# **Lower Cretaceous pterosaurs from Colombia**

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ABSTRACT

The global fossil record of lowermost Cretaceous pterosaurs is meagre, and much of the material is fragmentary. Here we report three occurrences of pterosaurs from the Rosablanca Formation (Valanginian), the first records of this extinct group of flying reptiles from Colombia. Specimens from Zapatoca, Santander Department, consist of fragments of the left mandible and the proximal portion of a wing phalange. A third specimen, from Cundinamarca Department, is the proximal termination of a radius. Although fragmentary, these remains are clearly pterosaurian, on account of their remarkably thin bone walls and provide evidence of pterodactyloids, including a large non-pteranodontian ornithocheiroid, in the northernmost part of South America in the early Lower Cretaceous.

*Keywords*: Pterosauria, Ornithocheiroidea, South America, Colombia, Lower Cretaceous, Valanginian.

**1. Introduction**

Pterosaurs have a fossil record that is distinctly patchy, both in time and space. Relatively large numbers of taxa have been reported from the Upper Jurassic and the late Lower Cretaceous, intervals for which the record exhibits relatively high degrees of completeness at more inclusive taxonomic levels (Dean et al., 2016). By contrast, very few remains have been recovered from intervals such as the early Lower Cretaceous. Only six named taxa have been reported from the 12 million year long Berriasian-Valanginian interval (Witton et al., 2009; Rodrigues and Kellner, 2013; Rigal et al., 2017) and only five of the eleven principal clades known to have existed during these two stages are represented by fossils. This corresponds to one of the lowest rates of completeness for any part of the pterosaur fossil record (Dean et al., 2016).

Similarly, the geographic distribution of finds within the Berriasian-Valanginian is also highly uneven with essentially no records, to date, from Gondwanaland or North America, one from Morocco and a few from Europe and East Asia respectively (Barrett et al. 2008). Fossil material from this interval consists almost exclusively of isolated fragmentary bones, the one exception being Tatal in Western Mongolia, which has yielded several partial skeletons (Lü et al., 2009) alongside numerous well-preserved, isolated bones (Bakhurina, 1982; Bakhurina and Unwin, 1995). (We note there is some controversy over the age of these Mongolian strata, known as the Tsagaantsav Svita with some authors referring them to the ?Berriasian-Valanginian [see Unwin and Bakhurina 2000], while others prefer a younger age of Aptian to Albian [e.g. Lucas, 2006]. The marked incompleteness of the lowermost Cretaceous pterosaur fossil record, presumably a consequence of the lack of Konservat Lagerstätten deposits in this time interval, is in sharp contrast to well documented assemblages from the Upper Jurassic (e.g. plattenkalk sequences of Germany; Kimmeridge Clay of southern England) and mid Lower Cretaceous (e.g. Yixian and Jiufotang Formations of China; Crato limestone of Brazil).

Pterosaur assemblages from the Upper Jurassic, contain basal forms (rhamphorhynchids, anurognathids), basal monofenestratans and several pterodactyloid lineages (basal ctenochasmatoids, ctenochasmatids and basal dsungaripteroids). This assemblage is very different from that of the mid Lower Cretaceous, which is dominated by dentate (ornithocheirids, istiodactylids, ctenochasmatids, lonchodectids) and edentate forms (tapejarids and chaoyangopterids). Clearly, several important evolutionary events took place in the latest Jurassic-earliest Cretaceous, including the disappearance of many typical Jurassic clades (most notably all non-pterodactyloids) and the appearance of several important Cretaceous clades including the ornithocheiroids and azhdarchoids. The nature and timing of this transition remains poorly understood, however, in part because of the exceptionally poor fossil record for the Berriasian-Valanginian interval.

Here we describe new pterosaur material from the Lower Cretaceous Rosablanca Formation (Valanginian) of Colombia. Despite the abundant record of Lower Cretaceous vertebrates from Colombia (Cadena, 2015; Cadena and Gaffney, 2005; Cadena et al., 2013; Cadena and Parham, 2015; Carballido et al., 2015; Carrillo-Briceño et al., 2015; Páramo-Fonseca et al., 2016), pterosaurs have never been formally reported or described. Presently, the only potential record consists of a partial limb bone housed in the University of California Museum of Paleontology collections (UCMP 38367). This specimen was found by J. D. Macgregor from an unrecorded locality in Cundinamarca Department, but has never been described or published. Here we formally describe this specimen, UCMP 38367, and two new fossil occurrences of pterosaurs from Colombia, a partial lower jaw and a fragment of a wing phalange from Zapatoca, Santander Department. This new material adds to the meagre record of earliest Cretaceous pterosaurs, provides the first record of pterosaurs from the early Lower Cretaceous of South America and throws new light on pterosaur evolution during this interval.

*1.1 Abbreviations used*

AMNH, American Museum of Natural History; MB, Museum für Naturkunde, Berlin; NHMUK, Natural History Museum, London, UK; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.; UR CP, Paleontological Collection Universidad del Rosario, Bogotá, Colombia.

**2. Material and methods**

UCMP 38367 was collected by J.D. Macgregor in 1944 during fieldwork in Colombia, however it lacks precise geographical provenance data, only that it was collected from the Rosablanca Formation in Cundinamarca Department, Colombia. The two other specimens described here (UR CP 0002 and UC CP 0003), were found by the first author in 2017, during fieldwork in Zapatoca, Santander Department, Colombia (Fig. 1A), in different horizons of section I of the Rosablanca Formation (Guzman, 1985) (Fig. 1B). Specimens from Zapatoca were prepared with a mechanical airscribe tool and 5% HCl to remove excess carbonate rock matrix. Both specimens are housed at UR CP. All measurements are given in mm. The global Valanginian record shown in Fig. 1C was obtained from Paleobiology Database (fossilworks.org) using advanced tool options and palaeoreconstructions of continents at 135 Ma, adding the new records from Colombia described herein.

**3. Locality and stratigraphy**

The new specimens were recovered from the Lower Cretaceous Rosablanca Formation, an approximately 425 metre thick series of marine limestones, dolomites and shales (Wheeler, 1929). These strata crop out in the Altiplano Cundiboyacense, Eastern Ranges of the Colombian Andes and the Middle Magdalena Basin (Fig. 1). They are richly fossiliferous (molluscs, brachiopods and arthropods occur abundantly) and have been securely dated as Valanginian on the basis of ammonites, including the genera *Acantholissonia*, *Lissonia* and *Raimondiceras* (Gomez-Cruz et al., 2015).

**4. Systematic palaeontology**

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Ornithocheiroidea Seeley, 1891

?Ornithocheiridae Seeley, 1870

*Referred material*. UR CP 0002 six fragments of the left mandibular ramus; UR CP 0003, fragment of the proximal part of a wing phalange.

*Locality and horizon*. El Caucho farm locality, Zapatoca, Santander Department, Colombia (6°49′31.2′′N, -73°15′9.43′W). Rosablanca Formation. The occurrence of the ammonite *Saynoceras* *verrucosum* (Fig. 1B) indicates the base of the upper Valanginian (Lower Cretaceous) dated at approximately 138 Ma according to the biochronostratigraphic framework of Ogg et. al., (2008).

## Description

UR CP 0002. This specimen consists of a proximal portion of the left ramus of the mandible (Figs 2-3). It is broken into six pieces: four central pieces which fit together and two additional pieces, one from posterior to the four cojoined fragments and the other anterior to this set. As the broken surfaces of the anterior and posterior fragments do not match the corresponding surfaces of the cojoined set it is assumed that short intermediate portions of the mandible are missing (Figs 2A, B, G, H). The presence of all but the posterior termination of the Meckelian foramen shows that the six fragments represent a section of the mandible immediately anterior to, but lacking, the articular region (cf. Wellnhofer, 1985, fig. 5). Bones present in the preserved fragment are partially fused to one another, suggesting a degree of osteological maturity. Sutures remain, for example, between the dentary, the articular and the splenial, and allow bone contacts to be traced with some confidence.

The mandible was deep and narrow with a rounded ventral margin, a flatter dorsal margin and slightly dorso-ventrally convex lateral and concave medial surfaces. This portion of the mandibular ramus was slightly curved, seen in dorsal or ventral view, with a gentle anterior-posterior convexity of the lateral surface and correspondingly concave medial surface. The width of the ramus gently tapers anteriorly. In lateral, or medial view the ramus has a near straight ventral margin and a slightly convex dorsal margin, declining in height from 30.5 mm posteriorly to 24.3 mm anteriorly.

A deep, oval Meckelian foramen perforated the posterior portion of the medial surface of the mandible. The long axis of the opening is inclined from anterodorsal to posteroventral such that the anterior termination is level with the dorsal margin. Overall, the shape of the opening corresponds closely to that described for several ornithocheirids (e.g. Wellnhofer, 1985, fig. 5; Veldmeijer, 2003, fig. 4).

A ridge-like structure, present on the lateral surface of the jaw just below, and parallel to, the dorsal margin may represent a suture between the coronoid (dorsally) and the dentary (ventrally). The bone is poorly preserved on the dorsal margins of the medial surface, but faint traces of a ridge-like structure might indicate the contact between the coronoid and the splenial. If these interpretations are correct, the coronoid was a lath-like bone capping the posterior part of the dorsal surface of each mandibular ramus. On the medial surface of the anterior and cojoined fragments an antero-posteriorly trending suture someway below the dorsal margin of the mandible likely represents the contact between the splenial (below) and the dentary (above). A low antero-posteriorly oriented ridge running parallel to and a little above the ventral margin of the medial surface of the mandible would appear to mark the boundary between the angulare (below) and the splenial (above) (Fig. 2). The splenial formed much of the medial wall of the mandibular ramus (Fig. 2A,B), decreasing slightly in height anteriorly (Fig. 2A-L), while the elongate angulare formed the ventral margin of the ramus (Fig. 2E,F) (see Wellnhofer, 1985 for a comparator).

Well preserved portions of periosteal bone on the lateral surface of the mandible bear a series of fine (possibly vascular) anteroventrally directed grooves that branch along the length of the ramus (Fig. 3I, J). Elongate foramina pierce the medial surface adjacent to its ventral margin (Fig. 4) (cf. Wellnhofer, 1985, fig. 5e).

The total length of the preserved portion of the specimen, restored as in life, is estimated at 150 mm, although it is possible that the gaps between preserved fragments were larger than assumed here. Typically, in ornithocheirid pterosaurs, the length of the mandible is approximately fifteen times its depth just anterior to the articular region (based on seven examples; Frey et al., 2003; Veldmeijer, 2005). On this basis the mandible of UR CP 0002 is likely to have reached approximately 0.4 m in length, comparable in size to the mandible of *Anhanguera santanae* Wellnhofer, 1991 (AMNH 22555) which has an estimated wingspan of 4.0 m

UR CP 0003. This specimen is a proximal fragment of a ?right wing phalange (Fig. 5A-D). The periosteal bone has largely flaked away revealing the internal trabecular framework which has a lineation reflecting the long axis of the bone. The bone has an oval-shaped cross-section, the ventral profile being markedly more convex than that of the dorsal. In cross-section, both proximally and distally, the trabeculae occupy only the outer portion of the bone’s interior, resulting in a lumen that occupies approximately 80% of the bone interior. The lumen and trabeculae are filled with sediment, suggesting the bone was fragmented prior to burial, thus allowing the ingress of sediment. The fragment has a maximum length of 51 mm, a maximum width of 37.5 mm and a depth of 18 mm proximally and 13.2 mm distally.

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Family indet.

*Referred material*. UCMP 38367, proximal portion of a radius.

*Age and horizon*. Rosablanca Formation. Late Valanginian (Early Cretaceous).

*Locality***.** Unknown locality, Cundinamarca Department, Colombia.

## Description.

UCMP 38367. This specimen consists of the proximal end of a left radius, identified on the basis of the near circular cross-sectional shape of the diaphysis and the distinctive shape of the articular surface (Fig. 5 E-I). The bone, exposed in posterior view, lies on a slab of buff coloured marly limestone, and displays a sharp break at the end of the slab revealing its near circular cross section, a partial geopetal sediment infill and an empty void in which can be seen a few trabeculae with a thin drusy ?calcite coating. The cross-section diameters are 9.5 mm x 8.4 mm. The bone wall is 0.36 mm thick. The maximum length of the specimen is 31.6 mm, and the width across the proximal articulation is 13.8 mm. Comparison with more complete remains (primarily azhdarchoid material from the Santana Formation of Brazil) suggests a wingspan within the range of 2-3 m.

The articular expansion consists of a sub-hemispherical ventral condyle that projects a little below the ventral margin of the shaft in anterior view. The ventral condyle is rounded and separated from a dorsal tubercle by a saddle-shaped excavation forming the cotylar surface that articulated with the radial condyle of the humerus. The dorsal tubercle is more angular in appearance than the ventral condyle and projects well above the dorsal margin of the shaft.

4.1 *Taphonomy*.

The material described here is fragmentary and largely lacks contextual data. From its general appearance it appears to have been weathered at the surface, resulting in surficial bone having fallen away to reveal internal moulds or the internal trabecular structure (e.g. Fig. 5A,B). The generally 3-D preservation of the material, and the infilling of void specimen with (presumably) early diagenetic calcite is comparable to pterosaur material from the slightly younger Santana Formation fossil Lagerstätte of north east Brazil (Martill, 2007). The Santana Formation pterosaurs occur within rounded carbonate concretions, that often reflect the general shape of the elements contained within. The block of matrix for specimen 38367 appears to have rounded margins on one side (the other side appears to be a break) suggesting that this specimen too is enclosed with a carbonate concretion (Fig. 5H,I). It is tempting the think that this new Colombian site may have similarities with the Santana Formation of Brazil and efforts should be made to obtain additional field data.

**5. Discussion.**

5.1 *Affinities*

Despite the highly fragmentary nature of the material described here, the remains can be confidently identified as pterosaurian based on the remarkable thinness of the cortical bone and the presence of large internal spaces (lumen) in the long bones and jaw fragment.

Comparison of the radius (UCMP 38367) with well-preserved examples for a range of pterosaurs including basal forms, basal monofenestratans and pterodactyloids suggests that the Colombian specimen is likely pterodactyloid. This assignment is supported by two features: the remarkably thin cortical bone, which tends to be relatively thicker in non-pterodactyloids (and dsungaripteroids) and the relatively robust construction of the proximal articulation, which tends to be much more flattened (antero-posteriorly) in non-pterodactyloids. The morphology of the articular region of the radius, most notably the well-developed somewhat angular dorsal tubercle of the radius, is quite unlike that of ornithocheiroids (e.g. Wellnhofer, 1985, fig. 19), but compares closely to that of azhdarchoids (e.g. Wellnhofer, 1985, figs 45f-i). However, a similar morphology is also present in some ctenochasmatoids (e.g. *Pterodactylus* sp. MB R 3657). At present therefore, it seems likely that UCMP 38367 is pterodactyloid, and possibly ctenochasmatoid, or azhdarchoid, but almost certainly not ornithocheiroid, or dsungaripteroid.

The jaw fragment (UR CP 0002) compares closely to the mandibles of Lower Cretaceous pterosaurs such as *Anhanguera santanae* (Wellnhofer, 1991) and is highly likely to be ornithocheirid. The mandible is preserved in several istiodactylids including *Istiodactylus* (Hooley, 1913) and *Nurhachius* (Wang et al., 2005; Zhou et al., 2019) and seems comparable in its general morphology to that of ornithocheirids. However, well preserved examples exhibiting the medial aspect of the mandible have yet to be described, precluding further comparison with UR CP 0002. The construction of the mandibular ramus of pteranodontians is markedly different from that of ornithocheirids or istiodactylids. Most notably the mandibular ramus rapidly deepens anterior to the articular region (e.g. Bennett, 2001, fig. 22; Frey et al.. 2006, fig. 4), quite unlike UR CP 0002 which, as in ornithocheirids and istiodactylids, remains of similar, or slightly decreasing, depth throughout its length.

The specimen identified as a partial wing phalanx (Fig. 5A-D) has a slightly flat oval cross section. Such a cross-sectional outline is typical for Ornithocheiroidea, whereas that for many azhdarchoids is sub-triangular or even T-shaped in cross-section (Martill and Frey, 1999).

5.2 *Temporal and palaeobiogeographical implications*

The new finds from Colombia add some important data to the meagre fossil record of early Lower Cretaceous pterosaurs and throw some light on pterosaur evolution in this interval. Although pterosaurs have been reported from the Jurassic and Cretaceous of South America (e.g. Barrett et al., 2008; Codorniú and Gasparini, 2013; Manzig et al., 2014; Codorniú et al., 2016; Ortiz et al., 2017; Perea et al., 2018; Kellner et al., 2019) these are the first finds from the early Lower Cretaceous of South America and, currently, the earliest records of pterosaurs from the northern half of South America.

These discoveries represent one of the earliest records for ornithocheiroids, predated only by an ornithocheirid mandible from the Purbeck Limestone (Tithonian-Berriasian) of England (Howse and Milner, 1995), and the earliest record of this clade in Gondwana.

The new finds are consistent with current understanding of pterosaur evolution. Ornithocheiroids have a fossil record that extends back to the start of the Cretaceous and, based on inferences from phylogenetic analyses (e.g. Zhou et al., 2017), originated in the Upper Jurassic, or possibly even earlier. The Colombian remains show that ornithocheirids achieved a wide, possibly global, distribution and large size early in the Cretaceous. Irrespective of whether the radius represents an azhdarchoid, or possibly a ctenochasmatoid, it is consistent with the known stratigraphic range of either group. Ctenochasmatoids are present in the Jurassic and Lower Cretaceous of South America (Perea et al., 2018), while the fossil record of azhdarchoids ranges from the Upper Jurassic to end Cretaceous (Averianov, 2010; Zhou et al., 2017).

Thus, the Colombian finds are consistent with, and further emphasise, two seemingly key features of pterosaur evolution in the latest Jurassic- earliest Cretaceous interval: (1) the absence of non-pterodactyloids; (2) The presence of widely distributed clades typical of the Early Cretaceous (e.g. ornithocheiroids) some species of which achieved relatively large size. This adds weight to the idea that the replacement of typical Late Jurassic pterosaur assemblages, by typical Early Cretaceous assemblages happened quite rapidly in the late Tithonian–early Berriasian.

**6. Conclusions**

New bone material from the Lower Cretaceous Rosablanca Formation is identified as fragmentary pterosaur jaw and wing elements on account of its thin bone wall and general morphology. The parallel sided mandibular dorsal and ventral margins and the suture of the splenial compare well with the same elements in ornithocheirid pterosaurs, and contrast with the situation seen on Cretaceous non-ornithocheirids such as azhdarchoids and dsungaripteroids. We are able therefore to assign the Colombian mandible to Ornithocheiridae. The material is confidently dated as Valanginian using biostratigraphically significant ammonite taxa. Although fragmentary, the new material represents the first occurrence of Pterosauria in Colombia, and suggests that further field work may discover better and more complete material.

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FIGURE CAPTIONS

Fig. 1. Locality and stratigraphic data for the new Colombian pterosaur material. A, locality maps showing the location of Colombia within South America, the locality of Santander Department and the locality of Zapotaca and Bucaramanga. B, stratigraphic log for the Rosablanca Formation and its age, with the index ammonite *Saynoceras* *verucossum* depicted. C, Map showing the distribution of Valanginian pterosaurs. The circular image depicts an exposure of the Rosablanca Formation near Zapatoca.

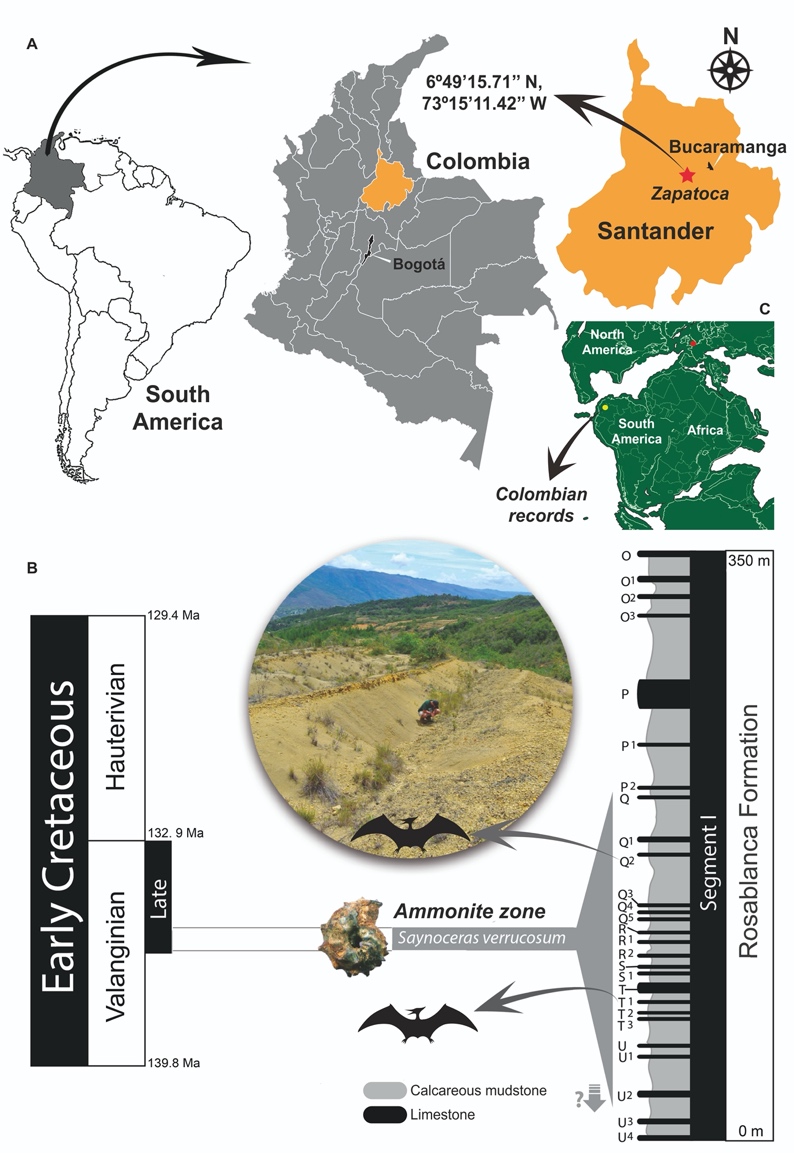


Fig. 2. Photographs and interpretive drawings of Colombian pterosaur specimen UR CP 0002. A,B, posterior left ramus of mandible in left lateral view; C,D, left ramus of mandible in occlusal view; E,F, left ramus of mandible in ventral view; G,H, left ramus of mandible in right medial view. Abbreviations used. co, coronoid; d, dentary, sp. splenial.



Fig. 3. Posterior left ramus of mandible UR CP 0002 in right medial view showing the adductor fossa (A,B), and the outline in cross section (C,D). Details of the internal trabeculae are visible where periosteal bone has flaked away (F-H) and fine grooving of the external bone surface is seen in I and J.

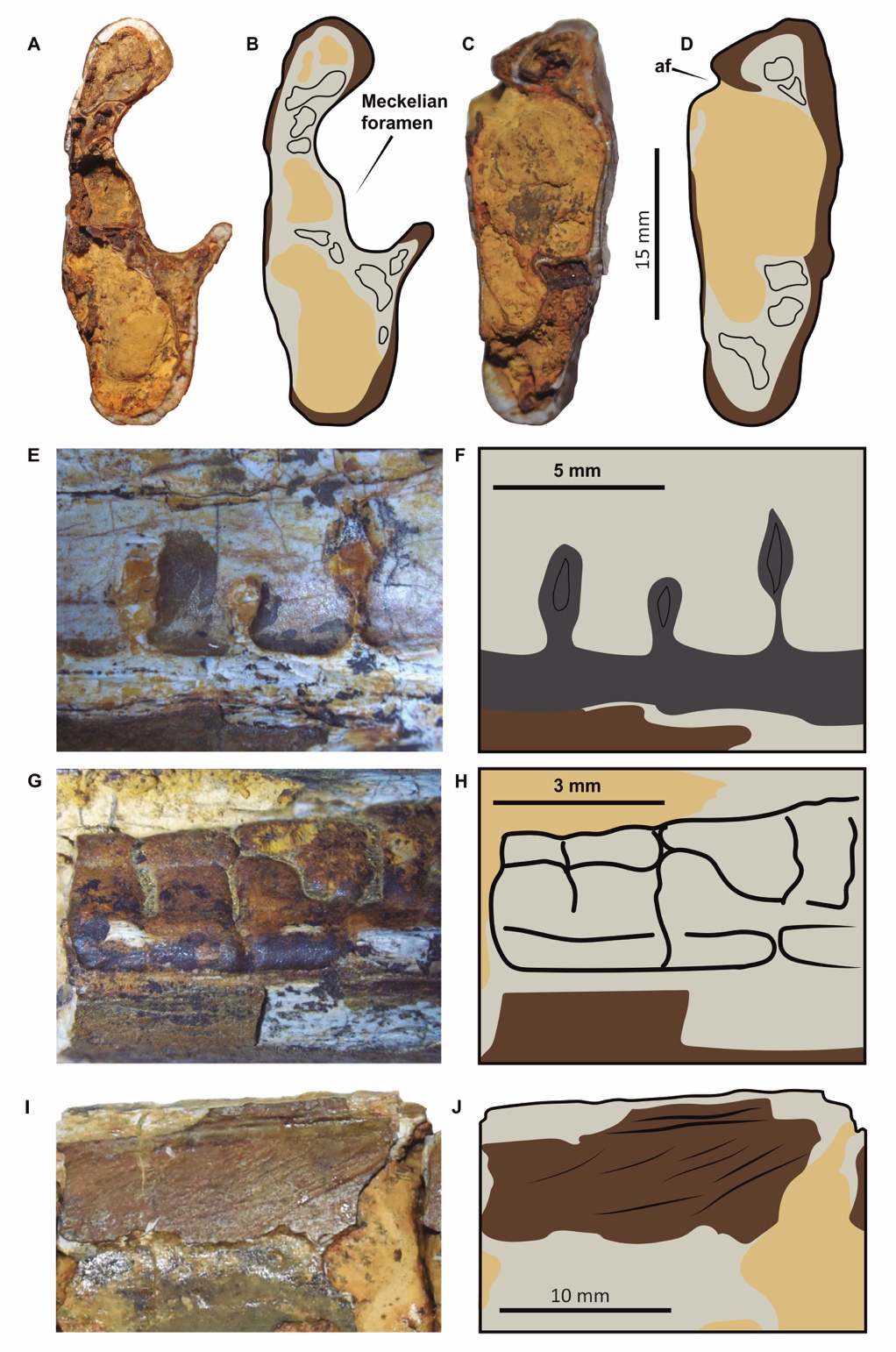


Fig. 4. Fragment of jaw ramus showing slit-like and oval foramina (arrowed) similar to those seen in some Azhdarchoidea.

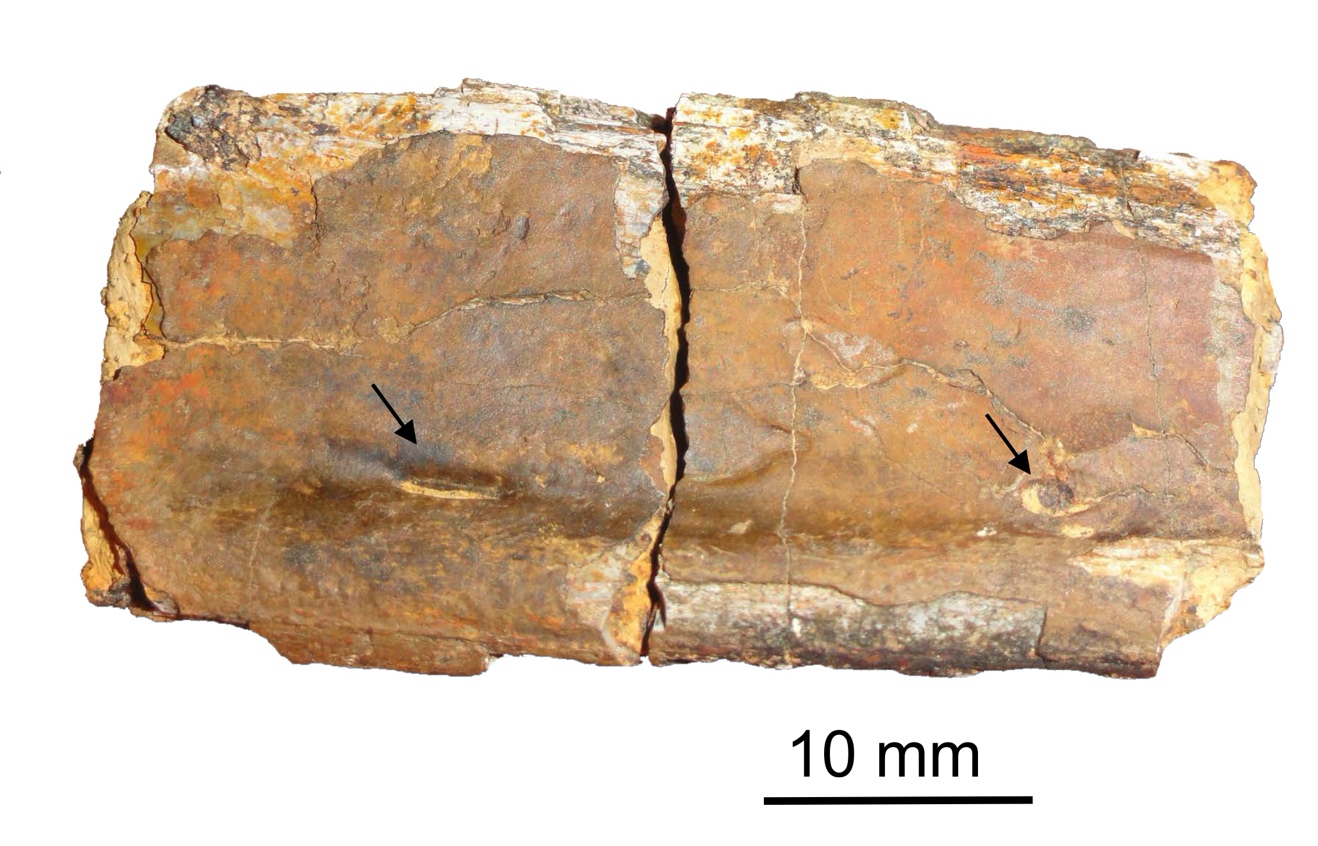


Fig. 5. Fragment of wing phalanx UR CP 0003, A, D, identified as ?Ornithocheiroidea on account of the cross sectional outline (C,D) of flat oval. We have assumed the wider end to be the proximal end, but note that some phalanges do expand slightly distally. E-I proximal end of long bone UCMP V4426/38367, here interpreted as a radius on account of the nearly circular cross-sectional outline and the rapid flaring of the proximal articulatory end.

