

Additional evidence for very large wing-span pterosaurs in the Wessex Formation (Early Cretaceous, Barremian) of southern England

David M. Martill^a and Robert A. Coram^b

^a*School of Earth and Environmental Science, University of Portsmouth, Portsmouth PO1 3QL, UK*

^b*School of Earth Sciences, University of Bristol,*

ABSTRACT

A partial distal left metacarpal IV of a pterodactyloid pterosaur is notable for its size. The specimen, from the Early Cretaceous (Barremian) Wessex Formation exposed on the southwest coast of the Isle of Wight, southern England is identified as an ornithocheirid, perhaps close to the *Ornithocheirus*, *Coloborhynchus*, *Caulkicephalus*, *Anhanguera* complex. A morphometric analysis suggests an original wing span of approximately 5.6 metres. With an early Barremian age, this pterosaur would have been a giant for its time.

1. Introduction

Pterosaur remains are a rare, but significant component of the Wessex Formation (Wealden Group, Early Cretaceous, Barremian) vertebrate assemblage of the Isle of Wight in southern England (Hooley, 1913; Howse et al., 2001; Steel et al., 2005; Witton et al., 2009; Sweetman and Martill, 2010; Martill et al., 2011; Martill, 2015). The Wessex Formation pterosaur assemblage includes two valid named taxa; *Istiodactylus latidens* (Hooley, 1913) and *Caulkicephalus trimicrodon* Steel, Martill, Unwin and Winch, 2005, and some fragmentary remains that have satisfactorily been referred to the genus *Coloborhynchus* (Martill, 2015). Other material generally lacks diagnostic features at generic level and has been referred to the higher pterodactyloid clades Gnathosaurinae (Ctenochasmatoidea) and Neoazhdarchia (Azhdarchoidea) (Martill et al., 2011) or is regarded as undiagnostic (Howse et al., 2001). Amongst this material, mostly housed in the collections of Dinosaur Isle Museum, Sandown, Isle of Wight (accession numbers MIWG and IWCMS) and the Natural History Museum, London (accession numbers NHMUK) are some fragmentary specimens indicating large individuals. Some of these have previously been described on account of their large size, but the remains are very scrappy, and accurate estimates of their size proved problematic (Green, 1995; Martill et al., 1996). A newly discovered specimen (IWCMS 2016.270) comprises a large distal metacarpal IV that indicates a very large individual and is placed on record here.

2. Locality and horizon.

The new specimen was discovered in rock-fall debris on the beach about 1.5 km north west of Chilton Chine on the southwest coast of the Isle of Wight, where over ten kilometres of excellent

exposures of the Wealden Group (both Wessex and Vectis formations: Barremian to lower Aptian) can be accessed. The section of coast between Chilton Chine and Sudmoor Point is known locally as The Undercliff (Fig. 1) and is well known to local fossil collectors as a rich source of vertebrate fossils, especially large dinosaurs (e.g. Martill and Naish, 2001; Naish et al., 2004; Sweetman, 2011). The cliffs at this locality comprise a sequence of red and variegated mudstones with channel sandstones representing a mud-dominated meander-belt river system (Stewart, 1978, 1981) punctuated by thin (10 cm to 1 m max) plant debris deposits representing large scale inundations in which plant and animal debris was washed into topographic lows on river floodplains (Sweetman and Insole, 2010). Vertebrate remains occur in three settings at this locality: as isolated or associated remains in plant debris beds; as rare, associated skeletons in overbank mudstones, and as worn and broken remains in channel lag deposits at the base of sandstone channels. Vertebrate trace fossils (footprints) also occur at some horizons, but none have yet been attributed to Pterosauria. The specimen is preserved in a matrix of a well-cemented pea-gravel of carbonate clasts of caliche origin (Fig. 2). This matrix is entirely consistent with derivation from intermittent channel fills in a plant debris bed overlying the Sudmoor Point Sandstone (L1 of Stewart, 1978, p. 35, fig. 7), a unit that is of lower Barremian age according to Batten (2011).

3. Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Ornithocheiroidea Seeley, 1891 *sensu* Unwin, 2003

Ornithocheiridae Seeley, 1870

Gen. et sp. indet.

Specimen. A single distal part of a left metacarpal IV of a pterodactyloid pterosaur cf. Ornithocheiridae. Accessioned in the collections of Dinosaur Isle Museum, Sandown specimen number IWCMS 2016.270 (Figs. 2-6; Table 1). Collected by R. A. Coram.

Locality. Coast between Chilton Chine and Sudmoor Point, Isle of Wight. National Grid references SZ 40907 82134 to SZ 39158 82807 respectively.

Horizon and age. Most likely from a plant debris bed (L1 of Stewart 1978) immediately above the Sudmoor Point Sandstone Member, Wessex Formation. Early Cretaceous, Barremian. Plant debris bed (L1), variably along its outcrop contains a basal "pea-gravel" and pebble bed from which most of the vertebrate remains found loose on the beach in this area are derived (Sweetman and Insole 2010)

3.1 Material

IWCMS 2016.270 is a partial left metacarpal IV comprising the metacarpal portion of the metacarpophalangeal joint with a short length of distal diaphysis in a matrix of pisolitic caliche gritstone. There is some damage to the surface bone of the distal condyles that is probably post mortem – preburial erosion. There is a partial, geopetal infill of fine siderite cemented mudstone with a surface lining of drusy calcite. The remainder of the diaphysis is hollow. The specimen has been removed from the matrix to reveal the ventral surface.

3.2 Description.

The specimen (Figs. 2,3) represents the distal portion, estimated to be approximately one third of the original length, of the left metacarpal IV of a pterodactyloid pterosaur. Some 84 mm are preserved. The distal diaphysis is irregularly broken to reveal a partially hollow interior (Fig. 3F). The cross sectional shape is oval with the anterior surface being somewhat flat and the posterior surface being shallowly depressed. The bone wall here is 3.2 mm thick on the dorsal margin, 1.5 mm thick on the anterior margin, 2 mm thick on the ventral margin and approximately 3.2 mm thick on the posterior margin. At the break the diaphysis is 32 mm dorso-ventrally and 14 mm antero-posteriorly. The articular surface for the metacarpophalangeal joint is considerably wider and higher than the diaphysis with a maximum height dorso-ventrally of 47 mm, with perhaps a millimetre missing due to some abrasion damage. The width antero-posteriorly is 32.5 mm with some lost to abrasion. The distal face of the metacarpophalangeal articular surface is deeply sulcate but with a smoothly rounded centrally located bulge, describing a shallow 'wave form' in anterior view. An oval fossa, elongate in the long direction of the bone, is located adjacent to the dorsal articular process measuring 21 mm long x 12 mm wide and contains an oval pneumatic foramen at its proximal end measuring 7 x 3 mm (Fig. 3C). There is some damage in this region of the bone obscuring detail of the pneumatic foramen.

The articular portion expands slightly more to the dorsal margin distally giving a slightly asymmetrical flaring to the element seen in anterior aspect (Fig. 3B, D). In distal view, the articular condyles appear slightly angled with respect to the vertical axis of the diaphysis cross section, but there is no condylar skew or narrowing of the diaphysis (neck) as seen in the slender metacarpal IVs of Azhdarchidae and Dsungaripteridae (Martill et al., 2013) (Fig. 5).

4. Dimensions.

Despite its fragmentary nature, IWCMS 2016.270 is sufficiently well preserved to determine a number of accurate measurements, allowing a tentative reconstruction of the entire bone (Fig. 4, Table 1). The width and depth across the distal articular condylar surface (38 and 43 mm respectively) compares closely with those of previously described Ornithocheiridae (e.g. Kellner and Tomida, 2000; Elgin and Frey, 2011). It possesses a distal condyle that is gently expanded distally seen in caudal aspect, and the shaft immediately behind the condyle is not constricted, as it is in Azdarchoidea (Martill et al. 2013). A pteranodontian affinity is ruled out because of the lack of prominent offset of the condyle seen in *Pteranodon* (Martill et al. 2013, fig. 7E). Comparable, and complete, three-dimensionally preserved ornithocheirid metacarpals are figured by Wellnhofer (1991), Kellner and Tomida (2000) and Elgin and Frey (2011), all derived from the Early Cretaceous Santana Formation of northeast Brazil (Figs. 5, 6). In *Santanadactylus araripensis* (Figs 5B, 6D), in which the width and depth of the condyle are 33 and 32 mm respectively, the total length of the metacarpal is 232 mm. Correspondingly, the length of metacarpal IV for IWCMS 2016.270 when complete is estimated at 280 mm.

Frey and Martill (1994) described the ornithocheirid *Arthurdactylus conandoylei* from the Early Cretaceous Crato Formation of north east Brazil. This ornithocheirid pterosaur, although lacking any cranial remains, represents the most complete postcranial skeleton of an ornithocheirid yet described, and permits the ratios of the wing skeletal components to be established with

certainty. The wing (humerus, radius, wrist, metacarpal IV, phalanges i-iv) has a straight length of 2.25 m. Thus, allowing for a body width of 100 mm, the total wingspan of *Arthurdactylus conandoylei* is ~ 4.5 m. In the wing of *Arthurdactylus* the metacarpal IV comprises approximately 10 percent of the single wing length. Thus the complete wing of IWCMS 2016.270 would likely measure about 2.75 m, suggesting a total wingspan of around 5.6 m. The specimen described here, although fragmentary, is evidence that pterosaurs were well on their way to achieving gigantic sizes perhaps 15 million years earlier than hitherto thought.

[Table of measurements here](#)

5. Discussion.

A wing span estimated at 5.6 m is large for Early Cretaceous pterosaurs. Pterosaurs with wingspans in excess of 5 m have hitherto only been reported from Aptian/Albian or younger strata, with most of the largest examples (wingspans estimated at 9 or more metres) being restricted to the Late Cretaceous (Maastrichtian) (see Witton, 2013) for Azhdarchidae (*Quetzalcoatlus*, *Hatzegopteryx*, *Arambourgiania* Lawson, 1975; Buffetaut et al., 2003; Martill et al., 1998). The largest ornithocheirids are reported from the Albian of Brazil (*Tropeognathus* Kellner et al., 2013) and the Albian of eastern England (Owen, 1859; Martill and Unwin, 2012), while a large ornithocheirid from the Aptian Crato Formation of Brazil has an estimated wingspan of 5.5 m (Cheng et al., 2018). An isolated ornithocheirid tooth from the Aptian of Tunisia was determined to come from an animal with a wingspan perhaps as large as 6 m by Martill et al. (2018). In China, ornithocheirid pterosaurs have been reported from the Barremian-Aptian age Jehol Group (Yixian and Jiufotang formations) of China (Wang and Lü, 2001). While the Barremian *Haopterus* only has a wingspan estimated at 1.35 m, the wingspan of *Liaoningopterus* from the Lower Aptian Jiufotang Formation has been estimated to have been ~5.0 m (Wang and Zhou, 2003).

Slightly older pterosaurs from the Berriasian to Late Valanginian Hastings Group of Sussex may also have achieved large sizes, but no material allowing reliable estimates of wing span has been recovered thus far (Martill et al., 2011). The presence of a large Barremian pterosaur in the Wessex Formation of the United Kingdom and in the Barremian of China shows that very large pterosaurs were already widespread early in the Cretaceous.

Although pterosaur remains are rare in the Wessex Formation of the Isle of Wight, their diversity (three named genera: *Coloborhynchus*, *Caulkicephalus*, *Istiodactylus* and an indeterminate azhdarchoid and ctenochasmatid) nevertheless suggests that they were an important part of the Wessex Formation ecosystem (Martill et al 2011). The taxonomic and morphological diversity suggests the pterosaurs were niche partitioned, with heterodont, fang-toothed ornithocheirids feeding on fishes, while isodont *Istiodactylus* may have been a meat scavenger (Witton, 2012; Martill, 2014). Probably edentulous azhdarchoids were also present in the Wealden Group, but are poorly known (Witton et al., 2009) and may have been terrestrial predators of small vertebrates (Witton and Naish, 2008). Evidence of small pterosaurs is rare, although approximately coeval pterosaur remains from the Wealden Group of Sussex do suggest smaller forms were present in southern England during the Early Cretaceous (Witton et al., 2009). The small azhdarchoid, *Vectidraco daisymorrisae* was described from the Aptian Atherfield Clay Formation that overlies the Wealden Group on the Isle of Wight (Naish et al. 2013).

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Figures

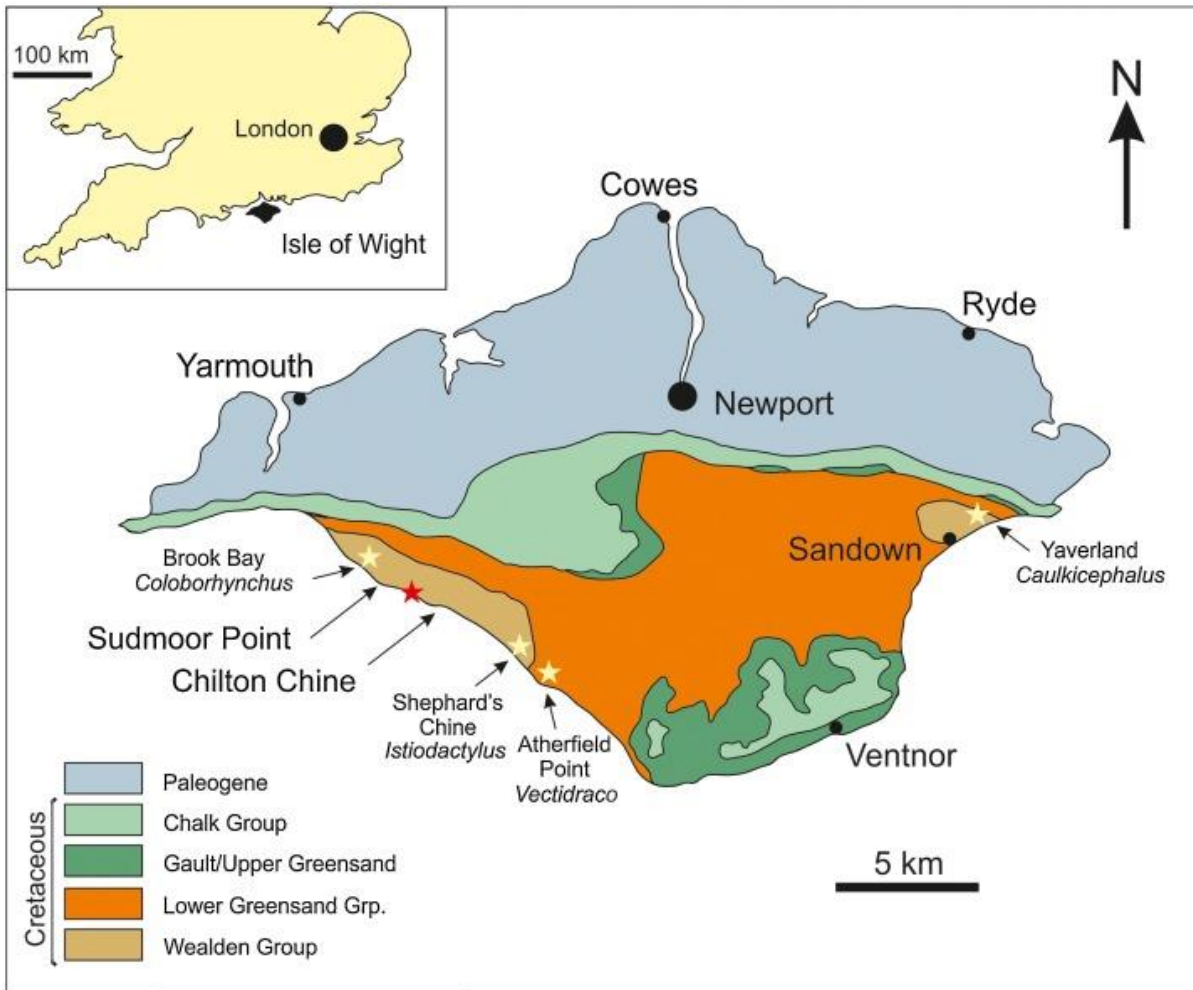


Fig. 1. Simplified geological map of the Isle of Wight with the outcrop of the Wessex Formation indicated. The discovery site of the specimen described here is between Chilton Chine and Sudmoor Point (large arrows), and other pterosaur localities are indicated with small arrows and the genus given.

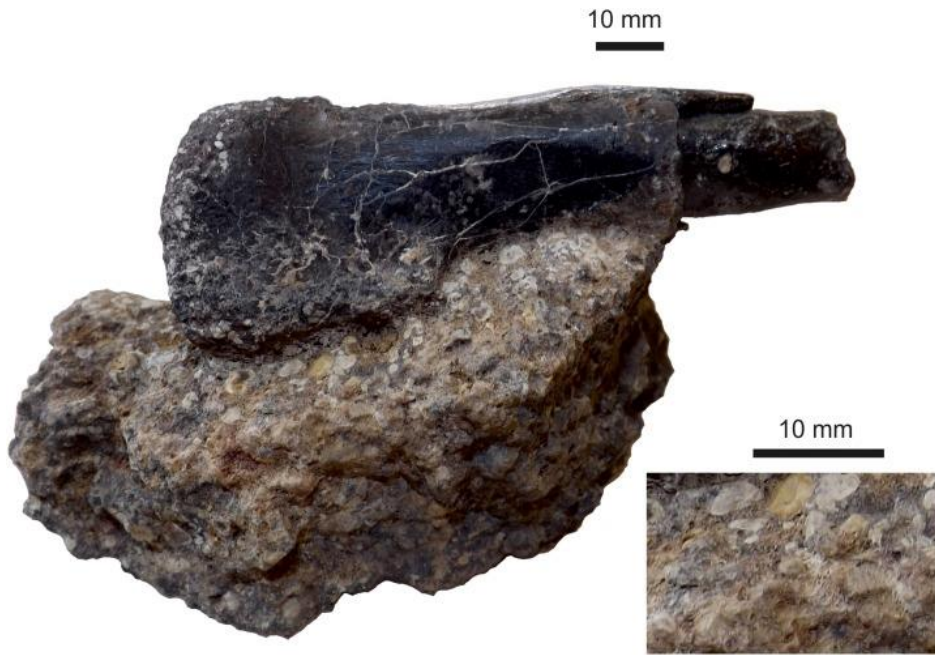


Fig. 2. New pterosaur metacarpal IV specimen viewed in dorsal view in caliche grit matrix typical of Wessex Formation fluvial channel deposits. Inset shows detail of caliche clasts.

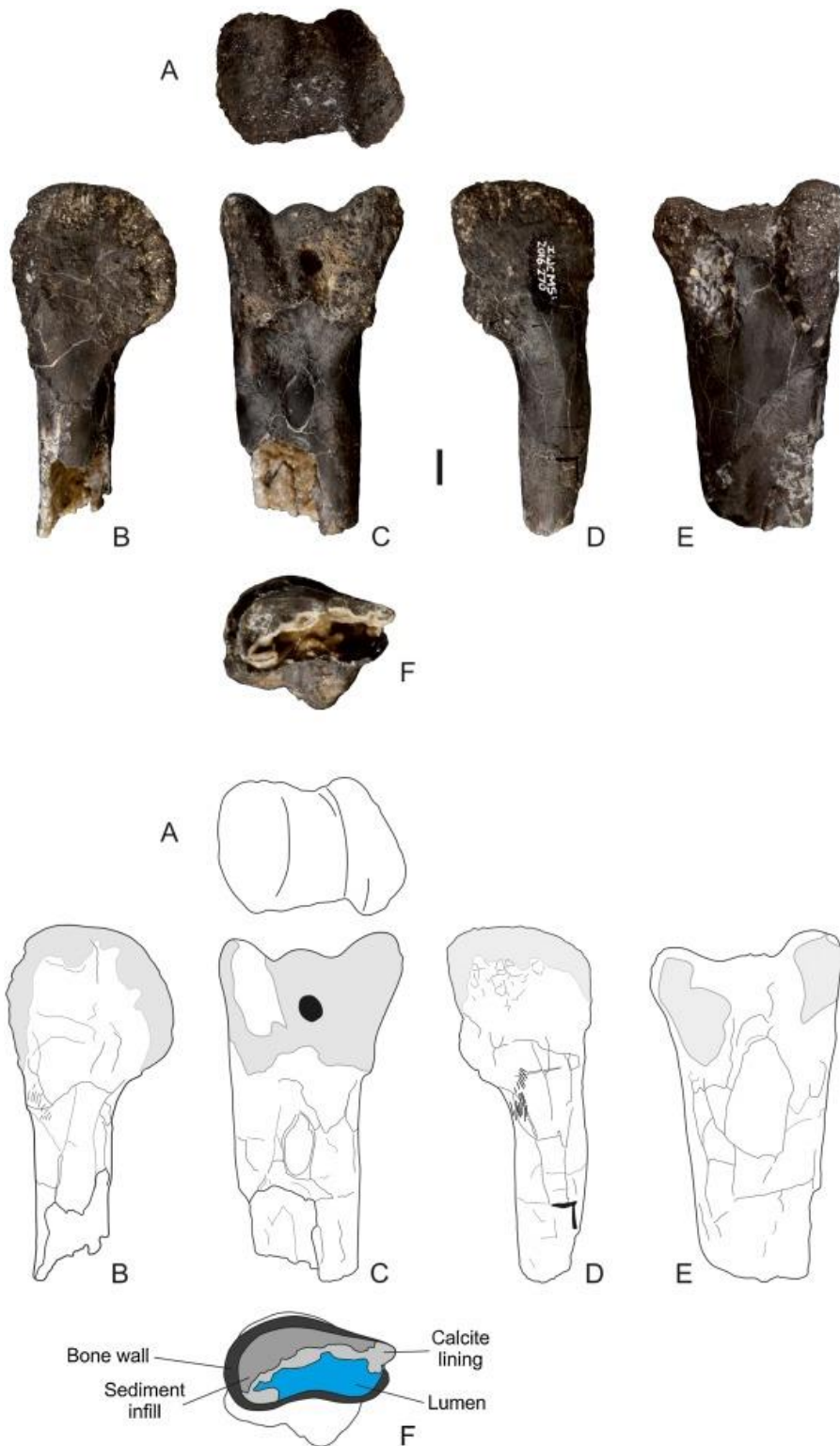


Fig. 3. New pterosaur specimen. Distal end of left metacarpal IV from the Wessex Formation of the southwest Isle of Wight after complete preparation from the matrix, accession number IWCMS 2016.270. Seen in distal (a), ventral (B), caudal (C), dorsal (D), cranial (E), proximal (F) views. Below interpretive drawings of the same views. Scale bar = 10 mm.

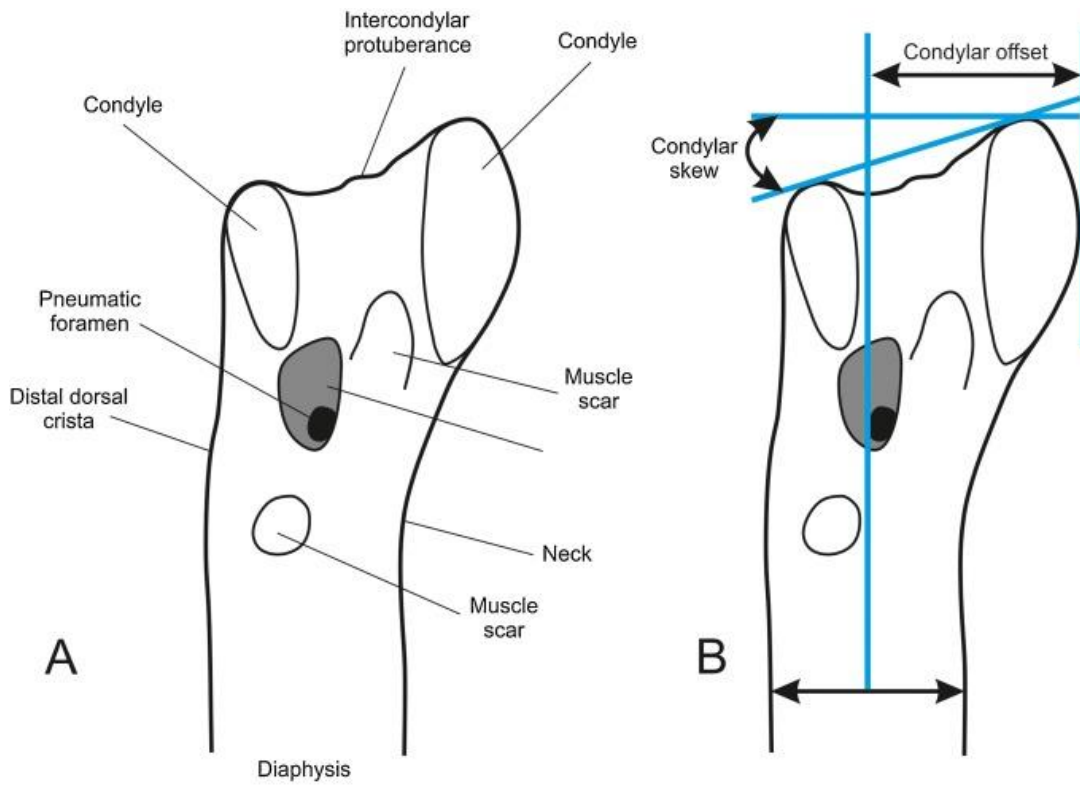


Fig. 4. Interpretative drawing of specimen IWCMS 2016.270 with morphology highlighted. seen in caudal view.

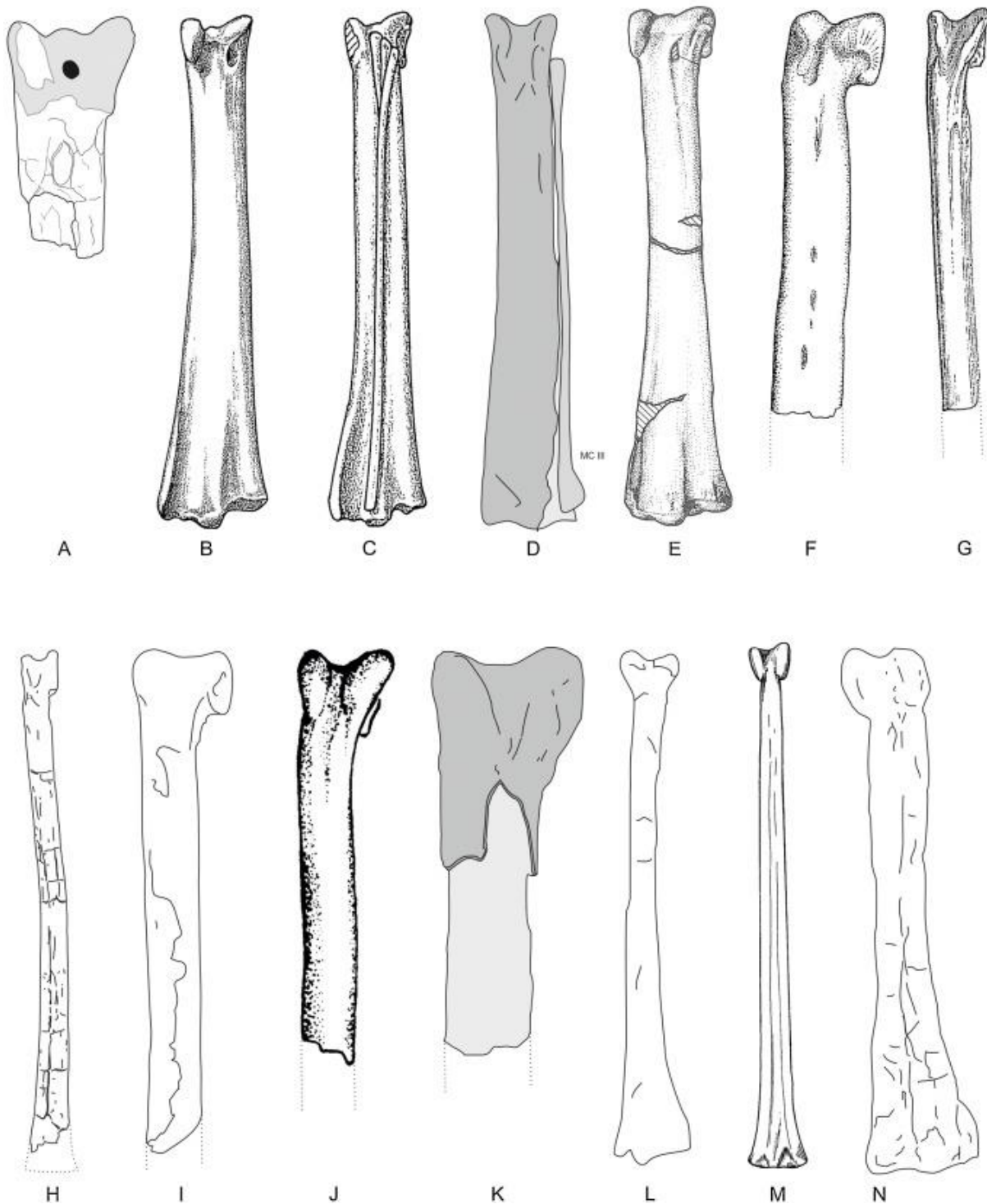


Fig. 5. Morphology of pterosaur metacarpals IV. A, IWCMS 2016.270 distal portion of left metacarpal IV; B, *Santanadactylus araripensis* (after Wellnhofer, 1991, fig. 39c); C, *Santanadactylus pricei* (after Wellnhofer, 1991, fig. 31a); D, *Barbosania gracilirostris* (drawn from holotype after Elgin and Frey 2011); E, *Coloborhynchus piscator* (after Kellner and Tomida, 2000; reversed); F, *Pteranodon* (after Bennett, 2001; flipped); G, *Dsungaripterus weii* (holotype; after Young, 1964, fig. 4c); H, *Dsungaripterus weii* (GIN125/1010-2, traced from Lü et al., 2009, fig. 4d); I, *Tupuxuara longicristata* (traced and reversed from Wellnhofer, 1991); J, *Dermodactylus montanus* (after Galton, 1981, fig. 2q; rotated); K, *Azhdarcho lancicollis* (after Averianov, 2010, fig. 30a; flipped); L, *Tapejara wellnhoferi* (juvenile) (after Eck et al., 2011, fig. 3a); M, *Cycnorhamphus suevicus* (after Wellnhofer, 1978); N, *Pterodaustro guinazui* (after Codorniú, PhD thesis). Not to scale.

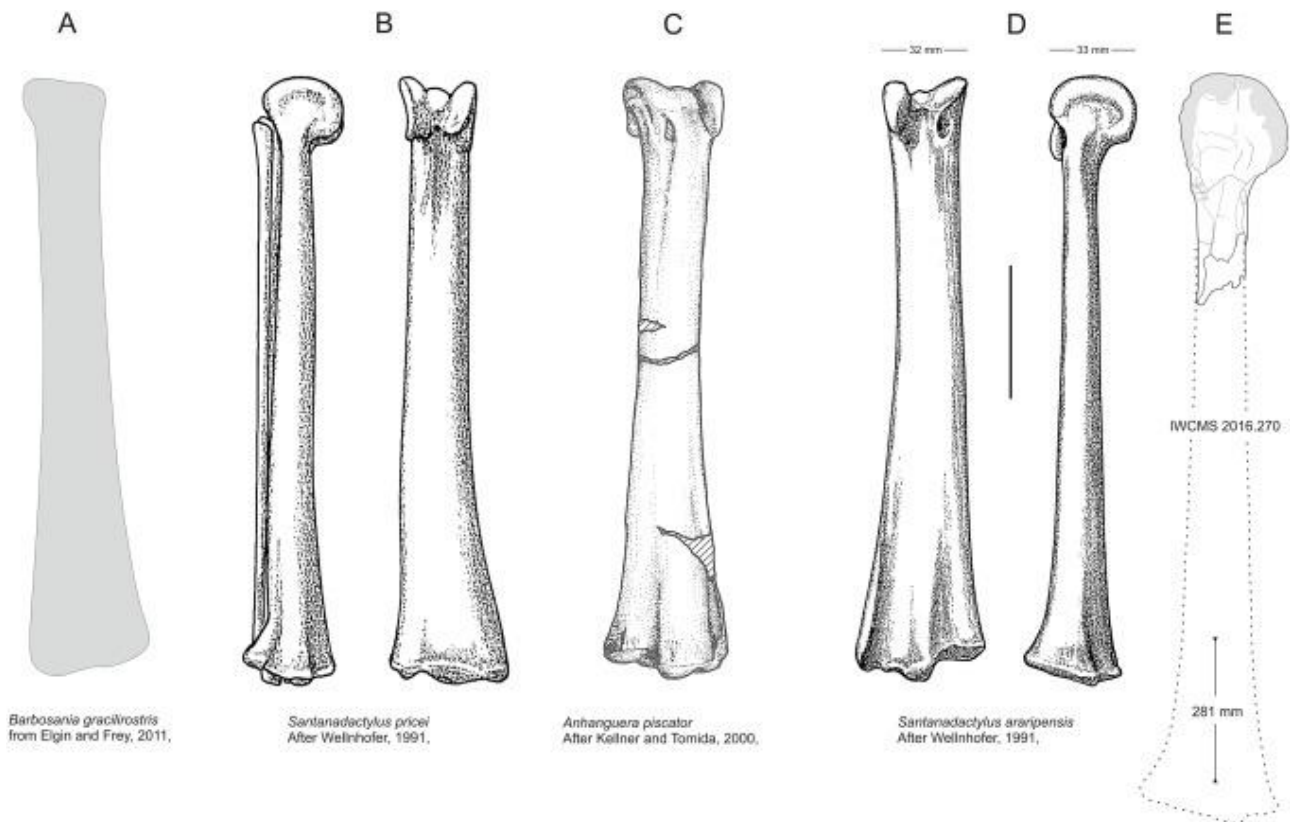


Fig. 6. Ornithocheirid metacarpals from the species (A) *Barbosania gracilirostris*, (B) *Anhanguera piscator*, (C) *Santanadactylus pricei*, (D) *Santanadactylus araripensis* and E, IWCMS 2016.270 showing consistency of form across ornithocheirid taxa. The scale bar is correct for *Santanadactylus araripensis*. All other taxa are scaled to the same length by using the drag function in Corel draw. E is to the same scale and the length of the metacarpal established using the drag function applied to D.

Table 1. Selected measurements for IWCMS 2016.270

| Measurement | Value in mm. |
|--|--------------|
| Maximum diameter of diaphysis behind condyle | 32 |
| Minimum diameter of diaphysis behind condyle | 20 |
| Maximum width of condyle | 38 |
| Height of articular surface of metacarpophalangeal joint | 47 |
| Minimum width of condyle | 32.5 |
| Maximum depth of condyle | 43 |
| Length of oval depression on anterior fascia | 21 |
| Maximum length of specimen as preserved | 84 |
| Maximum bone thickness at proximal end | 3.2 |
| Minimum bone thickness at proximal end | 1.5 |