A large pterosaur limb bone from the Kaiparowits Formation (late Campanian) of Grand Staircase-Escalante National Monument, Utah, USA (#54186)

First submission

Guidance from your Editor

Please submit by **18 Nov 2020** for the benefit of the authors (and your $200 publishing discount) .

Structure and Criteria
Please read the 'Structure and Criteria' page for general guidance.

Custom checks
Make sure you include the custom checks shown below, in your review.

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files

Download and review all files from the materials page.

2 Figure file(s)
2 Table file(s)

Custom checks

Field study

Have you checked the authors field study permits?

Are the field study permits appropriate?

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

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

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

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

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

EXPERIMENTAL DESIGN

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

VALIDITY OF THE FINDINGS

- Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- All underlying data have been provided; they are robust, statistically sound, & controlled.
- Speculation is welcome, but should be identified as such.
- Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

A large pterosaur limb bone from the Kaiparowits Formation (late Campanian) of Grand Staircase-Escalante National Monument, Utah, USA

Andrew A. Farke Corresp. 1

1 Raymond M. Alf Museum of Paleontology at The Webb Schools, Claremont, CA, United States

Corresponding Author: Andrew A. Farke
Email address: afarke@webb.org

Pterosaurs were widespread globally during the Late Cretaceous, but their fossils are comparatively rare in terrestrial depositional environments. A large pterosaur bone from the Kaiparowits Formation (late Campanian, ~76–74 Ma) of southern Utah, USA, is tentatively identified as an ulna, although its phylogenetic placement cannot be precisely constrained beyond Pterosauria. The element measures over 36 cm in preserved maximum length, indicating a comparatively large individual with an estimated wingspan between 4.3–5.9 m, the largest pterosaur yet reported from the Kaiparowits Formation. The size estimate places the individual at approximately the same wingspan as the holotype for *Cryodrakon boreas* from the penecontemporaneous Dinosaur Park Formation of Alberta. Thus, relatively large pterosaurs occurred in terrestrial ecosystems in both the northern and southern parts of Laramidia (western North America) during the late Campanian.

A large pterosaur limb bone from the Kaiparowits Formation (late Campanian) of Grand Staircase-Escalante National Monument, Utah, USA

Andrew A. Farke[1]

Raymond M. Alf Museum of Paleontology at The Webb Schools, Claremont, California, USA

Corresponding Author:

Andrew A. Farke

Raymond M. Alf Museum of Paleontology at The Webb Schools, 1175 West Baseline Road, Claremont, California, 91711, USA

Email address: afarke@webb.org

Abstract

Pterosaurs were widespread globally during the Late Cretaceous, but their fossils are comparatively rare in terrestrial depositional environments. A large pterosaur bone from the Kaiparowits Formation (late Campanian, ~76–74 Ma) of southern Utah, USA, is tentatively identified as an ulna, although its phylogenetic placement cannot be precisely constrained beyond Pterosauria. The element measures over 36 cm in preserved maximum length, indicating a comparatively large individual with an estimated wingspan between 4.3–5.9 m, the largest pterosaur yet reported from the Kaiparowits Formation. The size estimate places the individual at approximately the same wingspan as the holotype for *Cryodrakon boreas* from the penecontemporaneous Dinosaur Park Formation of Alberta. Thus, relatively large pterosaurs occurred in terrestrial ecosystems in both the northern and southern parts of Laramidia (western North America) during the late Campanian.

Introduction

Pterosaurs were a widespread component of terrestrial ecosystems during the Late Cretaceous, reconstructed as filling a variety of ecological niches (Barrett et al., 2008; Witton & Naish, 2008). However, the comparative rarity of skeletal material in most formations, due in part to strong taphonomic influences and other geological biases, have limited studies of this clade and clouded interpretations of pterosaur paleobiology and paleoecology (Butler et al., 2012; Butler, Benson & Barrett, 2013; Dean, Mannion & Butler, 2016). Thus, even isolated and incomplete bones can provide important information for establishing the distribution and general morphological attributes of pterosaurs (e.g., Kellner et al., 2019).

The Kaiparowits Formation preserves rocks deposited along the eastern margin of Laramidia during the late Campanian (~76–74 Ma; Roberts, Deino & Chan, 2005; Roberts et al., 2013), with significant exposures within Grand Staircase-Escalante National Monument (GSENM) in southern Utah. A rich fossil record includes exquisitely preserved specimens for numerous tetrapods, including birds, non-avian dinosaurs, crocodylomorphs, turtles, mammals, amphibians, and lepidosaurs (see Titus & Loewen, 2013, and references therein). Pterosaurs are known from only a handful of specimens. An isolated manual phalanx was the first published record of a pterosaur from the Kaiparowits Formation (Farke & Wilridge, 2013), suggesting a fairly small (<3 m wingspan) individual. A potential pteranodontoid metacarpal was later reported (McCormack & Sertich, 2016), as well as the incomplete but associated skeleton of an azhdarchid (Carroll, Farke, Chai, et al., 2017), both of which await formal description.

Here I report on RAM 22574 (Figure 1), an isolated ?ulna from the largest pterosaur (4.3–5.9 m estimated wingspan) yet known from the Kaiparowits Formation. Although it is only a single bone, this element demonstrates the ecological and morphological breadth occupied by

this clade in southern Utah during the Late Cretaceous, and the general distribution of large pterosaurs across terrestrial environments during the late Campanian of western North America.

Abbreviations. FHSM, Sternberg Museum of Natural History, Hays, Kansas, USA; NSM, National Science Museum, Tokya, Japan; RAM, Raymond M. Alf Museum of Paleontology at The Webb Schools, Claremont, California, USA; SMK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; TMM, Texas Memorial Museum, Austin, Texas, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

Geological Setting

RAM 22574 was collected at locality RAM V2005022 (colloquially known as the "Cripe Site"), within the middle unit of the Kaiparowits Formation. This site is a multi-taxon bonebed including multiple associated elements from a tyrannosaurid, at least two hadrosaurids, testudines, and a small (~3 m wingspan) azhdarchid pterosaur (Farke et al., 2016; Carroll, Farke, Chai, et al., 2017).

The bonebed at RAM V2000522 measures over 1 meter in thickness and is interpreted as including at least three main depositional events, with evidence of reworking and slight movement of bones towards the top of the sequence. RAM 22574 was collected at the stratigraphic top of the quarry, ~1.2 meters above the lowest fossil, in a sandy mudstone with extensive clay rip-up clasts and plant debris. The articular surfaces of the bone show some pre-depositional damage, potentially due to fluvial abrasion or decomposition. The fossil was found within 1 m of an azhdarchid associated skeleton (RAM 15445), partially in the same bedding plane. However, RAM 22574 is from a much larger individual, in that its ulna measures 36 cm

long, versus a radius length (which should be roughly equivalent to ulna length) of around 20 cm for RAM 15445.

Materials & Methods

Collection and preparation. RAM 22574 was collected during the summer of 2016, using standard paleontological excavation techniques. Observations in the field showed that it was damaged prior to burial (described in more detail below). Paraloid B-72 was used to stabilize the fossil in the field, and as a consolidant and glue in the preparation lab. The fossil was mechanically prepared using pneumatic hand tools of various sizes, with final preparation completed using dental picks. Fieldwork was completed under US Bureau of Land Management paleontology permits UT06-012E-GS and UT06-001S-GS, and the fossil is reposited at the Raymond M. Alf Museum of Paleontology, Claremont, California, USA.

Comparisons and measurements. Linear measurements of RAM 22574 were collected with a digital calipers, to the nearest millimeter or 0.1 mm (Figure 2; Table 1). Circumference was measured to the nearest millimeter with a cloth measuring tape. For anatomical comparisons, casts of *Montanazhdarcho minor* (MOR 691) and *Quetzalcoatlus northropi* (TMM 41450) were compared directly with RAM 22574.

Wingspan estimation. The wingspan of RAM 22574 was approximated by scaling from relatively complete wings of pterodactyloid pterosaurs. Here, wing length is calculated as the sum of all sequential forelimb bone lengths (humerus, ulna, metacarpal IV, phalanges in digit IV). Wingspan is approximated by doubling wing length. As noted by Hone and Benton (2007), this neglects the width of the torso, but that is offset in part by the flexion of the wings in life. Data (Table 1) were taken from measurements published by Unwin et al. (2000) and Bennett

(2001a). Assuming that RAM 22574 was an ulna, each wing was scaled by ulna size for that specimen. To reduce concerns about allometry, only specimens in the approximate size range of RAM 22574 were used (<25% difference in ulnar length). Because RAM 22574 was slightly "telescoped", two calculations were ~~run~~—one with the bone length as preserved, and another adding an additional 15 mm to the bone length to accommodate the effects of the crushing. Finally, the wingspan of *Cryodrakon boreas* (TMP 1992.83.4) was estimated by scaling the holotype humerus (measurements from Godfrey & Currie, 2005) relative to the humerus for *Quetzalcoatlus* sp. (TMM 42422).

Results

Systematic Paleontology

Archosauria (Cope, 1869)

Pterosauria (Kaup, 1834)

Pterosauria indet.

Referred material. RAM 22574, a nearly complete ?ulna (Figure 1).

Locality and horizon. Locality RAM V2005022, the "Cripe Site," located within Grand Staircase-Escalante National Monument, Garfield County, Utah. The site is situated in the middle unit of the Kaiparowits Formation, which is late Campanian in age (Roberts, Deino & Chan, 2005; Roberts et al., 2013).

Identification. This fossil is identified confidently as a pterosaur limb bone, and tentatively as an ulna. Because the descriptive terminology hinges upon these assumptions, I first address the underlying logic.

RAM 22574 is clearly hollow, which for the Late Cretaceous restricts possible identifications to either Theropoda or Pterosauria. The extremely thin cortical bone (between 0.7 and 1.7 mm) is distinct to pterosaurs (with the exception of dsungaripterids; Unwin, 2003), particularly for elements of this size. Thus, the identification to Pterosauria is quite confident.

Because key parts of RAM 22574 were damaged prior to fossilization (see below), identification of this bone within the skeleton is less certain. It is clearly a limb bone (rather than vertebra, ribs, or cranial material), but does not match well with morphology expected for any of the hind limb elements. There is nothing that resembles either the head or distal end of the femur, and the overall robustness of the bone (proportions of length vs. width) differs sharply from that seen in the tibia and fibula for typical Late Cretaceous pterosaurs of this size range (e.g., Bennett, 2001b; Averianov, 2010). A humerus can be excluded on the basis of a lack of a deltopectoral crest or the bulbous distal articular surface processes. Neither articular end shapes or element proportions fall within what would be expected for metacarpals or phalanges, regardless of clade. Thus, a radius or ulna seems to be the most likely identification.

The more heavily pre-depositionally damaged end of RAM 22574 shows topographic complexity that differs from what is seen in typical pterosaur radii (Wellnhofer, 1991; Bennett, 2001b; Veldmeijer, 2003). A prominent protrusion matches with a similar feature seen on *Montanazhdarcho minor* (MOR 691, personal observation on cast) and also material referred to *Cryodrakon boreas (TMP 19[5]4.398; Godfrey & Currie, 2005; Hone, Habib & Therrien, 2019)*. The relatively restricted nature of this protrusion differs from the more elongate anterior tuberosity seen on a radius referred to *Azhdarcho lancicollis (Fig. 26 in Averianov, 2010)*. Finally, large pterosaur radii (especially in Late Cretaceous clades; e.g., *Quetzalcoatlus northropi*, TMM 41450) tend to show substantial tapering on the shaft relative to the proximal

and distal ends. RAM 22574, at least relative to the more complete end, does not show substantial tapering, which is more consistent with an ulna than a radius.

The overall proportions (length vs. width) of RAM 22574 also are more similar to that of an ulna than a radius. For instance, in *Quetzalcoatlus northropi* (TMM 41450) shows that radii tend to be far more slender (proportionately) than ulnae. Similar proportions are seen in *Montanazhdarcho minor*, *Azhdarcho lancicollis*, and also in *Pteranodon* spp. (Bennett, 2001b; McGowen et al., 2002; Averianov, 2010), as a few examples.

Assuming that RAM 22574 is an ulna, it can be further identified as a right element, based on the position of a roughened area on the ?proximal end that may represent the bicipital tuberosity (Figure 1B, C). This area should be on the ventral edge of the element's anterior surface.

Description. RAM 22574 measures 366 mm in maximum preserved length. As outlined above, this description assumes that RAM 22574 is a right ulna, so that directional and anatomical terminology follow accordingly. Both proximal and distal ends were slightly abraded prior to fossilization, with the proximal end most damaged. Part of this end was broken open prior to burial, as evidence by some rip-up clay clasts inside the bone as well as field observations of the incomplete element.

The proximal end of the element is mostly incomplete, preserving only a portion of what is interpreted as the ventral cotylus. The cotylus projects ventrally, with much of its surface abraded away. A roughened patch of bone around 20 mm distal to the peak of the cotylus may represent the bicipital tuberosity, for attachment of *m. biceps brachii* (Figure 1B, C). There is no evidence of pneumatic foramina on the proximal end of RAM 22574, but the area where such foramina would be expected is broken.

The shaft broadens gradually from the proximal to the distal end of the element (Figure 1C, F, G), although this appears accentuated in part by crushing. At mid-shaft, the cross-section is oval and elongated in the dorso-ventral direction (width/height ratio of 0.51; see Table 1). At the distal third of the bone, cortical thickness ranges from 1.0 to 1.6 mm; at the proximal third, it is 1.7 mm thick. At least part of the shaft is mildly telescoped through proximo-distal distortion, as shown by displacement around the shaft. This would add another 15 mm or so to the total length of the bone. The distal third of the shaft in RAM 22574 is flattened on its ventral surface. This is somewhat accentuated by crushing, but appears to be at least partly original morphology.

The distal end of RAM 22574 is slightly abraded, but overall more intact than the proximal end. Its distal margin in anterior view is relatively straight, probably accentuated by abrasion. When viewed end on, the ventral condyle region is more expanded than the dorsal condyle, although it appears that the dorsal condyle is abraded (Figure 1D). A broad depression separates the condyles on the posterior surface of the element, although the extent of this depression appears accentuated by crushing. After accounting for the space between the crushed bone pieces, the width of the distal end is exaggerated by around 10 percent.

Discussion

Unfortunately, the incomplete and crushed nature of RAM 22574 limits substantial interpretation of the element and the animal. In general, neither the radius nor ulna exhibit major diagnostic features in pterosaurs, so the element cannot currently be identified beyond Pterosauria. Nevertheless, RAM 22574 does represent the largest pterosaur bone yet known from the Kaiparowits Formation and only the second formally described element, and is thus useful for establishing the maximum size of pterosaurs in the Kaiparowits ecosystem.

The total wingspan for RAM 22574 is estimated at 4.3 to 5.9 m (Table 2). This places it within the same size range as *Quetzalcoatlus* sp. (TMM 42422; Maastrichtian, Javelina Formation, Texas) or *Cryodrakon boreas* (TMP 92.83.4; late Campanian, Dinosaur Park Formation, Alberta); the ulna of RAM 22574 is roughly the same length as that of TMM 42422. McGowen et al. (2002) estimated a 2.5 m wingspan for *Montanazhdarcho minor* (late Campanian, Two Medicine Formation, Montana), and Sullivan and Fowler (2011) estimated 3.5 m for *Navajodactylus* (late Campanian, Kirtland Formation, New Mexico). Thus, RAM 22574 stands alongside *C. boreas* as one of the largest pterosaurs known from late Campanian-aged terrestrial deposits of North America. Furthermore, it demonstrates that pterosaurs in this size range occurred in ecosystems both in the northern and southern parts of Laramidia (western North America) during the late Campanian. Future discoveries will undoubtedly help clarify phylogenetic relationships between pterosaurs living in terrestrial environments at this time, to see if they were relatively geographically restricted, or if individual species had continent-level ranges. Additionally, additional work is required to determine if large pterosaurs played similar ecological roles across their various environments.

Acknowledgments

This specimen would never have been revealed without the sharp eyes of Jeff Cripe, who discovered the locality where this bone was collected. The 2016 field crew of volunteers and museum staff from the Alf Museum assisted in collection of this fossil, and Jared Heuck skillfully completed preparation. Discussions with Dave Hone, Nate Carroll, and others were helpful in establishing and confirming the identity of this fossil. We thank Valeria Pellicer for her renderings of the bone. Fieldwork in GSENM was completed under US Bureau of Land

Management paleontology permits UT06-012E-GS and UT06-001S-GS, with facilitation by Alan Titus and Greg MacDonald.

References

Averianov AO. 2010. The osteology of *Azhdarcho lancicollis* Nessov, 1984 (Pterosauria, Azhdarchidae) from the late Cretaceous of Uzbekistan. *Proceedings of the Zoological Institute of the Russian Academy of Sciences* 314:264–317.

Barrett PM, Butler RJ, Edwards NP, Milner AR. 2008. Pterosaur distribution in time and space: an atlas. *Zitteliana* B28:61–107.

Bennett SC. 2001a. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon* Part II. Size and functional morphology. *Palaeontographica Abteilung A* 260:113–153.

Bennett SC. 2001b. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon* Part I. General description of osteology. *Palaeontographica Abteilung A* 260:1–112.

Butler RJ, Benson RBJ, Barrett PM. 2013. Pterosaur diversity: Untangling the influence of sampling biases, Lagerstätten, and genuine biodiversity signals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 372:78–87. DOI: 10.1016/j.palaeo.2012.08.012.

Butler RJ, Brusatte SL, Andres B, Benson RBJ. 2012. How do geological sampling biases affect studies of morphological evolution in deep time? A case study of pterosaur (Reptilia: Archosauria) disparity. *Evolution* 66:147–162. DOI: 10.1111/j.1558-5646.2011.01415.x.

231 Carroll N, Farke AA, Chai S, Oei A. 2017. A new azhdarchid pterosaur from the Kaiparowits
232 Formation (late Campanian) of southern Utah, USA. *Journal of Vertebrate Paleontology,*
233 *Program and Abstracts* 2017:94.
234 Cope ED. 1869. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America.
235 *Transactions of the American Philosophical Society* 14:1–252.
236 Dean CD, Mannion PD, Butler RJ. 2016. Preservational bias controls the fossil record of
237 pterosaurs. *Palaeontology* 59:225–247. DOI: 10.1111/pala.12225.
238 Farke AA, Chai S, Diepenbrock J, Gonzalez D. 2016. From the quarry to the classroom: a case
239 study in field- and museum-centered research for high school students. *Journal of*
240 *Vertebrate Paleontology, Program and Abstracts* 2016:191.
241 Farke AA, Wilridge CA. 2013. A possible pterosaur wing phalanx from the Kaiparowits
242 Formation (late Campanian) of southern Utah, USA. *PalArch's Journal of Vertebrate*
243 *Palaeontology* 10:1–6.
244 Godfrey SJ, Currie PJ. 2005. Pterosaurs. In: Currie PJ, Koppelhus EB eds. *Dinosaur Provincial*
245 *Park: A Spectacular Ancient Ecosystem Revealed*. Bloomington, Indiana: Indiana
246 University Press, 292–311.
247 Hone DWE, Benton MJ. 2007. Cope's Rule in the Pterosauria, and differing perceptions of
248 Cope's Rule at different taxonomic levels. *Journal of Evolutionary Biology* 20:1164–
249 1170. DOI: 10.1111/j.1420-9101.2006.01284.x.
250 Hone DWE, Habib MB, Therrien F. 2019. *Cryodrakon boreas*, gen. et sp. nov., a Late
251 Cretaceous Canadian azhdarchid pterosaur. *Journal of Vertebrate Paleontology*
252 39:e1649681. DOI: 10.1080/02724634.2019.1649681.

253 Kaup JJ. 1834. Versuch einer Eintheilung der Saugethiere in 6 Stämme und der Amphibien in 6
254 Ordnungen. *Isis* 3:311–315.
255 Kellner AWA, Rodrigues T, Costa FR, Weinschütz LC, Figueiredo RG, Souza G a. D, Brum AS,
256 Eleutério LHS, Mueller CW, Sayão JM, Kellner AWA, Rodrigues T, Costa FR,
257 Weinschütz LC, Figueiredo RG, Souza G a. D, Brum AS, Eleutério LHS, Mueller CW,
258 Sayão JM. 2019. Pterodactyloid pterosaur bones from Cretaceous deposits of the
259 Antarctic Peninsula. *Anais da Academia Brasileira de Ciências* 91:e20191300. DOI:
260 10.1590/0001-3765201920191300.
261 McCormack L, Sertich JJW. 2016. A possible late Campanian record of Pteranodontia from the
262 Kaiparowits Formation of Grand Staircase-Escalante National Monument, southern Utah.
263 *Journal of Vertebrate Paleontology, Program and Abstracts* 2016:186.
264 McGowen MR, Padian K, Sosa MAD, Harmon RJ. 2002. Description of *Montanazhdarcho*
265 *minor*, an azhdarchid pterosaur from the Two Medicine Formation (Campanian) of
266 Montana. *PaleoBios* 22:1–9.
267 Roberts EM, Deino AL, Chan MA. 2005. 40Ar/39Ar age of the Kaiparowits Formation, southern
268 Utah, and correlation of contemporaneous Campanian strata and vertebrate faunas along
269 the margin of the Western Interior Basin. *Cretaceous Research* 26:307–318.
270 Roberts EM, Sampson SD, Deino A, Bowring S, Buchwaldt R. 2013. The Kaiparowits
271 Formation: a remarkable record of Late Cretaceous terrestrial environments, ecosystems
272 and evolution in Western North America. In: Titus AL, Loewen MA eds. *At the Top of*
273 *the Grand Staircase: The Late Cretaceous of Southern Utah*. Bloomington, Indiana:
274 Indiana University Press, 85–106.

275 Sullivan RM, Fowler DW. 2011. *Navajodactylus boerei*, n. gen., n. sp.,
276 (Pterosauria, ?Azhdarchidae) from the Upper Cretaceous Kirtland Formation (Upper
277 Campanian) of New Mexico. *New Mexico Museum of Nature and Science Bulletin*
278 53:393–404.
279 Titus AL, Loewen MA. 2013. *At the Top of the Grand Staircase: The Late Cretaceous of*
280 *Southern Utah*. Bloomington, Indiana: Indiana University Press.
281 Unwin DM. 2003. On the phylogeny and evolutionary history of pterosaurs. *Geological Society,*
282 *London, Special Publications* 217:139–190. DOI: 10.1144/GSL.SP.2003.217.01.11.
283 Unwin DM, Lü J, Bakhurina NN. 2000. On the systematic and stratigraphic significance of
284 pterosaurs from the Lower Cretaceous Yixian Formation (Jehol Group) of Liaoning,
285 China. *Mitteilungen aus dem Museum für Naturkunde, Berlin, Geowissenschafilichen*
286 *Reihe* 3:181–206. DOI: 10.1002/mmng.20000030109.
287 Veldmeijer AJ. 2003. *Coloborhynchus spielbergi* sp. nov. (Pterodactyloidea) from the Albian
288 (Lower Cretaceous) of Brazil. *Scripta Geologica* 125:35–139.
289 Wellnhofer P. 1991. Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do
290 Araripe, Brasilien. *Palaeontographica Abteilung A* 215:43–101.
291 Witton MP, Naish D. 2008. A reappraisal of azhdarchid pterosaur functional morphology and
292 paleoecology. *PLOS ONE* 3:e2271. DOI: 10.1371/journal.pone.0002271.

Figure 1

RAM 22574, ulna of Pterosauria ~~indet.~~

A) ?dorsal; B) ?proximal; C) ?anterior; D) ?distal; E) ?ventral; and F) ?posterior views; with G) showing interpretive drawing of ?posterior view, including missing parts; and H) showing restored view of bone in ?posterior view. Scale bars equal 10 cm. Abbreviations: ?bt, ?bicipital tuberosity; ?dist, ?distal end; ?prox, ?proximal end.

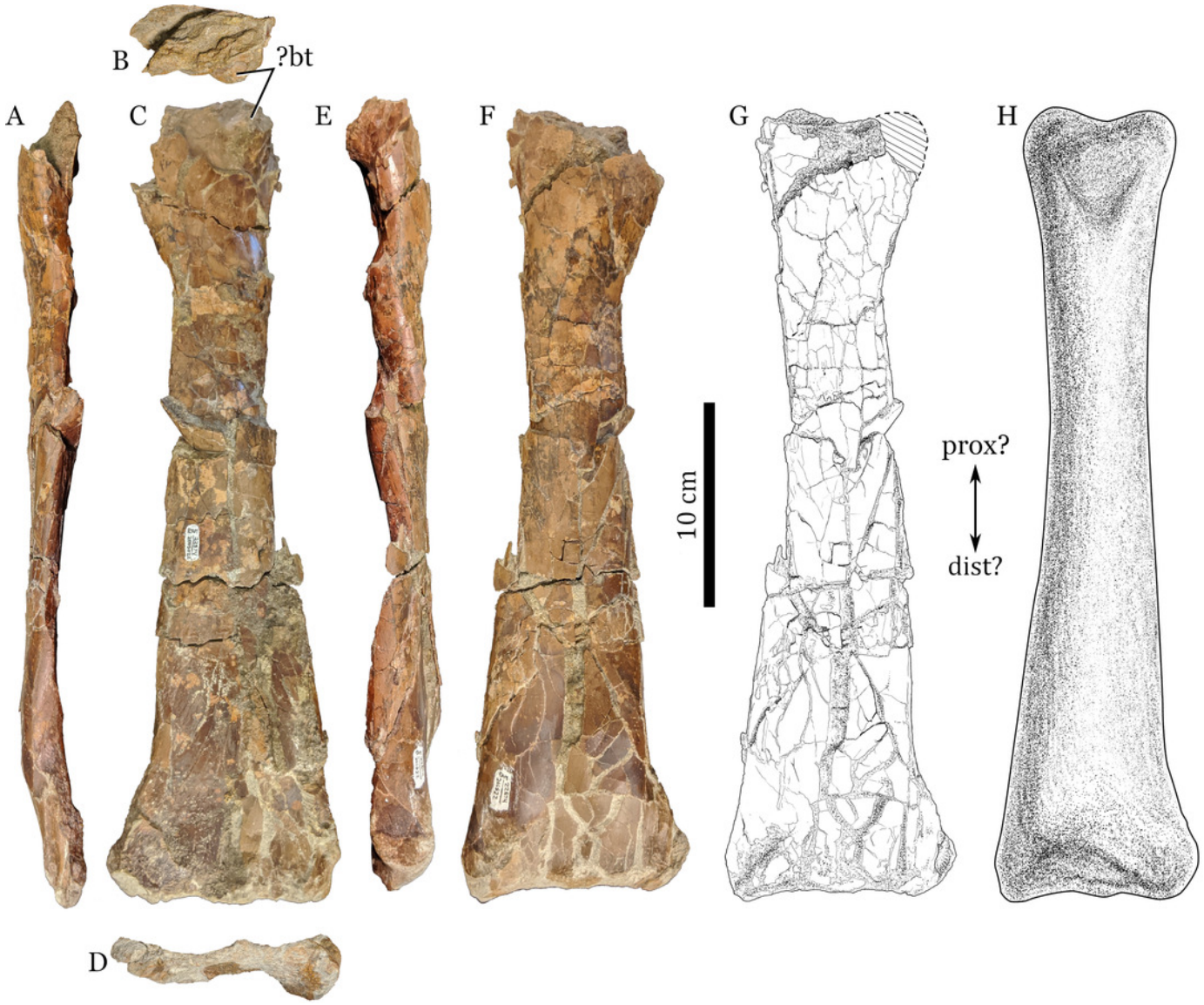

Figure 2

Interpretive drawing of RAM 22574, showing measurements taken here.

Measurements include: 1a, maximum proximo-distal length; 1b, maximum proximo-distal length (adjusting for telescoping); 2, maximum dorso-ventral width of proximal end; 3, minimum antero-posterior width of proximal end; 4, antero-posterior width of proximal end at ventral cotyle; 5, dorso-ventral width at narrowest point of shaft; 6, dorso-ventral width at mid-shaft; 7, antero-posterior width at mid-shaft; 8, circumference at mid-shaft; 9, maximum dorso-ventral width of distal end; 10, maximum antero-posterior width of distal end; 11, minimum antero-posterior width of distal end. Data are provided in Table 1.

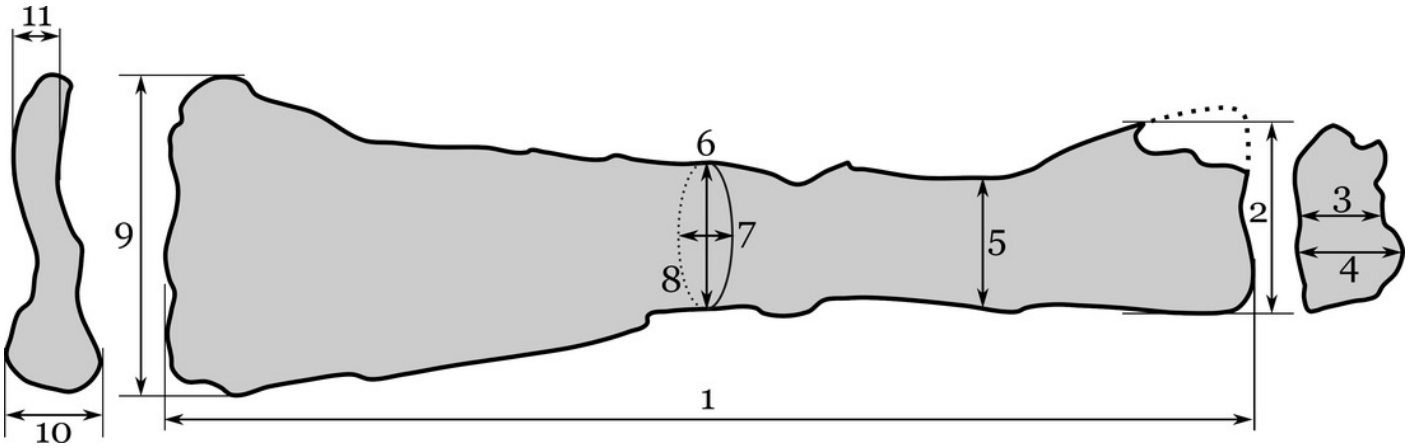

Table 1(on next page)

Measurements of pterosaur ?ulna, RAM 22574, in millimeters.

All measurements were taken with sliding digital calipers, except for 6, which was measured with a cloth measuring tape. See Figure 2 for explanation of measurements.

	Standard	Measurement
1a	Maximum proximo-distal length (as preserved)	366
1b	Maximum proximo-distal length (adjusting for telescoping)	381
2	Maximum dorso-ventral width of proximal end (as preserved)	71
3	Minimum antero-posterior width of proximal end (as preserved)	32
4	Antero-posterior width of proximal end at ventral cotyle	48
5	Dorso-ventral width at narrowest point of shaft	49
6	Dorso-ventral width at mid-shaft (as preserved)	52
7	Antero-posterior width at mid-shaft (as preserved)	27
8	Circumference at mid-shaft (as preserved)	133
9	Maximum dorso-ventral width of distal end (as preserved)	106
10	Maximum antero-posterior width of distal end (as preserved)	31
11	Minimum antero-posterior width of distal end (as preserved)	17

Table 2 (on next page)

Comparative measurements of selected pterodactyloid pterosaurs, with wingspan for RAM 22574 scaled from those measurements.

Two ulna lengths are provided for RAM 22574, representing the element as preserved (the smaller number) and a second estimate accounting for mild telescoping that reduced the preserved length of the element. Measurements for *Pteranodon* are taken from Bennett (2001a), and those for *Cryodrakon* are from Godfrey and Currie (2005); all others are from Unwin et al. (2000). Measurements are in millimeters, except for wingspan estimates, which are in meters. Abbreviations: H, humerus length; MC-IV, metacarpal IV; IV-1,-2,-3,-4, fourth digit manual phalanges 1 through 4; RAM WS, range of wingspans estimated for RAM 22574 based on direct scaling from each specimen; WS, wingspan (calculated by summing forelimb bone lengths and multiplying by 2).

Taxon	Specimen	H	U	MC-IV	IV-1	IV-2	IV-3	IV-4	WS	RAM WS
Arthurdactylus conandoylei	SMK 1132 PAL	230	312	227	445	402	312	275	4.41 m	5.2–5.4 m
Anhanguera santanae	NSM PV 19892	257	384	257	462	387	270	225	4.48 m	4.3–4.5 m
Cryodrakon boreas	TMP 1992.83.4	245							4.57 m (est.)	
Pteranodon sp.	FHSM 184	269	393	583	653	539	390	194	6.04 m	5.6–5.9 m
Quetzalcoatlus sp.	TMM 42422	250	358	620	602	305	156	39	4.66 m	4.8–5.0 m
Pterosauria indet.	RAM 22574		366/ 381							4.3–5.9 m