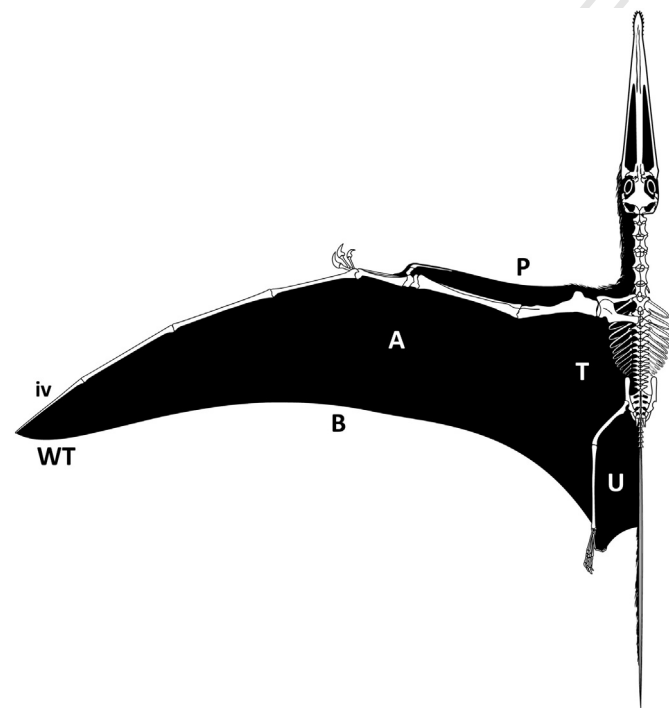


Fig. 1. Pterosaurian bauplan (*Darwinopterus*) showing key wing membranes and anatomical features in a flight posture but with the wings not loaded. Abbreviations as follows: A – actinopatagium, B – brachiopatagium, P – propatagium, T – tenopatagium, U – uropatagium, WT – wingtip, iv – fourth wing phalanx.

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

179 preserved *Anhanguera* specimen described by Kellner and Tomida
180 (2000) it is certainly plausible that this feature is much more wide-
181 spread in pterosaurs than noted here and is simply not apparent on
182 many two dimensionally flattened specimens.

183 There is no evidence for pneumaticity in the distal phalanx in basal
184 pterosaurs and the internal structure of the bone is uncertain. Various
185 pterodactyls however possess pneumatic distal wing phalanges,
186 though the number identified to date is limited. *Pteranodon* exhibits
187 this condition (Bennett, 2001), and a pneumatopore is also apparently
188 present in the ventral side of an unidentified azhdarchid (SMNK PAL
189 6409). The number of taxa showing this condition is perhaps limited
190 owing to a lack of specimens that preserve a pneumatopore and/or
191 show clear evidence of internal invasions of the bone, though
192 given the extensive pneumaticity of elements in clades such as the
193 ornithocheirids (Kellner and Tomida, 2000) and the pneumatisation of
194 even elements such as ribs, sterna and ilia in azhdarchoids (Elgin and
195 Hone, 2013), then this is likely more extensive and may be present in
196 a variety of pterodactylid pterosaurs.

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

204 Soft tissues

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

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

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

238 In life position

239 The life position and shape of the wingtip might not have been the
240 same as seen in fossil specimens. In particular, both theory and

241 anatomical observations predict that the wingtip would take on a no-
242 ticeably different shape during flight. To be functionally tensioned for
243 flight, the trailing edge of the wing membrane in pterosaurs must
244 have been either straight (if there was a trailing edge tendon), or at
245 least slightly concave (Palmer and Dyke, 2010). Because the distalmost
246 phalanx of the pterosaur wing was often quite gracile, it is probable that
247 it would flex when the wing was tensioned, adding to the concavity of
248 the trailing edge and producing a lunate wingtip.

249 The degree to which the wingtip would deform depends on the ma-
250 terial properties of the original bone, in addition to its shape. The degree
251 of mineralization in the original bone is not immediately apparent from
252 the fossil remains. Bennett (2001) referred to the distal wing in ptero-
253 saurs as a ‘flexible spar’, with Steel (2008) describing the histology as
254 “Longitudinal section (Section 3) through the proximal end of UP
255 2000.9 (wing phalanx 4), showing calcified cartilage supported by col-
256 umns of bone”. These observations, while inconclusive, support the pos-
257 sibility of the distal wing in pterosaurs having been composed, in part, of
258 bone with low mineral content (and therefore potentially a low elastic
259 modulus). Thus may have been curved in flight, but would appear
260 straight ‘at rest’ and thus as preserved.

261 2. Methods

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

272 Curvature was measured by marking a straight line between the tip
273 of the phalanx and posterior edge of the proximal face. This was then
274 bisected by a perpendicular line until it reached the phalanx. From
275 this point, lines were drawn out to the two original points and the
276 angle of the crux measured (see Fig. 3) to give a value. Note that this
277 value will likely never reach 180° because the proximal part of the pha-
278 lanx extends slightly posteriorly in its articulation with the preceding
279 element. Thus, even a totally straight phalanx will have a value of
280 a few degrees below 180°. While this method provides a highly simplified
281 measure of curvature, it is sufficient in this case since we are testing
282 against a null model of a straight phalanx. The simple curve measure
283 used here is sufficient, even for our sample sizes, to differentiate even
284 a relatively weakly curved phalanx from a straight one (see Fig. 2). It
285 is also sufficient to differentiate overall strength of curvature (i.e.
286 strongly curved vs weakly curved). More specific details of curvature
287 (such as those sometimes employed to look at claws – e.g. Feduccia,
288 1993; Birn-Jeffrey et al., 2012) are not elucidated by our simplified met-
289 ric, and we therefore do not make fine scale differentiations in phalanx
290 curvature or shape in this analysis. Because the primary interest is the
291 potential response of the phalanx to total-element bending under
292 wing tension loads, the more specific details of curvature would effec-
293 tively constitute noise in our analysis. Construction of the lines and
294 measurements of the angles were completed in Photoshop.

295 3. Results

296 Not all pterosaurs exhibit curved distal phalanges. Measurements of
297 *Pterodactylus* (BSPG 1937.1.18X) for example show minimal curvature
298 (i.e. almost 180°) with values of 177.0° and 170.6° recorded and a spec-
299 imen of *Darwinopterus* (YH 2000) was 170.4°. These are extremely
300 straight, although other pterosaurs do exhibit distal phalanges with
301 only very moderate curvature. Here we define a straight phalanx as
302 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	<i>Jeholopterus</i>	IVPP V 12705	161.7, 168.6
Anurognathidae	<i>Dendrorhynchoides</i>	GMV 2128	160.4
Dimorphodontidae	<i>Peteinosaurus</i>	Wellnhofer, 1991 p.66	165.2
Scaphognathinae	<i>Scaphognathus</i>	SMNS 59395	170.7, 169.7
Scaphognathinae	<i>Sordes</i>	PIN 2585/3	Moderate curvature to both phalanges.
Scaphognathinae	<i>Jianchangopterus</i>	Lü and Bo, 2011	161.5
?	<i>Austriadactylus</i>	SMNS 56342	168.3
Campylognathoidea	<i>Campylognathoides</i>	Padian, 2008b Plate 4	164.2, 163.8
Campylognathoidea	<i>Campylognathoides</i>	Padian, 2008b p90	Phalanx incomplete but curvature is visible.
?Rhamphorhynchinae	–	OXFUM 23047	170.7
Rhamphorhynchinae	<i>Dorygnathus</i>	SMNS 51827	170.2
Rhamphorhynchinae	<i>Dorygnathus</i>	SMNS 50164	168.2
Rhamphorhynchinae	<i>Dorygnathus</i>	SMNS 81205	168.3, 167.3
Rhamphorhynchinae	<i>Dorygnathus</i>	MBR 3665.1	171.7
Rhamphorhynchinae	<i>Dorygnathus</i>	BSPG 1938 I 49	170.7, 169.0
Rhamphorhynchinae	<i>Dorygnathus</i>	Padian, 2008a p15 MB. R 1920.16	163.8, 166.3
Rhamphorhynchinae	<i>Rhamphorhynchus</i>	Eichstätt collection. Figured in Wellnhofer, 1975 Plate 28.1	158.5, 168.3
Rhamphorhynchinae	<i>Rhamphorhynchus</i>	Wellnhofer, 1975 Plate 28.2	166.1
Rhamphorhynchinae	<i>Rhamphorhynchus</i>	TMP 2008.041.0001	165.7, 171.3
Rhamphorhynchinae	<i>Rhamphorhynchus</i>	RAM 14522	170.5
Rhamphorhynchinae	<i>Rhamphorhynchus</i>	SMNS 80429	155.9 (Near 90° turn in distal part of phalanx).
Rhamphorhynchinae	<i>Rhamphorhynchus</i>	BMMS 3	168.9, 172.5
Rhamphorhynchinae	<i>Rhamphorhynchus</i>	BMMS 6 AS 7	166.5, 170.7
Rhamphorhynchinae	<i>Bellubrunnus</i>	BSPG 1993 XVIII 2	198.2, 206.6
Wukongopteridae	<i>Kunpengopterus</i>	IVPP V 16047	168.7, 166.8 (second tip broken?)
Wukongopteridae	<i>Wukongopterus</i>	Wang et al., 2009	175., 163.9 *
Monofenestrata Indet.	Unnamed 'Pro-pterodactylid'	Tischlinger and Frey, 2014	169.3
Pterodactyloidea Indet.	–	MBR 5591.1	162.7
Ctenochasmatoidea	<i>Ctenochasma</i>	CM 11425	166.9 (Juvenile specimen).
Ctenochasmatoidea	<i>Pterodactylus</i>	BSPG AS V 29	165.6
Ctenochasmatoidea	<i>Elanodactylus</i>	Zhou, 2010a	156.4
Ornithocheiridae	<i>Anhanguera</i>	NSM-PV 19892	175.5
Boreopteridae	<i>Zhenyuanopterus</i>	Lü, 2010	170.9, 171.7
Pteranodontidae	<i>Nyctosaurus</i>	NHMUK R4810	151.1
Pteranodontidae	<i>Nyctosaurus</i>	Bennett, 2003 p.67	148.5
Pteranodontidae	<i>Pteranodon</i>	NHMUK 4538	163.0
Pteranodontidae	<i>Pteranodon</i>	LACM 50921	163.3
Pteranodontidae	<i>Pteranodon</i>	LACM 51132	159.4
Pteranodontidae	<i>Pteranodon</i>	Bennett, 2001 p.95	163.0
Pteranodontidae	<i>Pteranodon</i>	Bennett, 2001 p.95	140.4
Dsungaripteridae	<i>Germanodactylus</i>	BSPG 1892 IV 1	170, 167
Azhdarchoind Indet.	–	Unwin and Martill, 2007 Fig. 17.1e	Slight curvature on the one preserved phalanx.
Azhdarchoind Indet.	–	SMNK PAL 6409	156.0
Chaoyangopteridae	<i>Eoapteranodon</i>	Lü et al., 2006 p.74	159.9
Chaoyangopteridae	<i>Chaoyangopterus</i>	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	<i>Nemicopterus</i>	IVPP V 14371	165.6, 166.3
Tapejaridae	<i>Sinopterus</i>	IVPP V 13363	157.8, 162.4
Tapejaridae	<i>Sinopterus</i>	Lü et al., 2006 p.54	Strong curvature to the one preserved phalanx.
Tapejaridae	<i>Huaxiapterus</i>	Lü et al., 2006 p.60	Moderate curvature to both phalanges.
Tapejaridae	<i>Tapejara</i>	Eck et al., 2011 p.2	158.2
Azhdarchoidae	<i>Eoazhdarcho</i>	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).

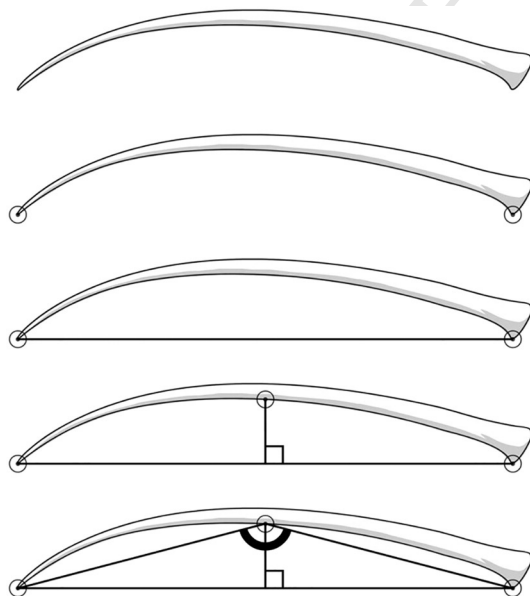


Fig. 3. Diagram to demonstrate measurement of the angles of the wingtips. Points are taken from the distal tip and the posterior most part of the proximal articulation, a line is drawn between them, this is then bisected by a perpendicular line until it contacts the ventral margin of the bone, from this 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° recorded 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.

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

It is worth noting that presumably these pathological features as seen in pterosaur phalanges took some time to develop into the shapes seen through healing, and thus although they may well have had a detrimental effect on the performance of the animals bearing them, nevertheless they presumably survived for some considerable time with these 'distorted' wingtips. Wingtip damage may have been common in pterosaurs through ground strike during take-offs, or as the most likely part of a wing to hit an object when flying in a cluttered environment or close to the ground.

On the other hand, at least some of the above described curved wingtips must be considered genuine anatomical features on the animals in question. When the curvature is uniform to both wingtips (especially when these lie in different orientations to one another and thus confounding crushing effects) and indeed across multiple specimens of a species, it would be more parsimonious to interpret these as being genuine. In at least some cases (e.g. *Sinopterus*, *Dorygnathus*) multiple specimens are seen with similar curvature both within and between specimens, further supporting the inference that these features are genuine and that in life these animals bore curved distal phalanges. This may still be a polymorphic characteristic with perhaps some individuals bearing curved tips and others not (or varying degrees of curvature), but the repeated presence suggests it was at least common.

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

Effect of wingtip shapes

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

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

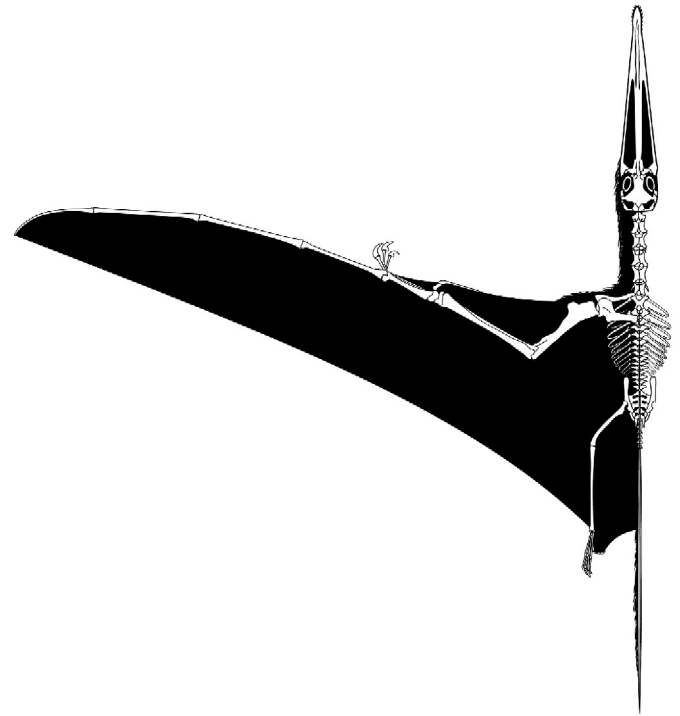


Fig. 5. Hypothetical alteration to the wingtip under loading in flight (cf Fig. 1).

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

A strongly curved distal phalanx is also potentially more resistant to impact and may more effectively offload sudden gusts, particularly if the distal phalanx is comprised of relatively low modulus bone (some bats, for example, can actually launch off of the distal phalanges, e.g. see figures in Adams et al., 2012). Wings with a deeper chord may also provide greater total load to the distal phalanx since the force required to tension the larger area of membrane can be greater than for a small membrane area, assuming a similar degree of active camber control. A phalanx with greater capacity to flex under these loads (i.e. greater compliance) could help to offset the high forces produced within broader tensile membranes. These considerations all indicate that inland flying species should be expected, on average, to possess distal phalanges with greater curvature (assuming that inland flying pterosaurs, as in modern thermal soaring birds, tended to possess comparatively broad wings and spend long periods of time in slow flight at high lift coefficients).

Ecology

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

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

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

466 distal phalanges. This is seen in anurognathids that show values of
 467 around 160–170° (see Table 1). Anurognathids are known from terres-
 468 trial deposits (e.g. Bakhurina and Unwin, 1995; Bennett, 2007) includ-
 469 ing those that were likely cluttered based on the presence of gliding
 470 taxa (Sullivan et al., 2014) indicating large numbers of trees. Impact re-
 471 sistance would be conferred by short, low modulus wing tips for two
 472 reasons — short phalanges would be less prone to bending, and low
 473 modulus bone should improve impact resistance (greater toughness, in-
 474 creased low alleviation). Since a low elastic modulus in the distal phal-
 475 anx would also increase its tendency to bend under wing tension,
 476 impact resistance is likely to be correlated with wing tip curvature.
 477 We confirm that this is the case in anurognathids, which matches the
 478 predictions. We therefore suggest that this apparent absence may be a
 479 preservation bias resulting from the distal phalanx being exceptionally
 480 low modulus bone, possibly to the point of being primarily cartilaginous
 481 or comprised of collagen (to an even more extreme extent than in living
 482 bats, which have low modulus bone in the distal phalanges but do pre-
 483 serve them regularly in fossils). This hypothesis would also explain the
 484 apparent reduction of the wingfinger in a specimen of *Anurognathus*
 485 that is both very young and lacks a fourth phalanx (Bennett, 2007).
 486 The high degree of wing tip curvature seen is expected to help prevent
 487 tip stall during slow speed, high maneuverability flight while simulta-
 488 neously being related to wing tip fracture resistance in cluttered
 489 environments.

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

503 We expected that azhdarchids would have somewhat straighter
 504 wing tips than tapejarids, working under the assumption that
 505 azhdarchids would prefer more open habitats. The single azhdarchid
 506 we recorded does not match this pattern, possessing a relatively strong-
 507 ly curved wingtip. However, it is likely that azhdarchids utilized thermal
 508 soaring and therefore would have benefited from adaptations to slow,
 509 maneuverable, flight. Since curved wingtips can reduce induced drag,
 510 curved wingtips might have been important for azhdarchids even if
 511 they lived in open habitats. The situation in the azhdarchids may also
 512 be complicated by the fact that the distal phalanx is proportionally
 513 very short (typically circa 10% of the length of the wing phalanges —
 514 based on data in Elgin, 2014). We originally suspected that this would
 515 make the wingtips relatively robust and might mediate the risk of dam-
 516 age through wingtip strikes. However, this might also simply reduce the
 517 importance of impact adaptations for the wingtips in azhdarchids, living
 518 the distal phalanx under selection primarily related to flight gait and
 519 speed. Additional data should resolve this issue; it is possible that curva-
 520 ture is generally reduced in the azhdarchids despite the curved condi-
 521 tion in the only measured specimen.

522 Pteranodontids: Although a curved wingtip would be predicted for
 523 pterosaurs living primarily in terrestrial environments, there are some
 524 taxa interpreted primarily as pelagic animals that also show some
 525 strong curvature (e.g. *Pteranodon* — Bennett, 2001). We note that
 526 wingtip strikes might be a constraint when launching from water
 527 (Habib and Cunningham, 2010). *Nyctosaurus* was likely a pelagic animal
 528 that rarely came to shore given its limited terrestrial abilities (Witton,
 529 2013), and it therefore may have water launched with more regularity
 530 than other taxa. Palmer and Dyke (2010) predicted that a lunate tip
 531 would be highly advantageous with forward swept wings in particular.

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

Bellubrunnus

Q3

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

559 If the wingtip of *Bellubrunnus* was deflected anteriorly in flight, the
 560 wing membrane would be forced to take on a convex shape at the
 561 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

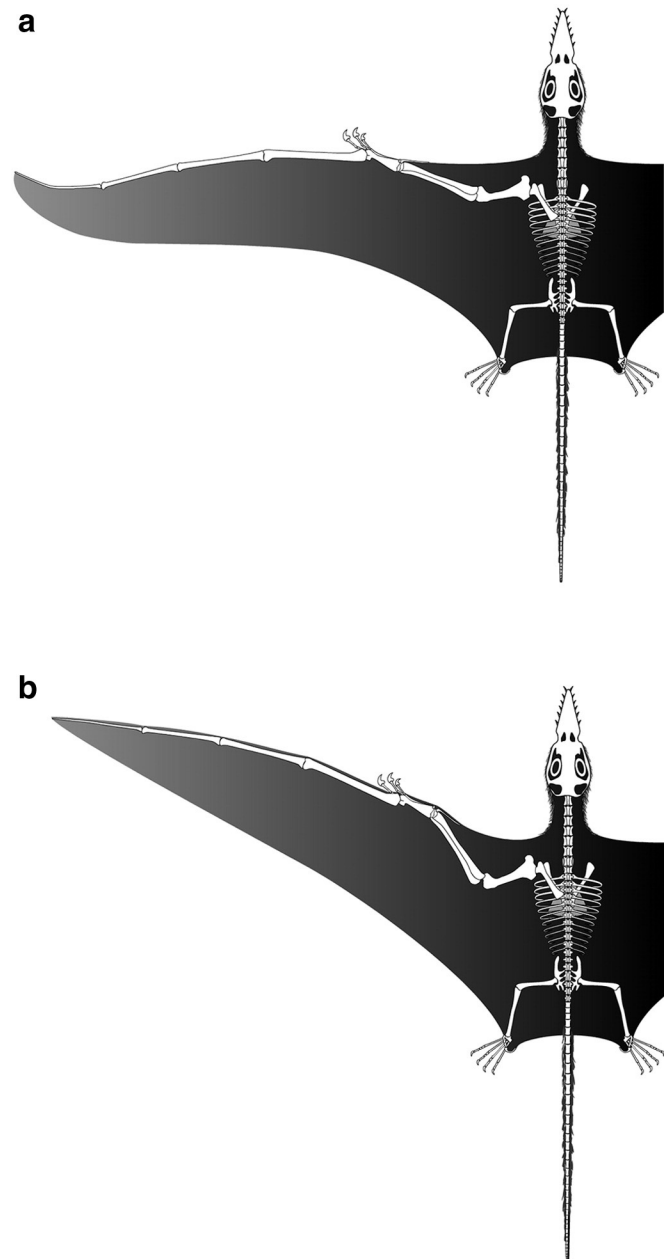


Fig. 7. Differing wing profiles for *Bellubrunnus* with A) laterally directed wings and B) anteriorly directed wings also showing straightening of the curved tip under stress in flight.

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 is 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

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