



A new pterodactyloid pterosaur from the Wessex Formation (Lower Cretaceous) of the Isle of Wight, England

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Abstract

A new pterosaur specimen comprising a partial skull and associated postcranial elements from the Lower Cretaceous Wessex Formation of Yaverland, Isle of Wight, southern England, is assigned to a new genus and species of ornithocheirid pterosaur, *Caulkicephalus trimicrodon* gen. et sp. nov., based on several unique features including a heterodont dentition in which the fifth, sixth and seventh teeth are reduced in size compared with those at positions 1–4 and 8–9; the presence of a frontoparietal crest and maxillopremaxillary crest that do not unite over the antorbital fenestra or cranium; a palatal ridge that extends no further forward than the eighth to ninth tooth pairs. The new taxon is the second species of pterosaur from the Wealden Group of the Wessex Basin. © 2005 Elsevier Ltd. All rights reserved.

Keywords: Reptilia; Pterosauria; *Caulkicephalus*; Early Cretaceous; Wealden Group; England

1. Introduction

Pterosaurs are rare in the Wealden Group of the UK with only three described species currently considered valid: *Coloborhynchus clavirostris* Owen, 1874 and *?Lonchodectes sagittirostris* (Owen, 1874) from the Hastings Sand Formation of Hastings, Sussex and *Istiodactylus latidens* (Seeley, 1901) from the Vectis Formation of the Isle of Wight (Unwin et al., 2000; Howse et al., 2001; Unwin, 2001). Other named taxa [*O. clifti*] (Mantell, 1844) and [*O. curtus*] (Owen, 1870) from the Wealden of Sussex and [*Ornithocheirus nobilis*] (Owen, 1870) from the Wealden of the Isle of

Wight] are considered nomina dubia, because they are based on non-diagnostic features (Howse et al., 2001). Only the distinctive *Istiodactylus latidens* is known from the Isle of Wight Wealden Group, and the two specimens that can definitely be assigned to this taxon (CAMMZ T707, BMNH R3877) both appear to have come from the lagoonal sediments of the Vectis Formation (Hooley, 1913; Howse et al., 2001).

Fragmentary, often indeterminate remains of pterosaurs, some possibly referable to the Ornithocheiridae, have previously been reported from the Wessex Formation (Martill et al., 1996). These include a partial postcranial skeleton (MIWG 5579) from the Wealden Group, an isolated ornithocheirid tooth (MIWG 5318) from the Vectis Formation of Barnes High, Isle of Wight, a similar tooth from the Wessex Formation of Yaverland (MIWG 2756), and the proximal part of a left humerus in the collections of the Natural History

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Museum, London (BMNH R558), that was only tentatively referred to *Ornithocheirus* by Lydekker (1888). A considerable amount of well-preserved and potentially diagnosable material has also been reported from several private collections on the island (Green, 1995).

The new material described here represents the first specifically identifiable pterosaur to have been discovered in the Wessex Formation. It comprises parts of a skull and possibly associated postcranial remains that were discovered on the foreshore near Yaverland, Sandown, Isle of Wight, throughout 2002 (some material was obtained as early as 1995 by one of us: JDW) by several independent collectors on a number of separate occasions. Most of the material was found loose on the beach, but one wing element, a quadrate and an indeterminate long bone were found in situ. Several bones in private collections, including one element figured by Green (1995, p. 23, specimen number 0037JW), that come from the same locality may also belong to this individual (JDW, pers. obs.). The material described here is housed in the Dinosaur Isle Museum at Sandown, Isle of Wight, under accession numbers IWCMS 2002.189.1–4, 2002.233, 2002.234, 2002.236, and 2003.2–4.

Abbreviations for institutions referred to in the text.

BMNH, the Natural History Museum, London; CAMMZ, Cambridge University Museum of Zoology; MIWG and IWCMS, Isle of Wight County Museum Service at Dinosaur Isle, Sandown, Isle of Wight.

2. Locality and stratigraphy

The new specimen was found on foreshore exposures of the Wessex Formation that are revealed from time to time at Yaverland on the north-east end of Sandown Bay, Isle of Wight (National Grid reference SZ 614852; Fig. 1). This locality is one of two coastal areas on the island where the Wessex Formation is exposed in cliffs and wave-cut platforms (Fig. 1A). Active erosion results in continuous new exposures, but landslips, especially during the winter months, can make visits dangerous while mudslides and beach sands can obscure outcrops. At the time of writing, much of the wave cut platform at Yaverland was covered by sand.

The section exposed at Yaverland comprises the upper part of the Wessex Formation and the overlying Vectis Formation of the Wealden Group, with younger beds, representing a marine transgression, exposed to the north-east of the bay (Fig. 2). Here the Wessex Formation is of Barremian (Early Cretaceous) age, and comprises a series of variegated mudstones with intermittent fluvial sandstones, silty clays and occasionally plant debris beds. The sequence represents a meander-belt floodplain

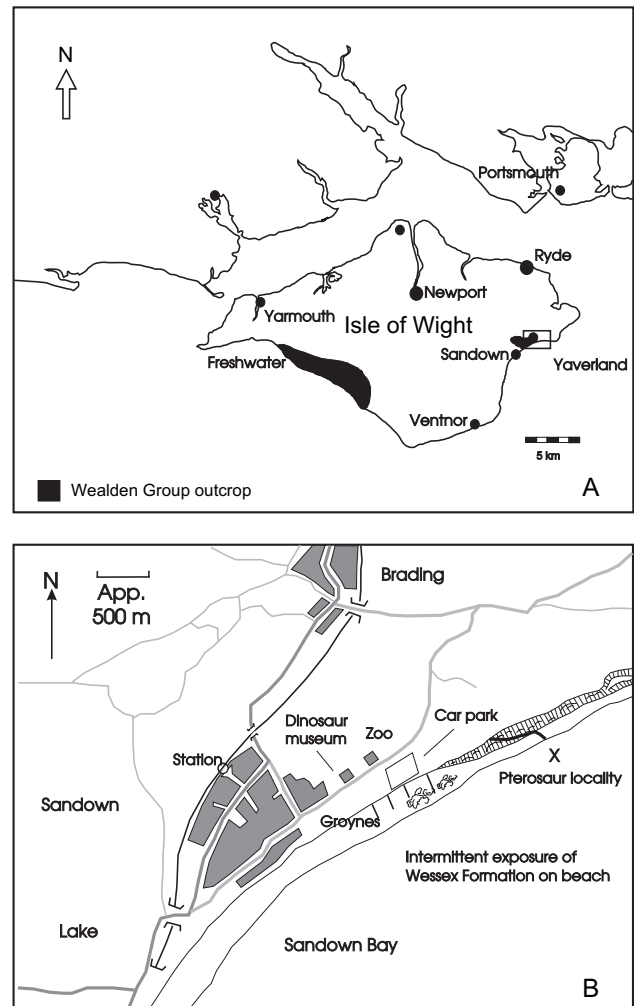


Fig. 1. Locality map showing the Cretaceous fossil vertebrate locality of Yaverland, Isle of Wight. In A, the shading represents outcrops of the Wealden Group. In B, the Yaverland Member (new name) is indicated as a black line in the cliffs and foreshore. The X marks the new pterosaur site.

system with pond and ephemeral lake deposits (White, 1921; Stewart, 1981; Radley, 1994; Wright et al., 2000). The plant debris beds are known for their abundant and often extremely well preserved macro- and micro-vertebrate remains, including dinosaurs, crocodylians, turtles, amphibians, mammals and fishes (Martill and Naish, 2001). The new pterosaur was obtained from one of the plant debris beds (Bed 33 of Radley, 1994). Typically, the plant debris beds are patchily cemented by nodular siderite, contain abundant intraclasts and a high percentage of plant remains ranging from leaf fragments to logs several metres in length. Both lignite and fusain occur. Pyrite, siderite, calcite and barite are common diagenetic minerals but, unfortunately, the pyrite is unstable and prone to decay in damp conditions. The plant debris beds are believed to be the result of intrabasinal flood events that transported plant debris and carcasses, depositing them on the floodplains (Martill

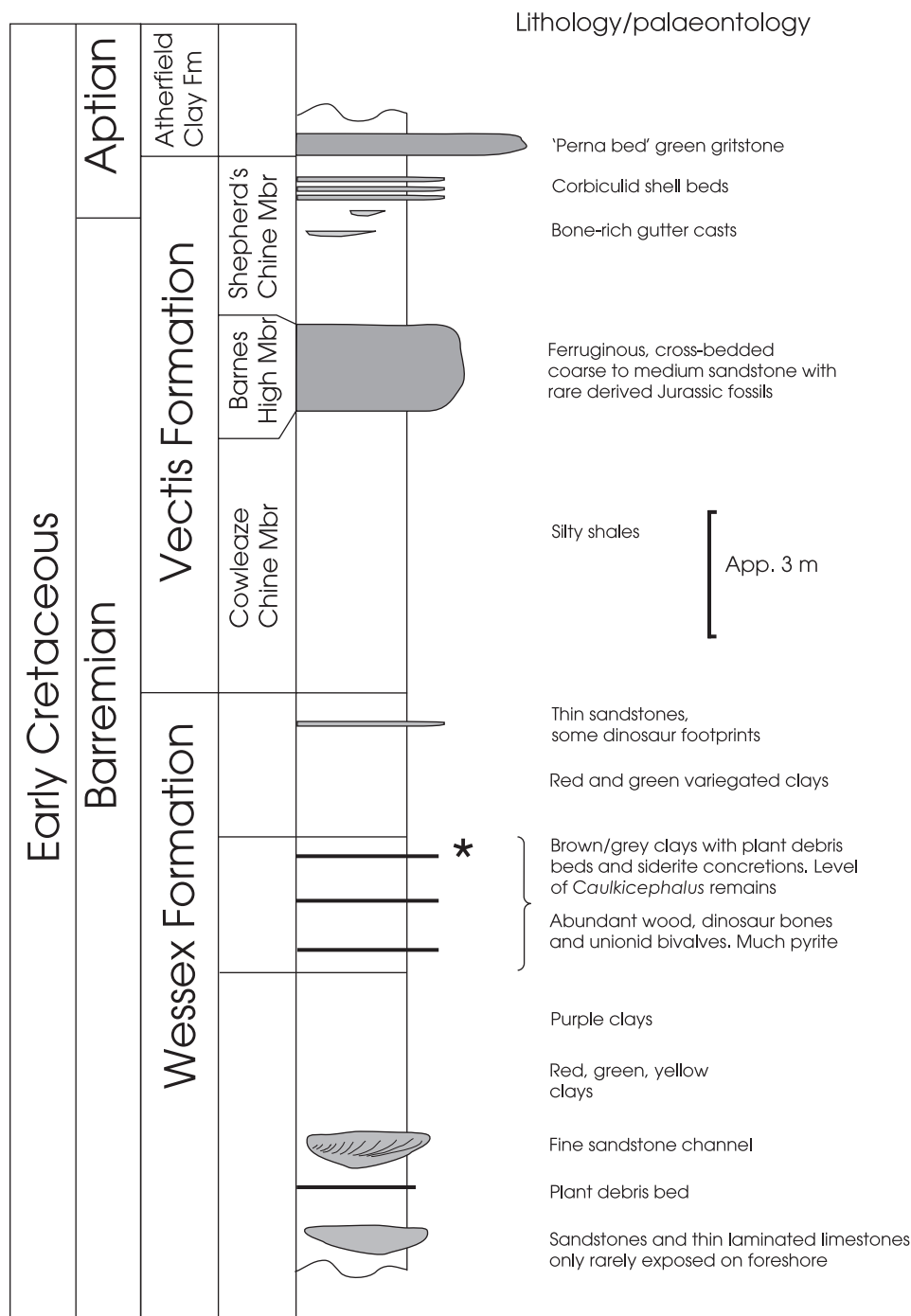


Fig. 2. Schematic stratigraphic section for the Wessex and Vectis formations at Yaverland, near Sandown, Isle of Wight, locating the horizon of *Caulkicephalus trimicrodon* gen. et sp. nov. with an asterisk; simplified from Radley (1994).

and Naish, 2001). Many of the skeletons are disrupted, possibly as a result of scavenging (Martill, 2001).

3. Preservation

The bones of the present specimen are black and well preserved although there is a small amount of compaction damage in places. A small area of compacta is

missing from the surface of the rostrum tip. Some parts of the bones are coated with a thin layer of iron pyrite, but most void space is filled with cemented mudstone (Figs. 3–5). A small amount of grey mudstone with abundant black plant debris has been left on one of the bones to confirm the provenance of the specimen. The surface of one bone is pitted, possibly as a result of pyrite growth, although bioerosion may be responsible.



Fig. 3. Rostrum of *Caulkicephalus trimicrodon* gen. et sp. nov., IWCMS 2002.189.1, 2. A, dorsal view. B, right lateral view. C, ventral view; D, anterior view. Scale bar represents 10 mm.

Some of the damaged surfaces are a consequence of recent marine erosion.

Several of the skull fragments fit together and clearly come from a single individual. It is assumed that the remaining skull fragments, including a braincase found in very close proximity to the holotype, and various portions of postcranial skeleton obtained from the same locality, all belong to the same individual. Although there is no direct fit to confirm this, this proposal is supported by several lines of evidence: the bones all came from the same site; there is no duplication of

bones; they exhibit the same style of preservation; they are completely consistent in size; and there is no indication of the presence of more than one taxon.

4. Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Ornithocheiridae Seeley, 1870

Genus *Caulkicephalus* gen. nov.

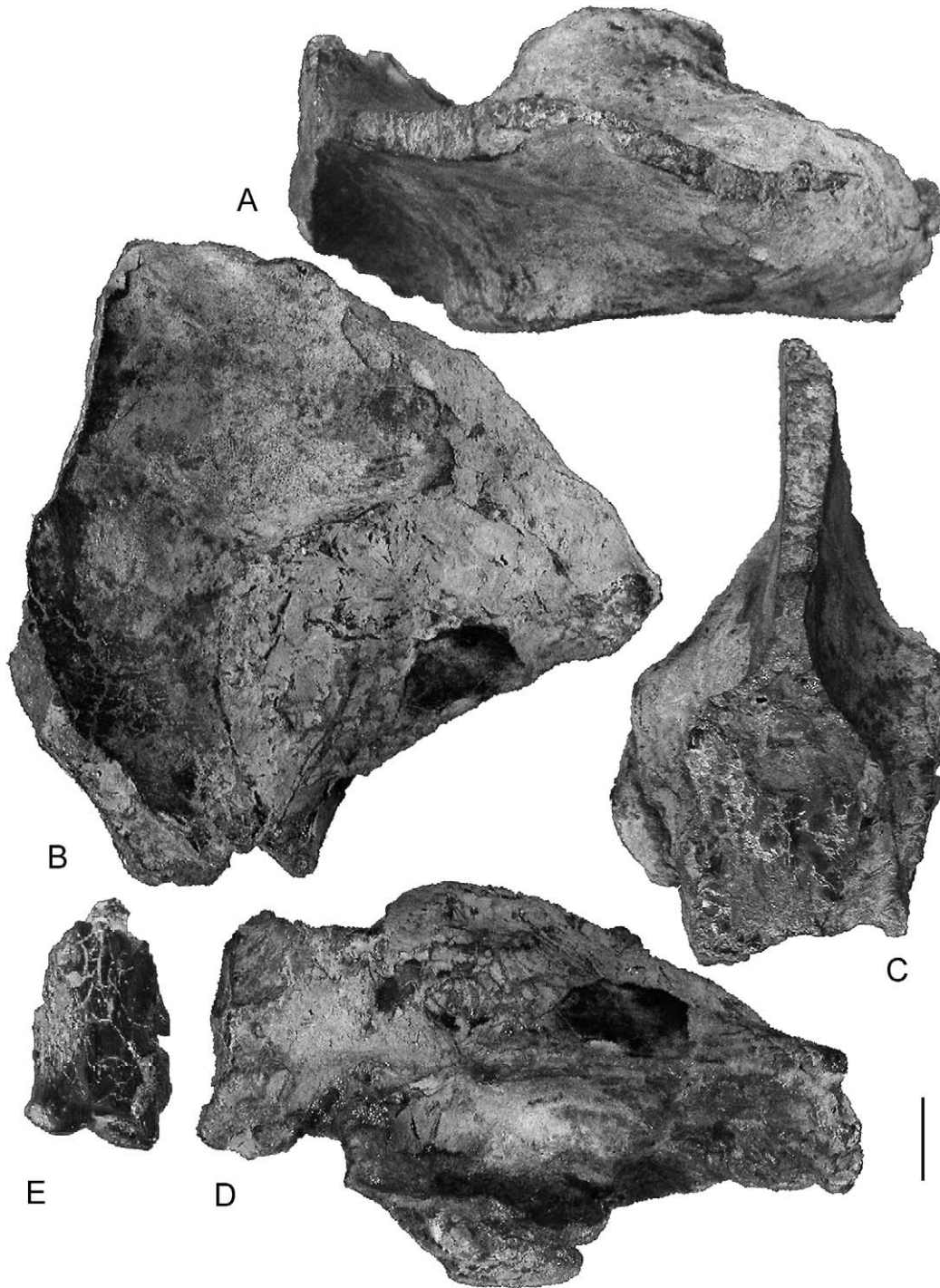


Fig. 4. Brainscase of IWCMS 2002.189.3 and quadrate referred to *Caulkicephalus trimicrodon* gen. et sp. nov. Brainscase in A, dorsal view, B, left lateral view, C, posterior view, D, ventral view. E, left quadrate, (IWCMS 2003.2). Scale bar represents 10 mm.

Derivation of name. Caulk; from Caulkhead, the informal name for natives of the Isle of Wight: workers from the Isle of Wight previously worked as caulkers in the Solent dockyards; and *cephalus*, Greek, head.

Diagnosis. As for type and only known species (see autapomorphies listed for type species below).

Caulkicephalus trimicrodon gen. et sp. nov.
Figs. 3–6

Derivation of specific name. A combination of *tri*, three; *micro*, tiny and *don*, tooth, referring to the small dental alveoli at tooth positions 5–7.



Fig. 5. Other elements referred to *Caulkicephalus trimicrodon* gen. et sp. nov. A, proximal part of the left wing-phalanx 1, ICWMS 2002.237. B, distal part of probable wing-phalanx 2, IWCMS 2002.233. C, four contiguous fragments of the shaft of wing-phalanx 1, IWCMS 2002.234.1–4. D, an element possibly from the hind limb, IWCMS 2003.3. E, cross section of phalange showing cortical bone and spongiosa. Scale bars represent 10 mm: left scale bar for A, B, D, E; right scale bar for C.

Holotype. IWCMS 2002.189.1, 2, 4, three contiguous elements that form the anterior portion of the rostrum (Fig. 3A–D).

Type locality and horizon. North-east Sandown Bay, Yaverland, Isle of Wight (Fig. 1); upper part of Wessex Formation, Lower Cretaceous (Barremian) (Fig. 2).

Referred material. Incomplete braincase bearing the base of a sagittal crest (IWCMS 2002.189.3; Fig. 4A–D); left quadrate (IWCMS 2003.2; Fig. 4E); a fragment of a possible jugal (IWCMS 2003.4); proximal part of the left wing-phalanx 1 (ICWMS 2002.237; Fig. 5A); four contiguous fragments of the shaft of a wing-phalanx 1 (IWCMS 2002.234.1–4; Fig. 5C); distal part

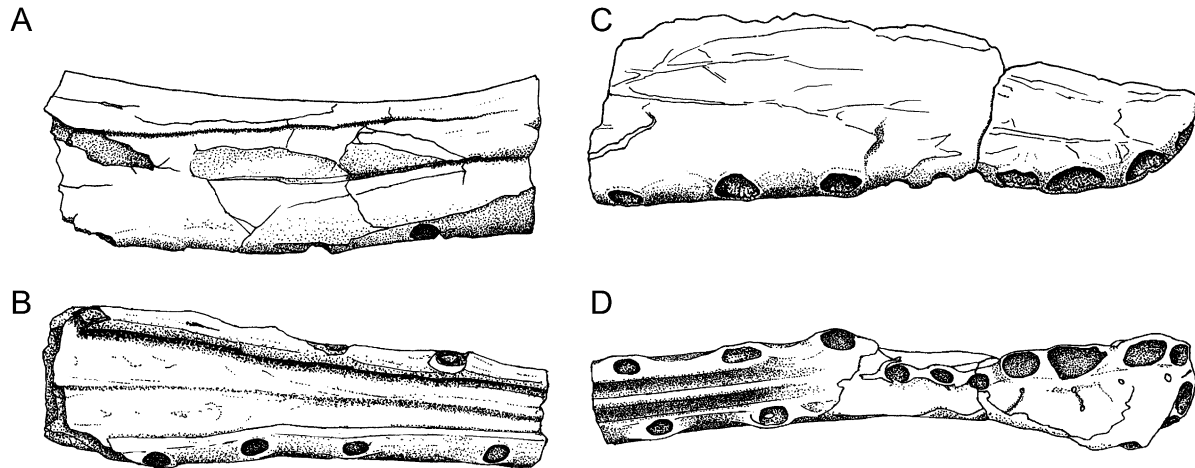


Fig. 6. Drawings of the holotype rostrum of *Caulkicephalus trimicrodon* gen. et sp. nov., IWCMS 2002.189.1, 2, 4 in right lateral view (A, C) and palatal view (B, D).

of wing-phalanx ?2 (IWCMS 2002.233; Fig. 5B); fragment of shaft of wing-phalanx ?4 (IWCMS 2002.236) and an element possibly from the hind limb (IWCMS 2003.3; Fig. 5D).

Diagnosis. Ornithocheirid pterosaur in which the maxillopremaxillary suture descends slightly posteriorly; the fifth to seventh pair of dental alveoli are significantly smaller than pairs 1–4 and 8–10, and the palatal ridge extends no further anteriorly than dental alveoli 8 and 9. Uniquely for the Ornithocheiridae this taxon possesses both frontoparietal and maxillopremaxillary crests and these do not merge over the nasoantorbital fenestra or cranium.

5. Description

The holotype consists of three contiguous fragments of the rostrum (Fig. 3, Table 1). These three pieces fit together to form the anterior part of the rostrum and include parts of the premaxillae and maxillae extending posteriorly to a position that terminates just prior to the anterior margin of the nasoantorbital fenestra. The margin of the nasoantorbital fenestra is not preserved, but an arc of crushed bone suggests that the margin of this fenestra may have been close to the edge of the preserved section. A fourth bone fragment, an incomplete braincase, is presumed to belong to the same individual as the rostral material (see “Preservation” above).

5.1. Rostrum

The preserved part of the rostrum is 290 mm in length and is laterally compressed for most of its length,

though some of this may in part be exaggerated by slight compaction, as indicated by numerous small cracks. It is 30 mm wide at the second tooth pair, narrowing to 20 mm in width between tooth pairs 9–10. It then expands in width posteriorly until it reaches a breadth of 42 mm at tooth pair 14. The dorsal margin of the

Table 1

Selected measurements of *Caulkicephalus trimicrodon* gen. et sp. nov. from the Wessex Formation (Lower Cretaceous, Barremian) of the Isle of Wight

Skull elements
<i>Rostrum (three pieces combined)</i>
Width of palate at third tooth pair 30 mm
Width of palate at ninth tooth pair 24 mm
Width of palate at fourteenth tooth pair 38 mm
Estimated length of rostrum from anterior tip to margin of nasoantorbital fenestra 300 mm
Height of rostrum at lowest point between maxillo/premaxillary crest and cranium 36 mm
Postcranial elements
<i>Posterior segment of proximal end of first phalanx of left wing IWCMS 2002.237 (as preserved)</i>
Length of fragment 44 mm
Width 30 mm
Depth 19 mm
Compacta thickness 0.2–0.8 mm
<i>Portion of wing-phalanx 1 IWCMS 2002.234.1–4 (as preserved)</i>
Length 245 mm
Width 29 mm
Depth 14 mm
Compacta thickness 0.5–2.5 mm
<i>Distal portion of wing-phalanx ?2 IWCMS 2002.233 (as preserved)</i>
Length 64 mm
Width proximally 30 mm
Width distally 30 mm
Depth 15 mm
Compacta thickness 0.1–0.2 mm

rostrum descends towards the anterior tip of the jaw and, as is in other ornithocheirids, the section anterior to the fifth pair of dental alveoli is transversely expanded to accommodate the first four pairs of large fang-like teeth (Unwin, 2001).

A premaxillary crest is present, but it is damaged and much of its dorsal margin is missing. The crest does not extend to the anterior tip of the snout, but commences a short distance posterior to it, level with the third alveolar pair. Several small nutritive foramina are visible on both lateral margins of the rostrum. They are evenly distributed; otherwise the surface of the bone is smooth.

The posterior most fragment of the rostrum (IWCMS 2002.189.4) measures 126 mm in length and is tapered, widening from 23 mm anteriorly to 38 mm posteriorly. Ventrally, it comprises the palate and dental borders, and bears a medial palatal ridge along its entire length. The dorsal surface is arcuate as it rises both anteriorly towards the maxillopremaxillary crest and posteriorly towards the cranium. The maxillopremaxillary suture is well defined on the left side. It is straight and extends ventroposteriorly.

The anterior tip of the palate begins to curve upwards from a point just behind the second alveolus, at an angle that gradually increases to about 80° from the horizontal. The dorsal margin of the rostrum arcs ventrally to meet the ventral margin forming a rounded anterior tip. The posterior part of the palate is encrusted with a thin coating of pyrite approximately 0.25–0.5 mm thick, but the median palatal ridge is clearly seen despite the pyrite coating. This ridge is not very pronounced and is not visible in lateral view. It is present on the posterior portion of the palatal surface, but becomes less pronounced anteriorly and disappears completely between the eighth and ninth alveoli.

The gradual upturn of the palate towards the tip of the rostrum means that the first two pairs of tooth sockets point anteroventrally, while the remaining alveoli are orientated ventrolaterally in the alveolar margin and the posterior most alveoli point ventrally. The interalveolar areas are gently concave while the rims of the alveoli project beyond the palatal surface. The palatal surface bears several paired nutritive foramina between the first four pairs of alveoli. The two foramina in each pair are linked by a groove that is 5–6 mm long. There is a small pit just posterior to the first alveolus on the right side. Whether this is a pathological feature, a nutritive foramen, or recent damage is uncertain, but a similar, though medially located pit, is seen in the ornithocheirid *Coloborhynchus wadleighi* (Lee, 1994).

The dental alveoli vary greatly in size, but are all approximately oval, with the longest diameter orientated anteroposteriorly. The first pair are of slightly different sizes (Table 2), the left being only slightly larger than the right. The second pair is substantially larger than the first

pair, while the third pair, only preserved on the right side, is the largest in the entire dental series. The fourth pair, again only preserved on the right side, is substantially smaller than the third and similar in size to the first pair. There is very little space between consecutive alveoli in this part of the rostrum: the interalveolar area is 4 mm between alveoli 2 and 3, but less than half this distance between alveoli 1 and 2 and between alveoli 3 and 4.

The first four pairs of dental alveoli are followed by three smaller alveoli that, again, are only preserved on the right side of the rostrum. The fifth pair of alveoli are less than half the anteroposterior width of the third, while the sixth and seventh are of almost the same size and slightly smaller than the fifth (Table 2). The space between consecutive alveoli in this group is almost equivalent to the length of individual alveoli. Posterior to the seventh pair of alveoli there is a marked increase in size with the eighth to tenth pairs of similar dimensions and almost reaching the size of the first pair of alveoli. These alveoli are also widely spaced; on the right side alveoli 8 and 9 are separated by a gap equivalent to one and one-half alveoli while the gap between alveoli 9 and 10 on the right side is equivalent to two alveoli, that on the left slightly less. Toward the anterior end of the rostrum the left and right alveoli of each pair are approximately parallel to one another, but in the region of the ninth and tenth alveoli they become increasingly staggered, those on the left side lying slightly anterior to those on the right side.

The tips of replacement teeth are visible in the first and ninth alveoli on the right side. They are oval in cross section and pointed. Immediately posterior to the tenth alveolus the specimen is broken. The third part of the rostrum bears four alveoli on the left side and four on the right side (alveoli 11–14) but they are not arranged in pairs. These alveoli are elongate, the best preserved measuring 7 × 4 mm (Figs. 3, 6), and with a long axis sub-parallel to the dental border.

5.2. Referred braincase

The braincase (IWCMS 2002.189.3) consists of the frontals, parietals, the supraoccipital and possibly dorsal

Table 2
Maximum diameters of the first ten pairs of dental alveoli (in mm)

Tooth pair	Left	Right
1	11	10
2	14	14
3	—	15
4	—	11
5	—	6
6	—	5.5
7	—	5.5
8	—	9–10
9	—	9–10
10	—	9–10

portions of the prootics, opisthotics and exoccipitals, all fused into a solid, largely uncrushed and undistorted box-like structure, in which all former bone contacts and sutures appear to be obliterated (Figs. 4A–D, 8). The ventral part of the braincase, composed of the basioccipital and parts of the prootics and opisthotics, is broken away and this fracture extends anteriorly through the upper part of the orbits. The outer margins of the braincase are eroded and the cranial crest is broken off at its base (see below).

In dorsal view the braincase is seen to expand laterally over the orbits, but then is strongly constricted posterior to this region before expanding again to form the occipital plate. The upper part of the inner wall of the orbits appears to have been ossified (possibly by the laterosphenoid).

The braincase bears evidence of a frontoparietal crest. The base of the crest begins anteriorly at a point between the orbits, and extends backwards along the midline, but is separated from the occipital plate by a small notch. The base of the crest seems to have been widest just behind the orbits and its orientation suggests that originally it extended posterodorsally. The left and right sides of the base of the crest are approximately parallel to each other, with some posterodorsally directed divergence, and the crest is 7 mm thick at its point of fracture. A little more posteroventrally the crest is only 2 mm thick. Thus it seems likely that the crest was relatively tall, narrow and posterodorsally directed, as in *Pteranodon* and *Ludodactylus* (Frey et al., 2003).

The occipital plate has thin margins and now has a relatively tall, narrow, pentangular outline, but may have been much broader when complete. The plate is slightly dished, concave both transversely and vertically and has a low, vertically orientated median ridge. Ventrally the plate is broken away along the dorsal margin of the foramen magnum.

5.3. Quadrate

The left quadrate (IWCMS 2003.2) has a slightly crushed dorsal region, but is well preserved ventrally. The articular surface is 18 mm wide (Fig. 4E).

5.4. Postcranial skeleton

An incomplete wing phalanx 1 consists of four contiguous pieces (IWCMS 2002.234.1–4; Fig. 5C, Table 1). The bone is slightly dorsoventrally crushed, but its original cross section was clearly an elongate oval. Pyrite and mudstone completely fill the large lumen of the bone and no trabeculae are visible on any of the broken surfaces. The compacta is generally thin (0.5 mm in places), but thickens to as much as 2.5 mm at

one end of the oval, which probably corresponds to the anterior margin of the bone as observed in more complete examples of ornithocheirids. The surface of the bone is remarkably smooth, but bears two small nutritive foramina that open on the better-preserved (probably ventral) side of the phalanx.

A short section of a large bone (ICWMS 2002.237) is identified as the posterior portion of the proximal end of the left wing-phalanx 1 (Fig. 5A). Both ends and one side are broken. The distal section reveals a loose network of very fine trabeculae, none of which completely crosses the lumen, just beneath the compacta. The thickness of the compacta varies from approximately 0.2–0.8 mm (Fig. 5E). The proximal region of the bone exhibits a dense spongiosa typical of the internal bone structure at an articulation. A small part of the articular surface is still preserved and bears a deep sulcus in which lie two pneumatic foramina. The preserved dorsal surface is flat.

The distal part of another wing-phalanx (IWCMS 2002.233; Fig. 5B) is too narrow to represent wing-phalanx 1, and probably represents part of a wing-phalanx 2. The bone is slightly crushed and cannot be assigned to a particular wing. Its surface is rather fibrous and distally it has an unfinished appearance lacking the compacta and exposing the bony trabeculae. This may indicate that this particular part of the skeleton was still growing, though in the braincase a lack of clearly visible sutures suggests a nearly mature individual. It is difficult to determine the thickness of the compacta at the broken end, but it appears to be approximately 0.1–0.2 mm thick.

A piece of wing-phalanx (IWCMS 2002.236), possibly representing wing-phalanx 4, has a compacta ranging from 0.2 to 0.5 mm in thickness. Again, the thickest compacta are found in the vertices of the oval cross section. A few tiny trabeculae are visible immediately beneath one area of the compacta, but they do not span the entire width of the lumen. The smooth surface of the bone is marked by clusters of shallow, irregular pits ranging from 0.3 mm to approximately 2.0 mm in diameter, while the majority are around 0.8 mm. They may be a consequence of bioerosion or the diagenetic ingrowth of pyrite aggregates.

Two small pieces of compacta with an underlying trabecular mesh were also recovered. They are both from the thickened margin of a long bone, but do not fit with any other preserved parts of the skeleton. Their value lies in that they show the three-dimensional structure of trabeculae in pterosaur long bones. What appears to be a network of bars when viewed in a two-dimensional surface, such as a transverse break or a thin section, is actually a system of closely opposed tubes running parallel to the long axis of the bone. This ‘tubular’ system is located between the compacta and the open lumen.

6. Relationships to other pterosaurs

Assignment of *Caulkicephalus* to Ornithocheiridae is supported by several synapomorphies including well-established diagnostic features of the rostrum and dentition (Bakhurina and Unwin, 1995; Unwin, 1995, 2001, 2002, 2003). As in other ornithocheirids, the anterior end of the rostrum of *Caulkicephalus* is transversely expanded, narrowest in the region of the fifth tooth pair and widens again posteriorly. The size distribution in the dentition shows a distinctive double peak, with the largest teeth occurring at position three and around position nine, and the smallest at position five. *Caulkicephalus* also exhibits several characters that appear to be restricted to ornithocheiroids (*Istiodactylus* + (Ornithocheiridae + Pteranodontia)). These include the presence of a low, bony sagittal crest with a smooth dorsal margin on the rostrum and a narrow, laterally compressed, posterodorsally directed, frontoparietal sagittal crest (though not certainly a synapomorphy of the Ornithocheiroidea; the crests of genera included within Ornithocheiroidea differ structurally from crests encountered in Azhdarchoidea) (NB: Unwin, 2003 lists “tall, narrow frontal crest” as a synapomorphy of Pteranodontia, though this feature was reported by Frey et al., 2003 for the ornithocheirid *Ludodactylus*. This feature may be synapomorphic for the Euornithocheira but was secondarily lost in some genera).

Caulkicephalus differs from *Istiodactylus*, the best known Isle of Wight pterosaur (Howse et al., 2001), which has a dorsoventrally compressed rostrum that superficially resembles a duck's beak and has labiolingually compressed, triangular teeth (Hooley, 1913; Howse et al., 2001). *Istiodactylus* is clearly distinct from *Caulkicephalus*, as are the edentulous pteranodontians (Pteranodontidae + *Nyctosaurus*) from the Upper Cretaceous of North and South America (Wellnhofer, 1991).

The ornithocheirid and ornithocheiroid characters cited above also show that *Caulkicephalus* cannot be assigned to any of the other three major pterodactyloid clades: Dsungaripteroidea (Germanodactylidae + Dsungaripteridae), Azhdarchoidea (*Tapejara* + (*Tupuxuara* + Azhdarchidae)) and Ctenochasmatoidea (*Cycnorhamphus* + (*Pterodactylus* + Lonchodectidae + Ctenochasmataidae). Dsungaripteroids have edentulous jaw tips and short, squat teeth in swollen alveoli that are largest toward the caudal end of the tooth row while azhdarchoids are toothless. Generally, ctenochasmatooids have relatively large numbers of teeth of sub-equal size but, in one case, *Cearadactylus*, the dentition is similar to that of ornithocheirids (Unwin, 2002). However, it is unlikely that this taxon and *Caulkicephalus* share a close relationship because *Cearadactylus* has a very distinctive step in the ventral profile of the rostrum (Leonardi and

Borgomanero, 1985), and the rostrum has a low lateral profile anteriorly, unlike that of *Caulkicephalus*, in which the rostrum is as deep as it is wide. *Cearadactylus* also lacks several key ornithocheiroid apomorphies, but shares a number of characters in common with ctenochasmatooids (see Unwin, 2002, for full discussion).

6.1. Comparison with other ornithocheirids

Several taxa are currently included within the Ornithocheiridae, though the validity of some remains in doubt. Unwin (2001, 2003), in a systematic revision of the Ornithocheiridae, included the genera *Anhanguera*, *Brasileodactylus*, *Coloborhynchus*, *Haopterus* and *Ornithocheirus*. Frey et al. (2003) considered *Anhanguera* to be a possible junior synonym of *Coloborhynchus* (see also Unwin, 2001, 2002) and proposed a new genus, *Ludodactylus*, to accommodate an ornithocheirid from the Aptian Crato Formation of Brazil that lacks a premaxillary crest, but possesses a pteranodontid-like parietal crest. Frey and Martill (1994) also consider *Arthurodactylus* from the Crato Formation (Lower Cretaceous, Aptian) of Brazil to belong within the Ornithocheiridae, an assignment tentatively supported by Unwin (2003), but this taxon is known only from postcranial remains. Here comparisons are made with those taxa in which the skull, or at least the rostrum, is preserved (Fig. 7).

Ornithocheirus, known from the Santana Formation of Brazil (Wellnhofer, 1987; Fastnacht, 2001) and the Cambridge Greensand of England (Unwin, 2001) is distinguished from all other ornithocheirids by the vertical orientation of even the anteriormost teeth, the absence of any anterior upcurving of the palate and the development of a large sagittal premaxillary crest, with a flat anterior face, that is situated on the anterior tip of the rostrum (Wellnhofer, 1987; Unwin, 2001). Not one of these characters is present in the new pterosaur material from Yaverland and it cannot be assigned to this taxon. All other ornithocheirids in which the rostrum is preserved, including *Caulkicephalus*, show some degree of upcurving of the palate anteriorly, and an anteroventral orientation of at least the first two pairs of teeth.

Haopterus, from the Yixian Formation of Liaoning Province, China (Wang and Lü, 2001), appears to be distinct from *Caulkicephalus* because in the former tooth pairs 5–7 show a marked increase in size (Wang and Lü, 2001), whereas in the latter they are subequal in size. In addition, the gaps between tooth positions are distinctly greater in *Haopterus*, and this ornithocheirid also lacks a sagittal rostral crest or frontoparietal crest (Wang and Lü, 2001), although this could be attributed to sexual dimorphism (Bennett, 1992) or the relative immaturity of the single known specimen of *Haopterus gracilis* compared to the single known example of *Caulkicephalus trimicrodon*.

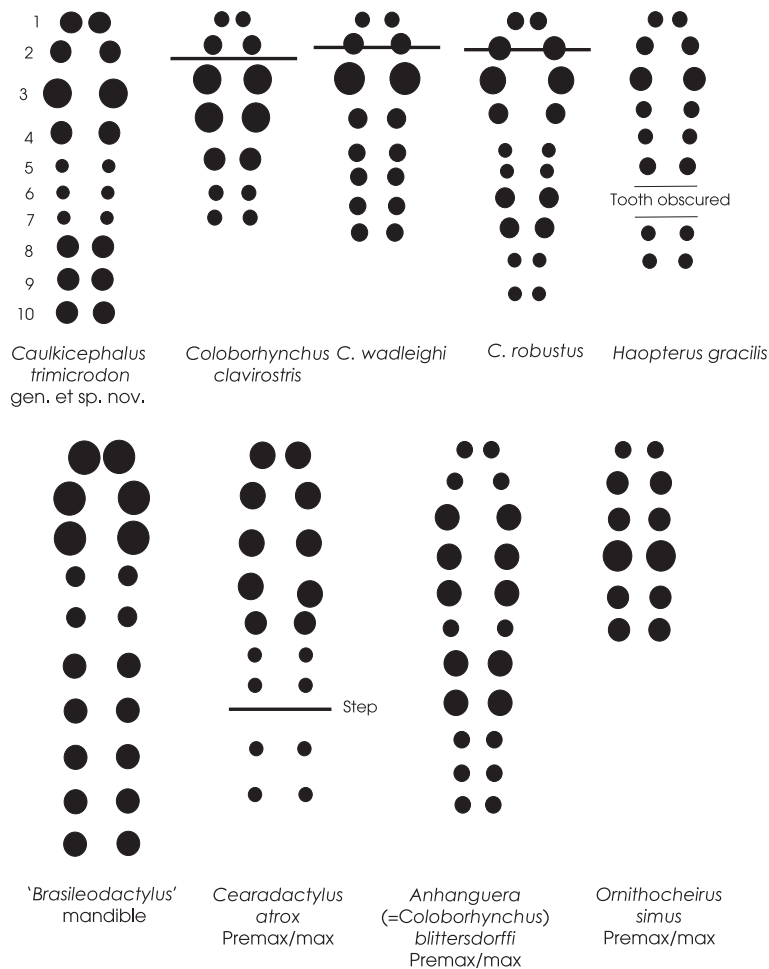


Fig. 7. Dental alveolar morphologies of pterosaurs. These diagrams are schematic and aim to show the distribution of large, medium-sized and small teeth in each taxon. Horizontal lines indicate points of upward flexure of the palatal surface. Data taken mainly from Kellner and Tomida (2000); Fastnacht (2001); Unwin (2001) and Wang and Lü (2001).

Ludodactylus, from the Crato Limestone Formation of Brazil (Frey et al., 2003) and the Yaverland pterosaur share one unique character in common when compared with other ornithocheirids, namely the presence of a narrow, posterodorsally directed frontoparietal crest, though quite how tall it was in *Caulkicephalus* cannot be established. This structure is absent in some ornithocheirids (*Istiodactylus*) or not known, but present in the pteranodontians *Pteranodon* (Bennett, 2001) and *Nyctosaurus* (Bennett, 2003). Currently, character state optimisations do not support a single origin for this character; thus it appears to have arisen independently in Ornithocheiridae and Pteranodontia (Unwin, 2003), but further exploration of relationships within Ornithocheiroidea is needed to establish this more firmly. *Ludodactylus* and *Caulkicephalus* also exhibit remarkably similar patterns of size distribution in the dentition, but are distinguished by the presence, in *Ludodactylus*, of a relatively large tooth pair at position seven, greater spacing between tooth positions 1–7, a less abrupt and more modest degree of upturn of the palate, the anterior

projection of the first three rather than just the first two pairs of teeth, a maxillo/premaxillary suture that meets the dorsal border of the nasoantorbital fenestra and the absence of a sagittal crest on the rostrum (Frey et al., 2003).

The Yaverland pterosaur exhibits numerous similarities to the nexus of species currently assigned to *Coloborhynchus* and *Anhanguera*. The degree of upturn of the palate is identical to that seen in many of these species, although an even greater degree of upturn is seen in some species of *Coloborhynchus* (e.g. Owen, 1874; Lee, 1994; Fastnacht, 2001). Patterns of tooth size, spacing and orientation (Kellner and Tomida, 2000; Fastnacht, 2001) are also remarkably similar, although only in *Caulkicephalus* is tooth pair 7 of similar size to 5 and 6. *Caulkicephalus* is also distinguished by the discontinuation, anteriorly, of the median ridge on the palate, in contrast to species of *Coloborhynchus*/*Anhanguera* where typically it extends forward to at least the fourth tooth pair (Wellnhofer, 1987, 1991; Lee, 1994; Unwin, 2001). Unlike *Caulkicephalus*, where the

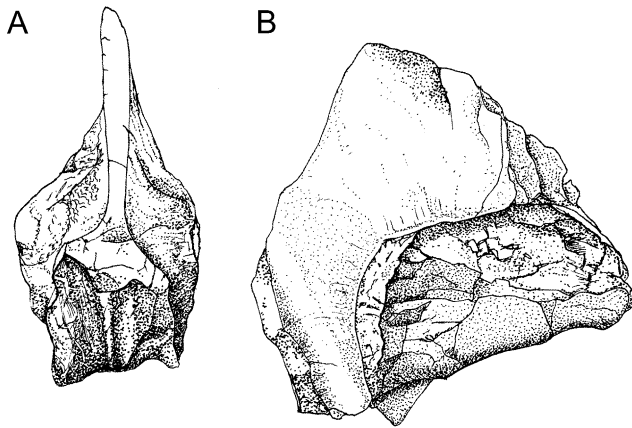


Fig. 8. Drawings of the braincase referred to *Caulkicephalus*, IWCMS 2002.189.3, in caudal view (A) and in right lateral view (B).

maxillo/premaxillary suture trends toward the ventral margin of the nasoantorbital fenestra, in *Coloborhynchus* and *Anhanguera* this suture meets the dorsal border of the fenestra (e.g., Kellner and Tomida, 2000).

6.2. Summary

The new Yaverland pterosaur is undoubtedly an ornithocheirid, and similar to several species that belong to this family. However, it lacks distinguishing features of all genera currently included in this taxon and represented by cranial material, but exhibits a number of characters (maxillo/premaxillary suture descends slightly posteriorly, fifth to seventh pair of dental alveoli of similar size and significantly smaller than pairs one to four; palatal ridge extends no further anteriorly than dental alveoli 8 and 9; and presence of fronto/parietal and maxillo/premaxillary crests that do not merge over the nasoantorbital fenestra or cranium) that are not found in any other ornithocheirid. Consequently, we assign this taxon to a new genus and species of the Ornithocheiridae.

In addition to their uncertain taxonomic status, several taxa currently assigned to Ornithocheiridae, including *Caulkicephalus*, are too poorly known for their interrelationships to be resolved with any certainty. Moreover, few, if any, of the character states discussed above that occur in more than one genus show clear cut patterns of distribution or some degree of correlation. Clearly, more complete specimens and much work will be needed to disentangle the systematics of ornithocheirids.

7. Discussion

Previous findings (Martill et al., 1996) hinted at the presence of ornithocheirids in the Wessex Formation (Barremian), and this is now confirmed by the discovery of *C. trimicrodon*. Ornithocheirids have already been widely reported from the Lower Cretaceous of Western

Europe (Unwin et al., 2000, table 1; Unwin, 2001), although not with any certainty from the Barremian. This new record fills that gap and further encourages the idea that ornithocheirids were present in Western Europe throughout the Early Cretaceous.

An unusual feature of the material described here is its discovery in a plant bed deposited within a fluvial continental setting. Most ornithocheirids have been recovered from marginal or fully marine sediments (Unwin, 2001, table 1) and they are thought to have had a life style broadly similar to that of some modern ocean-going birds such as the Albatross and Frigate Bird. This record of an ornithocheirid preserved in a continental environment adds to other recent reports of these pterosaurs from similar settings (Unwin et al., 2000; Unwin, 2001), although it is still not clear if these represent accidental occurrences or indications that some ornithocheirids lived in terrestrial environments.

Only one other pterosaur, *Istiodactylus latidens*, has so far been reported from the Isle of Wight and, at present, is only certainly known from the Vectis Formation (Martill and Naish, 2001). Recently, Mr. S. Sweetman recovered a small, laterally compressed, triangular tooth crown with thin enamel from a plant debris bed within the Wessex Formation that may be referable to *Istiodactylus*. If this preliminary identification is verified it would suggest that species of *Caulkicephalus* and *Istiodactylus* may have been sympatric, which is reasonable in that the dentition of these taxa is markedly different and hints at quite distinct and specialised life styles.

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