A new monofenestratan pterosaur from the Kimmeridge Clay Formation (Kimmeridgian, Upper Jurassic) of Dorset, England

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A specimen of slender skulled monofenestratan pterosaur from the Upper Jurassic Kimmeridge Clay Formation of Dorset, UK, is referred to the new genus and species *Cuspicephalus scarfi*. The dentition and posterior skull morphology suggest affinities with *Darwinopterus*, but a close relationship cannot be proved. There are also some similarities with the pterodactyloid *Germanodactylus cristatus*, but the presence of teeth on the distal rostrum excludes it from that genus. Pterosaur remains are rare in the Upper Jurassic of the UK and this specimen represents the first significant cranial remains of a pterosaur from the Kimmeridge Clay Formation, and possibly the first non-pterodactyloid monofenestratan outside China.

Key words: Pterosauria, Monofenestrata, *Cuspicephalus*, Jurassic, Kimmeridgian, United Kingdom.

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Introduction

Pterosaur remains are rare in the Upper Jurassic of the UK, having been reported only from the Oxford Clay Formation (only the upper parts are Late Jurassic, Oxfordian) of Huntingdonshire (Lydekker 1888), the Kimmeridge Clay Formation (Unwin 1988) and Portland Beds (Delair and Wimbledon 1993) of Dorset. None of these remains included substantial skull material that would enable accurate identification, and specimens have been referred only tentatively to valid genera (e.g., Unwin 1988, Etches and Clarke 2010). Here we describe the first substantial cranial remains of a monofenestratan pterosaur from the English Late Jurassic found at Kimmeridge Bay, Dorset, and consider its systematic position in the light of recent developments based on new Jurassic pterosaurs from China.

Institutional abbreviations.—BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germamy; DM, Dinosaur Museum, Blanding, Utah, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology (Chinese Academy of Sciences), Beijing, China; JME, Jura Museum, Eichstätt, Germany; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MGCL, Musée Géologique Cantonal de Lausanne, Laussanne, Switzerland; MJML, Museum of Jurassic Marine Life, Kimmeridge, Dorset, UK; NHMUK, Natural History Museum, London, UK; SMNK, Staatlisches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; SoS, Jura Museum (Solnhofen Sammlung), Eichstätt, Germany; ZMNH, Zhejiang Museum of Natural History, Hanzhou, Zhejiang Province, China.

Other abbreviations.—Naof, nasoantorbital fenestra; RI, rostral index.

Geological and geographical settings

The new specimen was collected by one of us (SE) from the foreshore of Kimmeridge Bay, Dorset at National Grid Reference SY90772 79118 in December 2009 (Fig. 1). This locality, situated on the Isle of Purbeck coast, is part of the Jurassic Coast World Heritage Site. Strata exposed on the wave-cut platform here belong to the lower Kimmeridge Clay Formation in the *Aulacostephanus autissiodorensis* Ammonite Biozone (Cope 1967). The lithology is a dark grey mudstone with fossils usually preserved in a highly compacted state but often

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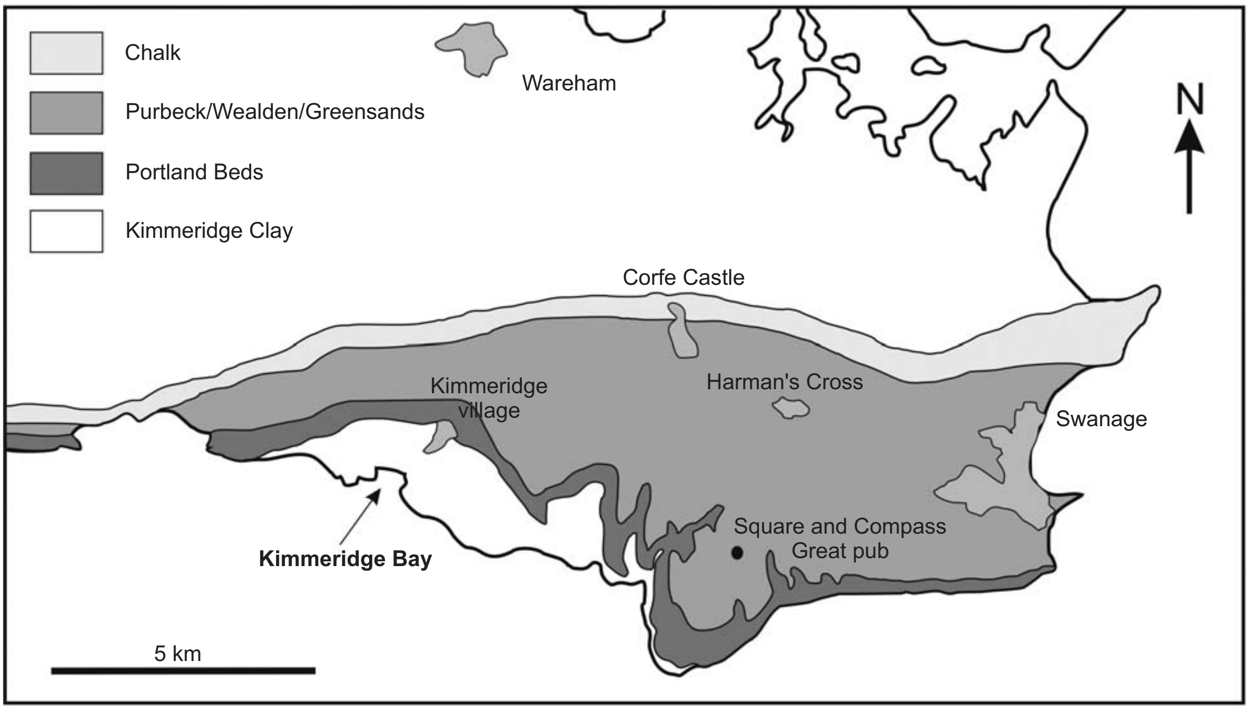


Fig. 1. Simplified geological map showing the distribution of the Kimmeridge Clay Formation on the Isle of Purbeck and the location of Kimmeridge Bay where *Cuspicephalus scarfi* was discovered.

retaining their original biominerals. This area is well known for the wide diversity of fossil vertebrates including both marine (chondrichthyan and osteichthyan fishes, turtles, ichthyosaurs, plesiosaurs, crocodiles) and terrestrial (theropod and sauropod dinosaurs) forms, as well as a diverse assemblage of marine shelly fauna and trace fossils (Wignall and Hallam 1991; Benton and Spencer 1995; Martill et al. 2006).

Systematic palaeontology

Pterosauria Kaup, 1834

Monofenestrata Lü, Unwin, Jin, Liu, and Ji, 2009

Genus *Cuspicephalus* nov.

Etymology: From Latin *cuspi*, pointed, after the pointed rostrum; and from Greek *cephalus*, pertaining to the head.

Type species: *Cuspicephalus scarfi* sp. nov., see below.

Diagnosis.—As for the type and only species.

Stratigraphic and geographic range.—As for the type species, see below.

Cuspicephalus scarfi gen. et sp. nov.

Figs. 2–4.

Etymology: After artist/cartoonist Gerald Scarfe whose vicious caricatures mostly have very pointy noses. http://www.geraldscarfe.com/

Holotype: MJML K1918 in the Museum of Jurassic Marine Life, Kimmeridge, Dorset.

Type horizon: Upper Jurassic, Kimmeridgian, Lower Kimmeridge Clay Formation, Upper Jurassic, *Aulacostephanus autissiodorensis* Ammonite Biozone.

Type locality: Kimmeridge Bay, Dorset, England.

Diagnosis.—Monofenestratan pterosaur in which the following unique combination of plesiomorphies define this metaspecies: skull very slender, triangular in lateral view with a pointed rostrum, straight dental border, at least 12 or 13 rostral teeth anterior of nasoantorbital fenestra (naof), and probably 30 tooth pairs in total for the rostrum, low fibrous bony crest on the dorsal surface of the premaxilla and nasals extending posteriorly from the 12th alveolus of the rostrum to at least one third the length of the naof. Rostral index 5.4.

Description

The holotype and only specimen of *Cuspicephalus scarfi* is a flattened skull preserved in right lateral aspect on a rectangular slab of dark grey mudstone measuring 389×135×24 mm. Some bones have been removed by marine erosion but substantial parts of the rostrum with alveoli, the ventral border of the nasoantorbital fenestra, the orbit, parts of the cranial roof and the atlas–axis complex are preserved. A partial sagittal crest and the nasals are also visible. There are some faint traces where removed bones have left an impression, or are represented by a thin film of calcite that was precipitated between the bone and the matrix. No teeth are preserved. A number of significant measurements are given in Table 1.

Rostrum and nasoantorbital fenestra (naof).—The rostrum is elongate, slenderly pointed with a rostral index of 5.4 (see Martill and Naish [2006] for discussion of the rostral index). It bears a series of alveoli with the first alveolus directed

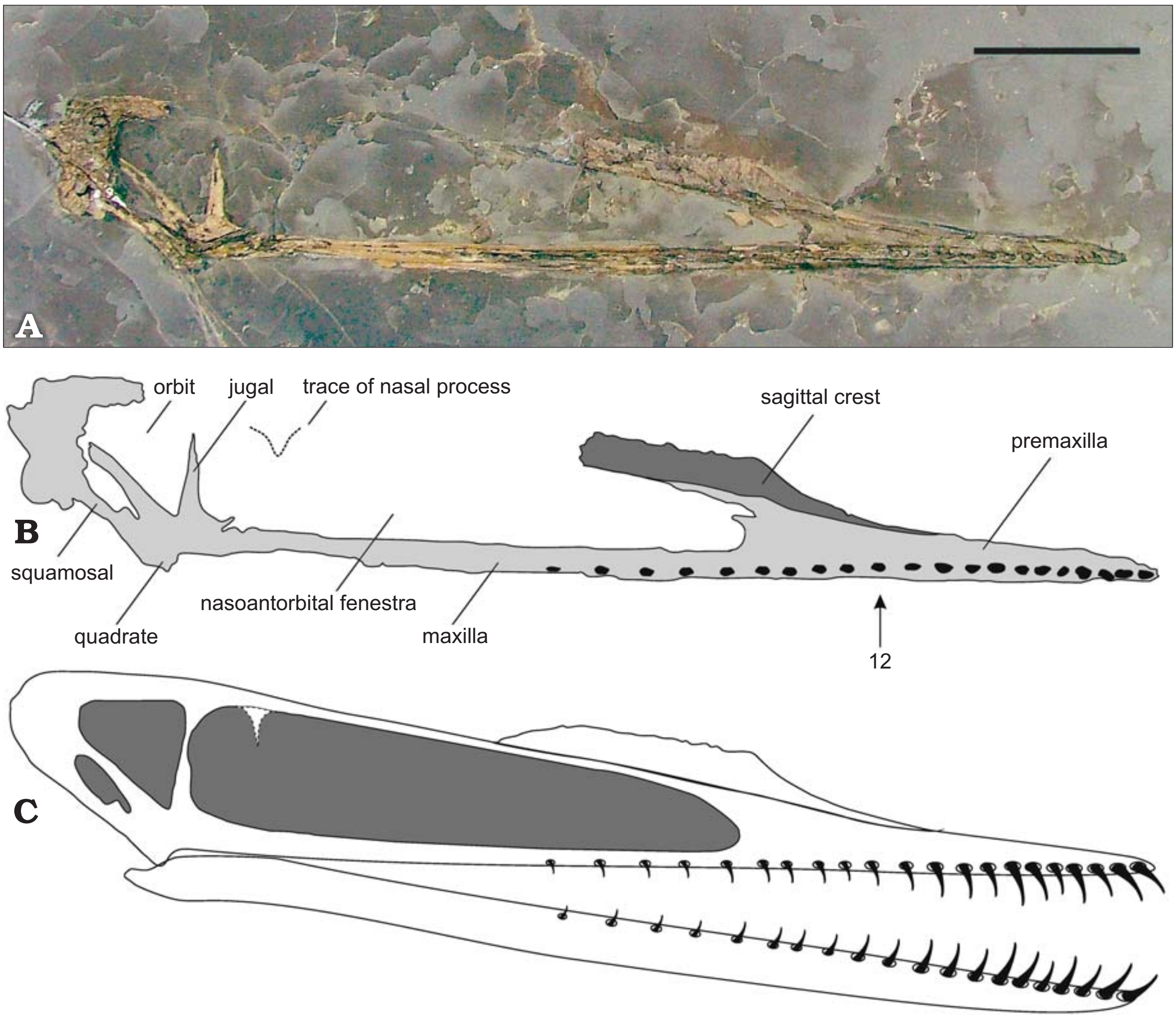


Fig. 2. A monofenestratan pterosaur *Cuspicephalus scarfi* gen. et sp. nov. from the Upper Jurassic of Kimmeridge Bay, England; MJML K1918. **A**. Original skull on slab of mudstone, lacking the mandible and dentition. **B**. Outline diagram of preserved bone. Light grey is bone, dark grey is fibrous bone of sagittal crest, black is dental alveoli where unambiguous. **C**. Restoration of skull outline, with hypothetical lower jaw. Scale bar 50 mm.

anteroventrally and all other alveoli directed ventrally. A total of 12–13 alveoli are clearly seen in front of the nasoantorbital fenestra, with the largest being 5.2 mm long and 2.2 mm high. Because of severe compaction, it is not clear if the present lateral direction of the alveoli is real, or a consequence of crushing. Behind the naof the alveoli become smaller and are less distinct. The smallest alveolus is 1.6 mm long and 1.2 mm high and the total tooth count is probably 25–30, allowing for places where alveoli cannot be seen or are obscured by compaction. The tooth-bearing part of the maxilla is very slender, as is the posterior process of the premaxilla, giving the rostrum a very delicate appearance. It is supposed that the naof has the same height as the orbit because the anterodorsal corner of the orbit and the posterodorsal margin of the naof and their morphology are unknown. The length of skull / length of naof ratio is 2.14. The posterior border of the naof is straight and vertical at its base with the dorsal process of the jugal, but the lachrymal is missing and so the upper part of the border is not seen.

Table 1. Key measurements of holotype skull of *Cuspicephalus scarfi*. Naof, nasoantorbital fenestra.

Measurement	mm
Skull length	326
Length from quadrate to rostral tip	284
Length of nasoantorbital fenestra	155
Max. height of naof (estimated)	30
Max height of skull	55
Length of largest dental alveolus	5.19
Width of largest dental alveolus	2.23
Length of smallest dental alveolus	1.65
Width of smallest dental alveolus	1.16

Orbit.—The orbit is almost entire, lacking only a small portion in the anterodorsal sector where the lachrymal and perhaps parts of the supraoccipital (sensu Wellnhofer 1991b) and prefrontal are missing. The overall shape however, can still be visualised (Fig. 2A). The anterior border is vertical and probably describes a near 90° angle with the dorsal border (there not being much space for a gentle curvature). The

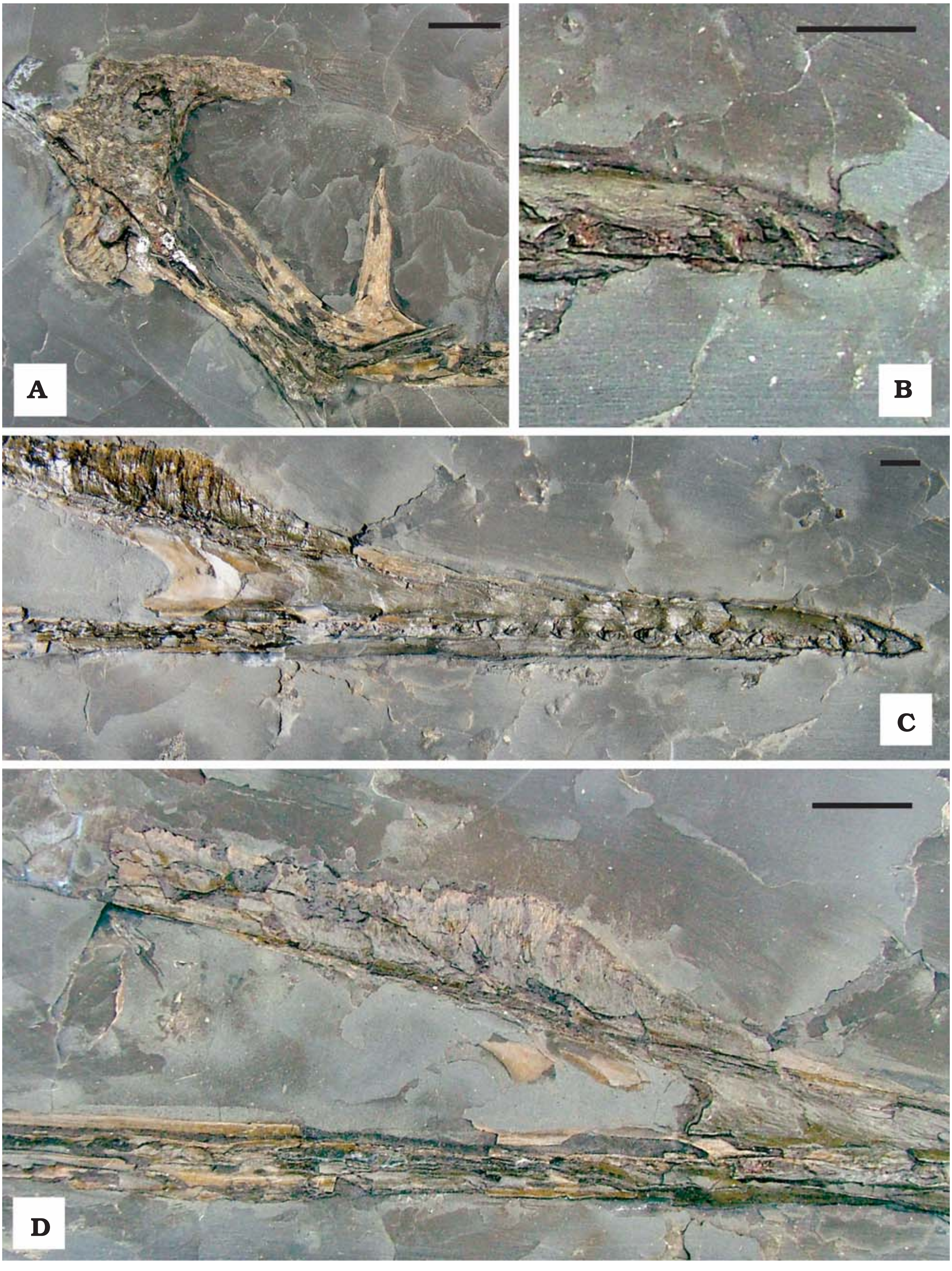


Fig. 3. A monofenestratan pterosaur *Cuspicephalus scarfi* gen. et sp. nov. from the Upper Jurassic, Kimmeridge Bay, Dorset; MJML K1918. **A**. Posterior of skull showing near complete orbit. **B**. Distal tip of rostrum showing anteriorly directed alveolus 1. **C**. Rostrum anterior of nasoantorbital fenestra. **D**. Sagittal crest. Scale bars 10 mm.

dorsalmost part of the posterior border is also vertical, or nearly so for one third of its length, but this curves sharply for the remaining two thirds where the posterior process of the jugal forms the border; thus the overall shape is sub-trapezoid. There is no sign of any sclerotic ring.

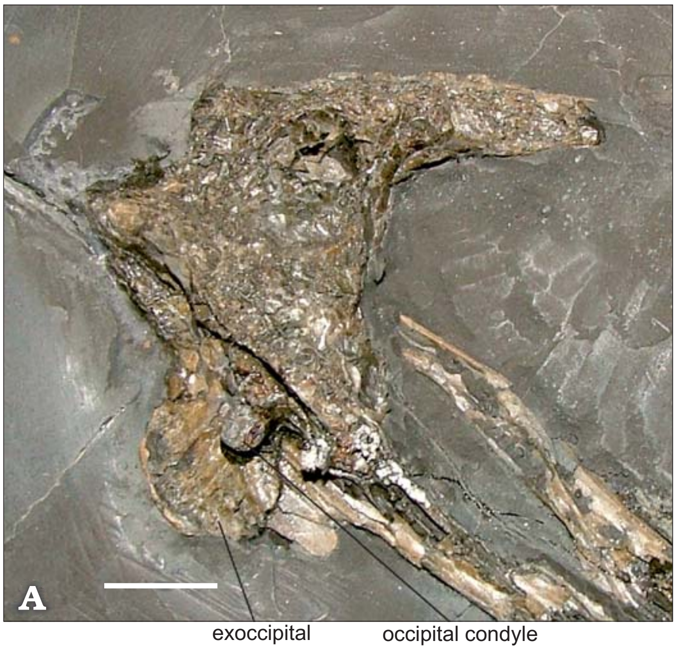
Jugal.—Several linear sutures can be seen that appear to define the boundaries of the jugal. The anterior process is short, especially so compared with the length of the posterior process of the maxilla, so it forms only about one-sixth of the length of the naof. The dorsal process has a slight indentation anteriorly, presumably to accommodate the descending process of the missing lachrymal, and reaches around 4/5 to the top of the naof. The posterior process is sharply deflected dorsoposteriorly at an angle of 45° with respect to the dorsal process (Fig. 4B).

Sagittal crest.—A bony sagittal crest is present on the rostrum extending from an anterior location on the dorsal surface approximately one third of the skull length from the rostrum tip. It rises gradually posteriorly with a smooth margin, becoming irregular and sub-parallel to the skull roof after reaching a height of approximately 10 mm. The dorsal margin of the crest is "ragged" and the bone is somewhat fibrous (Figs. 3C, D, 5A). The crest is incomplete posteriorly, but no trace is preserved on the posteriormost part of the dorsal cranium, suggesting that it did not extend over the orbit.

Exoccipital opisthotic and occipital condyle.—The exoccipital opisthotic of the left side is visible and projects posteroventrally giving the impression of a crest that is perhaps a consequence of rotation during compaction (Fig. 4A). Its posterior border (as seen) is hemispherical with a ventral process directed anteroventrally that may be part of the squamosal (possible sutures may be fractures). The occipital condyle is prominent, hemispherical with a diameter of 3.5 mm, and is approximately 45° to the jaw line when held horizontal. A fracture reveals it to be solid bone.

Remarks

Skull fenestration.—Only a single fenestra is present anterior to the orbit in *Cuspicephalus*, indicating monofenestratan affinities. Its posterior margin is the same height as the orbit, thus excluding azhdarchian affinities for this taxon. The orbit is somewhat rectangular, with a vertically straight anterior margin, a horizontal dorsal margin and a posterior margin with two components of approximately similar length (Fig. 2). This configuration distinguishes *Cuspicephalus* from *Pterodactylus* spp., which typically have a near circular orbit, as does *Dsungaripterus*, but is similar to the condition seen in *Germanodactylus cristatus*, *Darwinopterus* and taxa referred by Wang et al. (2010) to Wukongopteridae. (Note that the monophyly of this clade remains to be demonstrated; it may prove to be a series of stem taxa leading to Pterodactyloidea. Furthermore, it is likely that *Wukongopterus* is a junior synonym of *Darwinopterus*, with minor differences noted by Wang et al. (2010) arising from differing modes of preservation.). The inferior temporal fenestra is lenticular and about four times as long as it is wide (Fig. 2A).



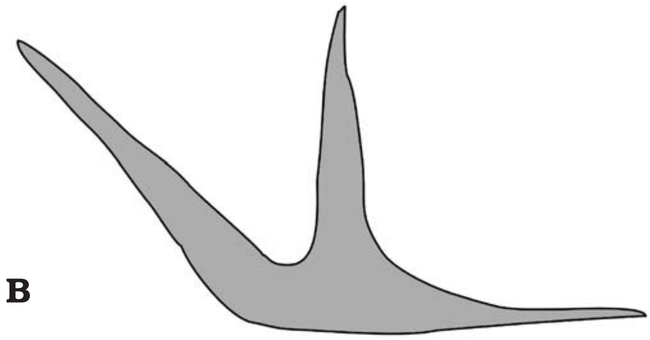


Fig. 4. A monofenestratan pterosaur *Cuspicephalus scarfi* gen et sp. nov. from the Upper Jurassic, Kimmeridge Bay, Dorset; MJML K1918. **A**. Left exoccipital and occipital condyle. Scale bar 10 mm. **B**. Outline of right jugal showing triangular shape of anteroventral border of orbit.

Dentition.—Although no teeth are preserved, the anteriormost 12 alveoli suggest a similar sized and more or less evenly spaced isodont dentition for the anterior rostrum. Posteriorly the alveoli are reduced somewhat, but many are difficult to discern. In some respects the dental pattern is comparable with *Germanodactylus cristatus* (Wiman 1925), although in this taxon teeth are not present in the very anterior part of the rostrum. Only the anteriormost alveolar pair in *Cuspicephalus* appears to have borne slightly prognathous teeth and in this respect it is similar to some ornithocheirids such as *Coloborhynchus* (Fastnacht 2008), *Darwinopterus modularis* (Lü et al. 2009b), and *D. robustodens* (Lü et al. 2011b). This feature is especially marked in *Rhamphorhynchus* spp. (Wellnhofer 1975). However, ornithocheirids have a heterodont anterior dentition set in an expanded rostrum not seen in *Cuspicephalus*, and *Rhamphorhynchus* has separate nasal and antorbital fenestrae. Some non-pterodactyloid

Table 2. Rostral indices (RI) of selected non-pterodactyloid monofenestratans, germanodactylid pterosaurs, and the crested "rhamphorhynchoid" *Pterorhynchus*.

Specimen	RI
Cuspicephalus scarfi, MJML K1918	5.4
Germanodactylus cristatus, holotype BSPG 1892 IV 1, Munich	3.07
Germanodactylus cristatus, SMNK PAL 6592, Karlsruhe	3.8
"*Germanodactylus*" *rhamphastinus*, JME Moe12, Jura Museum	4.06
"*Germanodactylus*" *rhamphastinus*, MCZ 1886, Cambridge Mass.	4.7
G. cristatus, SoS 4593, juvenile (Bennett 2006)	2.47
G. cristatus, SoS 4006, juvenile (Bennett 2006)	2.29
Darwinopterus modularis, restoration (Lü et al. 2009b)	5.4
D. modularis, holotype ZMNH M8782 (Lü et al. 2009b)	3.6
Darwinopterus sp. taken from image on Wikipedia http://en.wikipedia.org/wiki/Darwinopterus	3.8
Darwinopterus linglongtaensis, holotype IVPP V16049 (Wang et al. 2010)	3.46
Kunpengopterus sinensis, holotype IVPP V16047 (Wang et al. 2010)	5.06
Pterorhynchus wellnhoferi, holotype DM 608 taken from X-ray image (Czerkas and Ji 2002)	2.72
Darwinopterus, Mrs T, ZMNH M8802 (Lü et al. 2011a)	3.7

monofenestratans possess teeth beneath the naof (e.g., *Darwinopterus*, *Wukongopterus*) as seen in *Cuspicephalus*, but *Kunpengopterus* appears to have only ?8 tooth pairs in the anterior rostrum, and none beneath the naof (Wang et al. 2010). The holotype specimen of *Kunpengopterus* is severely crushed and it may be that teeth are present, but cannot be seen in the mass of crushed bone.

Sagittal crest.— Sagittal crests of fibrous bone are found in several pterosaur groups, including some stem-group pterosaurs (e.g., *Raeticodactylus filisurensis* Stecher, 2008) and the non-pterodactyloid monofenestratans *Darwinopterus*, *Kunpengopterus*, and ?*Pterorhynchus* (Fig. 5); the condition is not known for *Archaeoistiodactylus linglongtaensis* Lü and Fucha [2010] (which is probably a poorly preserved example of *Darwinopterus*), some Dsungaripteridae (*Domeykodactylus,* Martill et al. 2000; *Dsungaripterus,* Young 1964; *Lonchognathosaurus*, Maisch et al. 2004; *Noripterus* Lü et al. 2009a), and several ctenochasmatids, including *Huanhepterus*, *Gnathosaurus,* and a new species of ctenochasmatid referred to *Ctenochasma* sp. from the Mörnsheim Formation of Bavaria (Rauhut et al. 2011). Some tapejarids also bear a fibrous sagittal crest on the premaxilla, most notably *Tupandactylus imperator* and *T. navigans* (see Unwin and Martill 2007: 495, fig. 17.9c under the names *Tupandactylus imperator* and *Ingridia navigans* respectively). The sagittal crest of *Cuspicephalus* is comparable with that of several of these pterosaurs. Most notably, the gradual rise of the crest from the dorsal surface of the premaxilla is similar to that of *Pterorhynchus wellnhoferi* (Czerkas and Ji 2002), a stem-group pterosaur with affinities to *Rhamphorhynchus*, but it is not known if it descends gently as in *Pterorhynchus wellnhoferi* as more posterior parts of the crest of *Cuspicephalus* are missing, but clearly the crest does not extend as far posteriorly as the orbit, as it does in *Darwinopterus*. This gentle rise and decline of the crest is also seen in the *Ctenochasma* sp. nov. figured by Rauhut et al. (2011) from the Late Jurassic Mornsheim Formation, and in *Germanodactylus cristatus* (Wellnhofer 1991a). In dsungaripterids the rise of the crest is often abrupt, as in *Darwinopterus* and the putative germanodactylid *Normannognathus* (see below), or may even extend slightly forwards as in *Lonchognathosaurus acutirostris* (Maisch et al. 2004). Because of the mosaic of characters shared between several groups of pterosaurs, the affinities of *Cuspicephalus scarfi* are uncertain, but the preserved cranial features indicate it is closely allied to the non-pterodactyloid monofenestratans or the pterodactyloid Germanodactylidae. Given that the tooth count is high in *Cuspicephalus* (30 tooth pairs in the rostrum) and that the teeth are of uniform size along the entire tooth row (as suggested by the diameters of the alveoli) a non-pterodactyloid monofenestratan affinity is considered likely.

Rostral index.—The rostral index (RI) of *Cuspicephalus scarfi* at 5.4 is considerably larger than that for any comparable pterosaurs (Table 2). A similar RI of 5.4 was obtained for *Darwinopterus modularis* from the skull restoration presented by Lü et al. (2009b), but an RI of only 3.6 was obtained from photographs of the holotype. This lower value was consistent with values also obtained for *Darwinopterus* specimen ZMNH M8802 (3.7). The holotype of the non-pterodactyloid monofenestratan *Kunpengopterus sinensis* gave a RI of 5.06, comparable with that *Cuspicephalus scarfi*. In germanodactylids the RI is 3.07–3.8 for adult specimens of *Germanodactylus cristatus*, but only 2.29–2.47 for juveniles referred to that taxon by Bennett (2006). In adults of "*Germanodactylus*" *rhamphastinus* the RI varies between 4.06 and 4.7, which may reflect age differences between individuals. It is possibly the case that the rostral index is only a useful distinguishing feature when individuals can be confirmed as adults.

Jugal.—The jugal of *Cuspicephalus* is distinctive in that it has a short maxillary process compared to that described for wukongopterids by Wang et al. (2010). In *Darwinopterus linglongtaensis* the maxillary process of the jugal is a little over twice the length of the dorsal process and in *Kunpengopterus* it is nearly four times as long. In *Cuspicephalus* it is subequal in length (Fig 4B). A short maxillary processes of the jugal is also found in *Germanodactylus cristatus*, but in other pterodactyloids the maxillary process of the jugal is elongate: in *Pteranodon* (Bennett 2001), a specimen referred to *Pterodactylus kochi* (Wellnhofer 1970: pl. 2: 4) and *Tapejara wellnhoferi* (Wellnhofer and Kellner 1991) it is approximately twice as long as the dorsal process, while in the ornithocheirid *Coloborhynchus piscator* (Kellner and Tomida 2000) it is four times as long. Thus, the shortness of this process in *Cuspicephalus* might hint at a relationship with *Germanodactylus*.

Cranial angle.—The angle subtended between the back of the skull, formed by the squamosal and quadrate, with the jaw line, formed by the jugal, maxilla and premaxilla, is highly variable within the Pterosauria and may provide some clues to taxonomic affinity (e.g., Bennett [2006] notes the relative steepness of the quadrate in *Germanodactylus*). In wukongopterids this angle ranges from 132° in *Darwinopterus linglongtaensis* to 142° in *Kunpengopterus sinensis*, a range encompassing the 140° found in *Cuspicephalus* (Fig. 6). In more derived monofenestratans (i.e., Pterodactyloidea) cranial angles are generally larger, but that of "*Germanodactylus*" *rhamphastinus*, a probable basal pterodactyloid, at 148° is only slightly larger than that of *Cuspicephalus*.

Stratigraphical and geographical range.—Type locality and horizon only.

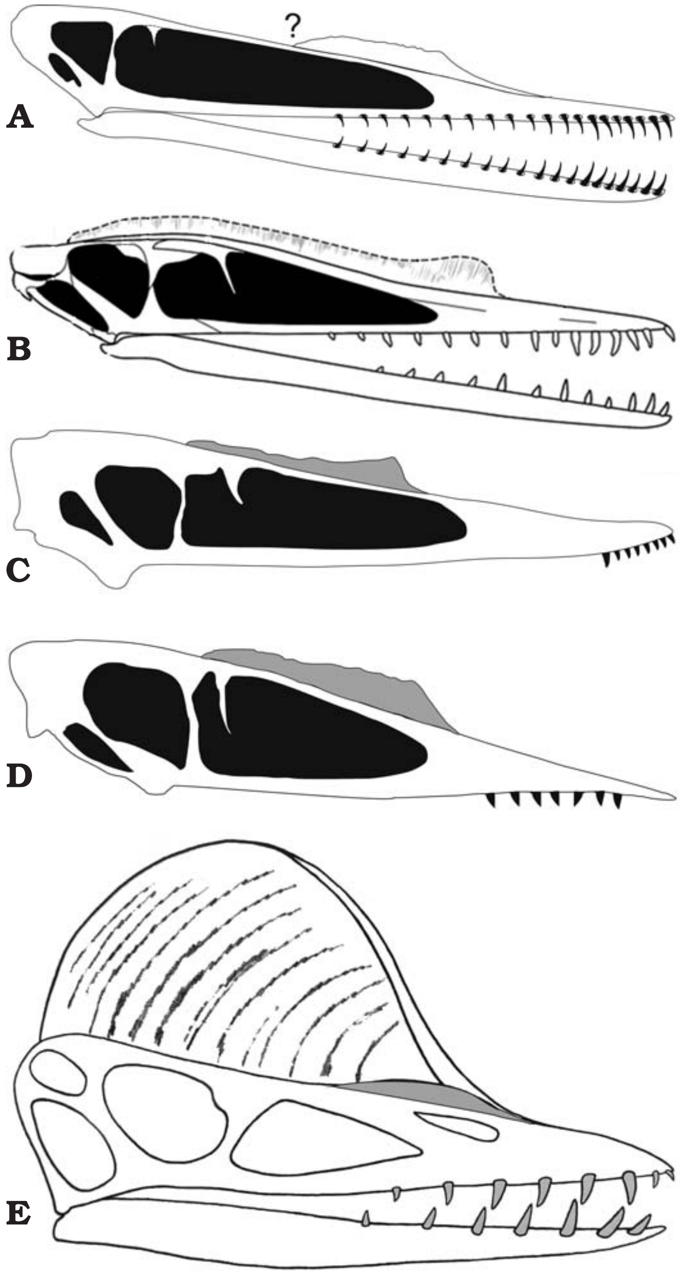


Fig. 5. Sagittal crest of *Cuspicephalus scarfi* gen. et sp. nov. from the Upper Jurassic, Kimmeridge Bay, Dorset (**A**) compared with *Darwinopterus modularis* (Lü, Unwin, Jin, Liu, and Ji, 2010) (**B**) (from Lü et al. 2009b), *Kunpengopterus sinensis* Wang, Kellner, Jiang, Cheng, Meng, and Rodrigues, 2010 (**C**) (based on Wang et al. 2010), *Germanodactylus cristatus* (Wiman, 1925) (**D**) (based on Wellnhofer 1970), and the elaborate crest-bearing *Pterorhynchus wellnhoferi* Czerkas and Ji, 2002 (**E**) (based on Czerkas and Ji 2002). Drawings not to scale.

Discussion

Upper Jurassic pterosaurs in the United Kingdom.—Pterosaurs are remarkably rare in the Upper Jurassic of the United Kingdom, having only been reported with certainty from the Kimmeridge Clay Formation (Unwin 1988) and Portland Beds. "*Rhamphorhynchus*" *jessoni* Lydekker, 1888 from the Oxford Clay, of St Ives, (now) Cambridgeshire was listed by Barrett et al. (2008) as coming from the late Callovian Middle Oxford Clay. St Ives is situated on the easternmost part of the Oxford Clay Formation outcrop and both Arkell (1933) and Edmonds and Dinham (1965) regard the St Ives clay pits as having been excavated in the Upper Oxford Clay (now called Weymouth Member; see Cox et al. 1992) and close to the Oxford Clay/West Walton Beds boundary. Thus "*Rhamphorhynchus*" *jessoni* is also from the Upper Jurassic, albeit the lowest part. The pterosaur remains collected by Alfred Leeds from the Oxford Clay of the Peterborough district (Leeds 1956) held in NHMUK are from the Peterborough Member and are therefore of late Middle Jurassic (Callovian) age (Cox et al. 1992).

Pterosaurs have previously been reported from the Kimmeridge Clay of Dorset, where fragmentary remains including two cervical vertebrae, a dorsal centrum and limb elements, were referred tentatively to *Germanodactylus* sp. (Unwin 1988). At the time, they were thought to represent the oldest known Pterodactyloidea, but a non-pterodactyloid monofenestratan affinity cannot be ruled out.

Other, highly fragmentary material from the Kimmeridge Clay of the Weymouth district, Dorset was reported

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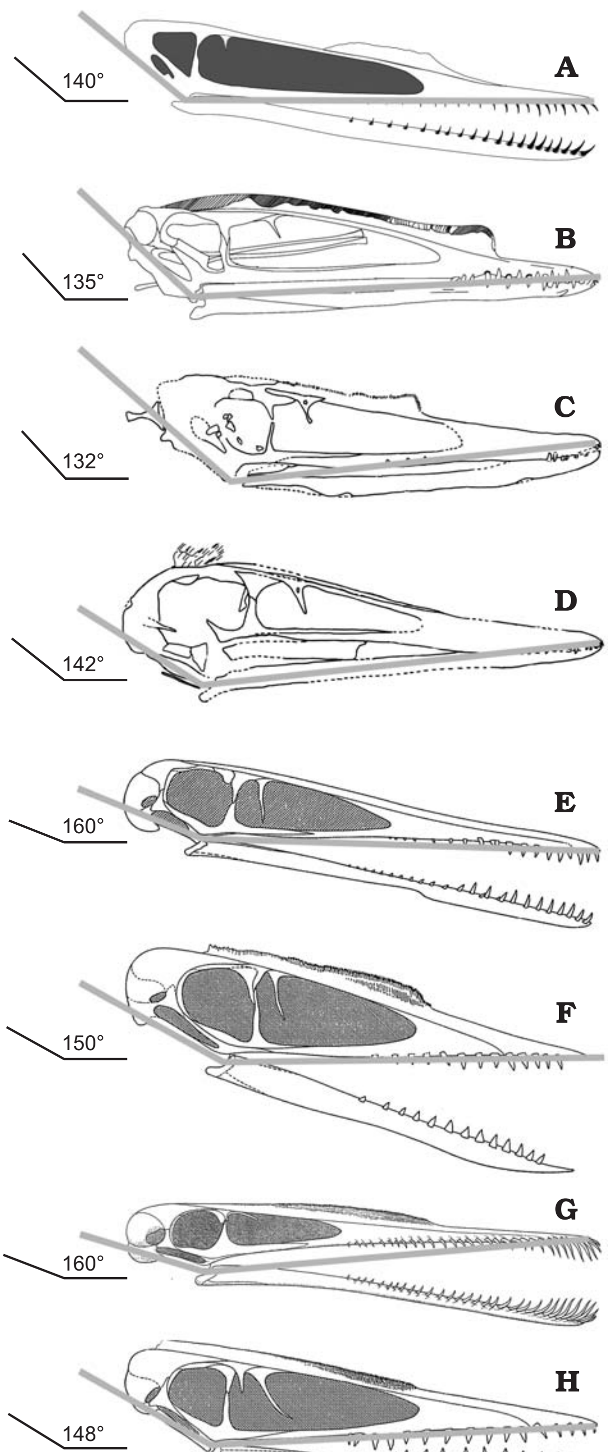

Fig. 6. Variation in cranial angle (subtended between the squamosal-quadrate and jugal-maxilla-premaxilla jaw line from a selection of Jurassic monofenestratans. **A**. *Cuspicephalus scarfi* gen et sp. nov. from the Upper Jurassic, Kimmeridge Bay, Dorset. **B**. *Darwinopterus robustodens* Lü, Xu, Chang, and Zhang, 2011b. **C**. *Darwinopterus linglongtaensis* (Lü, Unwin, Jin, Liu, and Ji, 2010). **D**. *Kunpengopterus sinensis* Wang, Kellner, Jiang, Cheng, Meng, and Rodrigues, 2010. **E**. *Pterodactylus antiquus* Sömmerring, 1812. **F**. *Germanodactylus cristatus* (Wiman, 1925). **G**. *Gnathosaurus subulatus* Meyer, 1834. **H**. "*Germanodactylus*" *rhamphastinus* (Wagner, 1851). B after Lü et al. (2011b); C–D after Wang et al. (2010); E–H after Wellnhofer (1970).

by Lydekker (1888) including the distal portion of a left humerus from the Kimmeridge Clay of Weymouth (NHMUK 41970), the holotype of "*Pterodactylus manseli*" Owen, 1874, and a distal left humerus (NHMUK 42378) which is the holotype of "*Pterodactylus pleydelli*" Owen, 1874. Lydekker (1888) hinted at a third taxon, which he listed as "species c" based on a distal metacarpal IV (NHMUK 41179) that is larger than Owen's two Kimmeridge Clay species.

More recently, Etches and Clarke (2010) figured a number of pterosaurian remains from the Dorset Kimmeridge Clay, including a complete mandible referred to as "rhamphorhynchoid" that may well be close to *Rhamphorhynchus*. This material requires further study to establish its true affinities.

An indeterminate fragmentary "wing bone" of a "pterodactyle" from Church Ope Cove on the Isle of Portland, Dorset was mentioned by Delair and Wimbledon (1993) and is apparently housed in the Portland Museum. They also allude to some isolated pterosaur bones and teeth form the Portlandian of Wiltshire, but provide no further details.

Kimmeridgian pterosaurs elsewhere in Europe.—Elsewhere in Europe, Kimmeridgian pterosaurs have been reported from the Kimmeridgian lithographic limestone of Cerin (Buffetaut et al. 1990), the Upper Kimmeridgian Kimmeridge Clay of Octeville-sur-Mer (Argiles d'Octeville), north of Le Havre (Buffetaut et al. 1998) and the Boulonnais (Sauvage 1873) in France. In particular, Buffetaut et al. (1998) described *Normannognathus wellnhoferi*, which they placed in Germanodactylidae. This taxon, based on a rostral and dentary apex with partial crest and numerous small alveoli, may well be a non-pterodactyloid monofenestratan. In the light of the discovery of non-pterodactyloid monofenestratans, the holotype and only specimen of *Normannognathus* (MGCL 59'583) can no longer be placed in Germanodactylidae with confidence, and should be regarded as Monofenestrata indet. A Lower Kimmeridgian pterosaur was reported from Goslar, Lower Saxony, Germany by Fastnacht (2005). This extremely well preserved pelvis, sacrum and partial limb skeleton was assigned to the Dsungaripteridae, but could not be identified with any more precision. A fragment of non-pterodactyloid pterosaur wing phalanx was reported from the Kimmeridgian Solothurn Turtle Limestone (Reuchenette Formation) of Switzerland by Billon-Bruyat (2005) and assigned to Rhamphorhynchinae indet. A pterosaur phalanx was also reported from this formation by Meyer and Hunt (1999) and interpreted as from a large pterodactyloid, but is otherwise indeterminate. Vullo (2001) reported two large pterosaur teeth from the early Kimmeridgian of La Rochelle, France, and pterosaur bones were also reported from Fumel by Sauvage (1902). *Gallodactylus* has been discovered in the Nusplingen Limestone fossil Lagerstätte (Bennett 1996) in Germany and fragmentary remains have been reported from the Kimmeridgian of Guimarota in Portugal (Wiechmann and Gloy 2000).

Ghost lineages of pterosaurs based on recent cladistic analyses (e.g., Unwin 2003; Lü et al. 2009b), clearly show that pterosaurs were diverse in the lower part of the Late Jurassic, but their remains are still proving elusive.

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