



## On pterodactyloid diversity in the British Wealden (Lower Cretaceous) and a reappraisal of “*Palaeornis*” *cliftii* Mantell, 1844

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### ABSTRACT

Pterosaur remains from Wealden strata of southern England have largely been referred to the Ornithocheiroidea, with only a solitary controversial claim of a lonchodectid providing evidence of heightened diversity. A reappraisal of a historic Wealden specimen suggests that “*Palaeornis*” *cliftii* Mantell, 1844, an isolated humerus from the Hastings Beds Group of West Sussex, is not an ornithocheiroid as previously reported but instead confirms the presence of lonchodectid pterosaurs in the British Wealden. The diversity of British Wealden pterosaurs is heightened further by a recently-discovered pterosaur humerus from the Wealden Group of the Isle of Wight, providing the first record of azhdarchoid pterosaurs in the British Lower Cretaceous. This specimen is thought to represent a non-azhdarchoid neoazhdarchoid and, being from Barremian deposits, represents the earliest known occurrence of such a pterosaur.

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### 1. Introduction

Lower Cretaceous pterosaur remains have been known from British Wealden strata since 1827 when Gideon Mantell reported the discovery of supposed ‘bones of birds’ in Tilgate Forest, Sussex (Martill, 2008). Pterosaur remains have continued to be recovered from these deposits (now part of the Weald Sub-basin, one of the two major divisions the British Wealden: see Radley, 2006a,b) and have since also been found in Wealden strata of the Isle of Wight (forming, along with Wealden sediments in Dorset, the Wessex Sub-basin; Figs. 1 and 2). The vast majority of British Wealden pterosaur material has been referred to the Ornithocheiridae (e.g. Howse et al., 2001; Steel et al., 2005) or Istiodactylidae (Hooley, 1913; Howse et al., 2001), and these groups are both found within the large pterosaur clade Ornithocheiroidea (Unwin 2003). Only a possible lonchodectid jaw provides a record of non-ornithocheiroid pterosaurs in the same strata (Unwin et al., 2000; Unwin, 2001), but this claim is mildly controversial. Kuhn (1967), Kellner (2003, 2004), Wang et al. (2005, 2008) and Andres and Ji (2008) suggest that lonchodectids lie within the Ornithocheiridae [=Anhangueridae]. If so, the British Wealden pterosaur assemblage has, to date, been represented exclusively by ornithocheiroids. Such

diversity is comparatively impoverished when contrasted against other pterosaur sites that, in Europe, yield dsungaripterids and ctenochasmatooids along with ornithocheirids and istiodactylids (Jursack and Pops, 1984; Benton et al., 1997; Sánchez-Hernández et al., 2007). Contemporaneous South American and Chinese deposits provide even higher diversity with tapejarids, thalassodromids, chaoyangopterids, dsungaripteroids, lonchodectids, ctenochasmatooids and ornithocheiroids found across several sites (e.g. Martill et al., 2000; Wang and Zhou, 2006; Lü et al., 2006; Unwin and Martill, 2007).

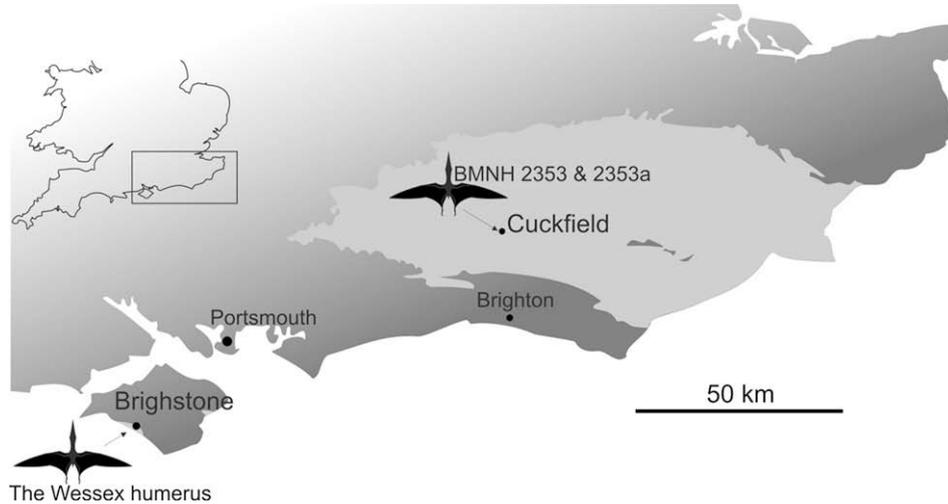
Here, new evidence is presented that suggests British Wealden pterosaur diversity is not as low as currently thought. A reappraisal of one of the first pterosaur fossils found in England, BMNH 2353 and 2353a (“*Palaeornis*” *cliftii* Mantell, 1844) suggests that its significance as strong evidence of non-ornithocheiroid Wealden pterosaurs has been overlooked by pterosaur workers for over 180 years. Adding further diversity to the English Wealden pterosaur assemblage is a new specimen from the Wessex Formation of the Isle of Wight, here suggested to represent a neoazhdarchoid azhdarchoid. This latter discovery marks the first reported occurrence of this group in Lower Cretaceous deposits of Europe.

### 2. Reappraisal of BMNH 2353 and 2353a, “*Palaeornis cliftii*”

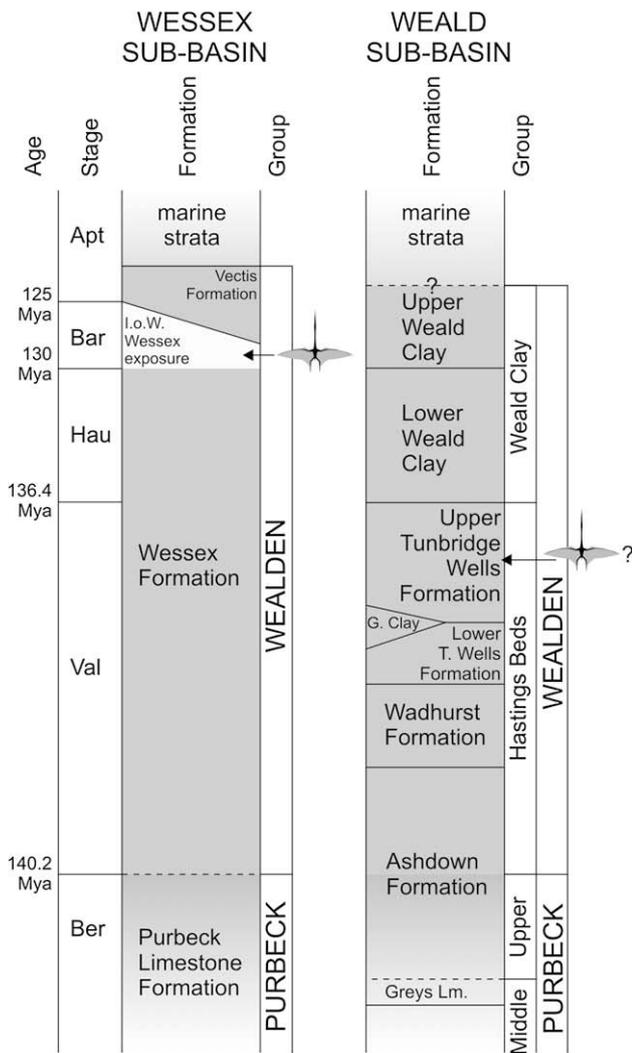
BMNH 2353 and 2353a (Figs. 3 and 4) represent one of the earliest discoveries of pterosaur material in England. The

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**Fig. 1.** Distribution of Wealden strata across southeast England (grey shading), and approximate localities of the pterosaur specimens described here. Wealden deposits of Dorset omitted for clarity.

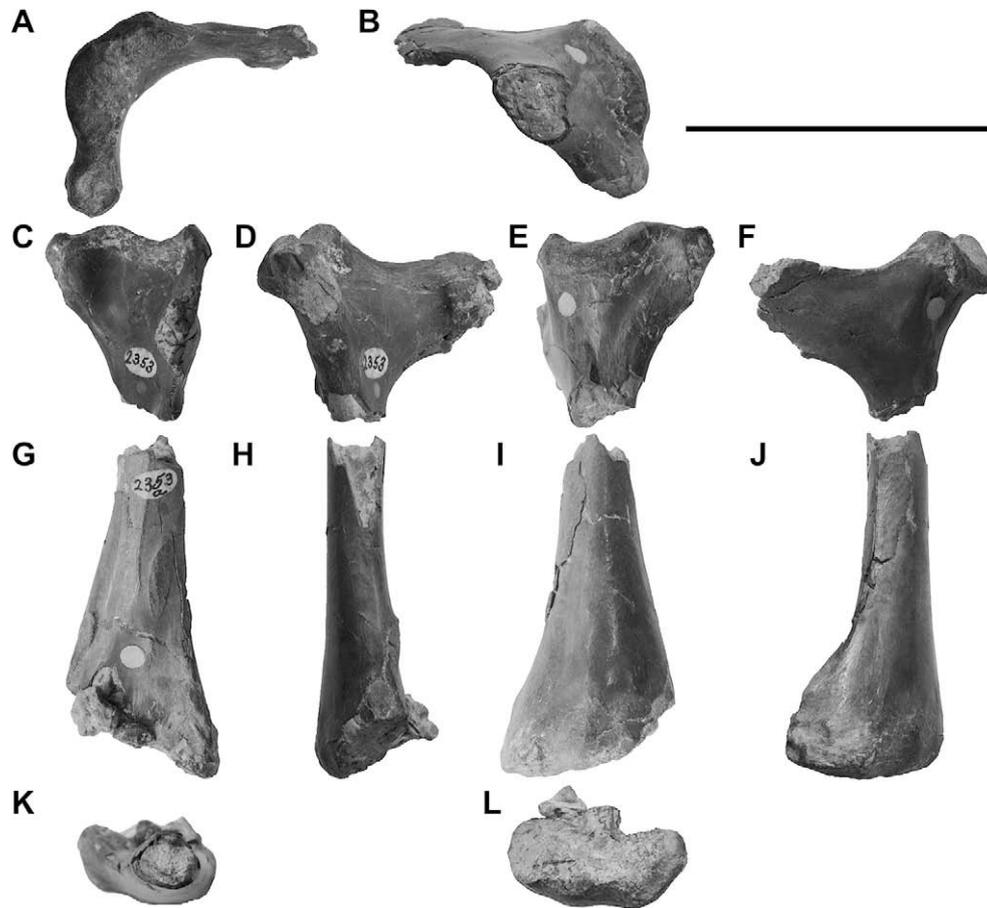


**Fig. 2.** Simplified stratigraphy of the Weald and Wessex Sub-basins based on Radley (2006a). Pterosaur silhouettes show approximate location of their source strata. Apt, Aptian; Bar, Barremian; Hau, Hauterivian; Val, Valanginian; Ber, Berriasian.

specimens, proximal (BMNH 2353, Figs. 3A–F, 4A–F) and distal (BMNH 2353a; Figs. 3G–L, 4G–L) portions of a left humerus, were the focus of a long-running controversy between Gideon Mantell and Sir Richard Owen over the presence of birds in the British Wealden during the 1800s and subjected to numerous nomenclatural revisions throughout the nineteenth century. Subsequently, the specimens have a long and somewhat complex history (Martill, 2008).

Although now recognised as components of the same bone, the relationship between BMNH 2353 and 2353a was not always appreciated. BMNH 2353 was first mentioned and figured by Mantell in his 1827 work, *Illustrations of the Geology of Sussex* (pl. VIII, Fig. 11), and was stated to come from Tilgate Forest, a locality that he placed in the ‘Hastings Sands and Clays’. This unit is now recognised as the Valanginian Hastings Beds Group of northeast West Sussex and it is likely that the specimen came from the Upper Tunbridge Wells Formation along with many famous early dinosaur discoveries (Figs. 1 and 2; Benton and Spencer, 1995; Radley, 2006a). Mantell’s first attempt at identifying BMNH 2353 was also his most insightful, suggesting it was analogous with the proximal region of a supposed bird bone from the Stonesfield Slate (Mantell, 1827). Because this alleged bird material was actually a non-pterodactyloid pterosaur humerus, Mantell had correctly – albeit unknowingly – identified BMNH 2353 as a pterosaur arm bone long before other workers. The British Museum acquired this piece and the as-yet-unpublished distal portion in 1836 when buying a part of Mantell’s collection (Lydekker, 1888). Mantell provided a new interpretation of BMNH 2353 in 1837 with his suggestion that it represented the head of a bird tibia. In the same publication, he figured BMNH 2353a for the first time and interpreted it as the distal tarsometatarsus of an *Ardea*-like bird (Mantell, 1837). Mantell’s opinion that his specimens were two separate avian bones was supported, and perhaps even suggested, by Georges Cuvier and Richard Owen (Mantell, 1834, 1837), both of whom are mentioned and directly quoted in Mantell’s work. In 1844, Mantell named BMNH 2353a *Palaeornis cliftii*, the specific name honouring the man responsible for providing Mantell with the iguana material integral to his work on *Iguanodon*, William Clift (Mantell, 1844).

The avian interpretation of “*Palaeornis*” *cliftii* was not to last, however. Through Mantell, Owen had suggested that several ‘bird bones’ from Tilgate Forest bore resemblance to those of pterosaurs (Mantell, 1837, 1844) and, in 1845, Owen not only demonstrated that BMNH 2353 and 2353a were extremities of the same humerus,



**Fig. 3.** BMNH 2353 and 2353a; Lonchodectidae indet. A, BMNH 2353, proximal view; B, distal; C, anterior; D, ventral; E, posterior; F, dorsal; G, BMNH 2353a, anterior; H, ventral; I, posterior; J, dorsal; K, proximal; L, distal. Scale bar represents 50 mm.

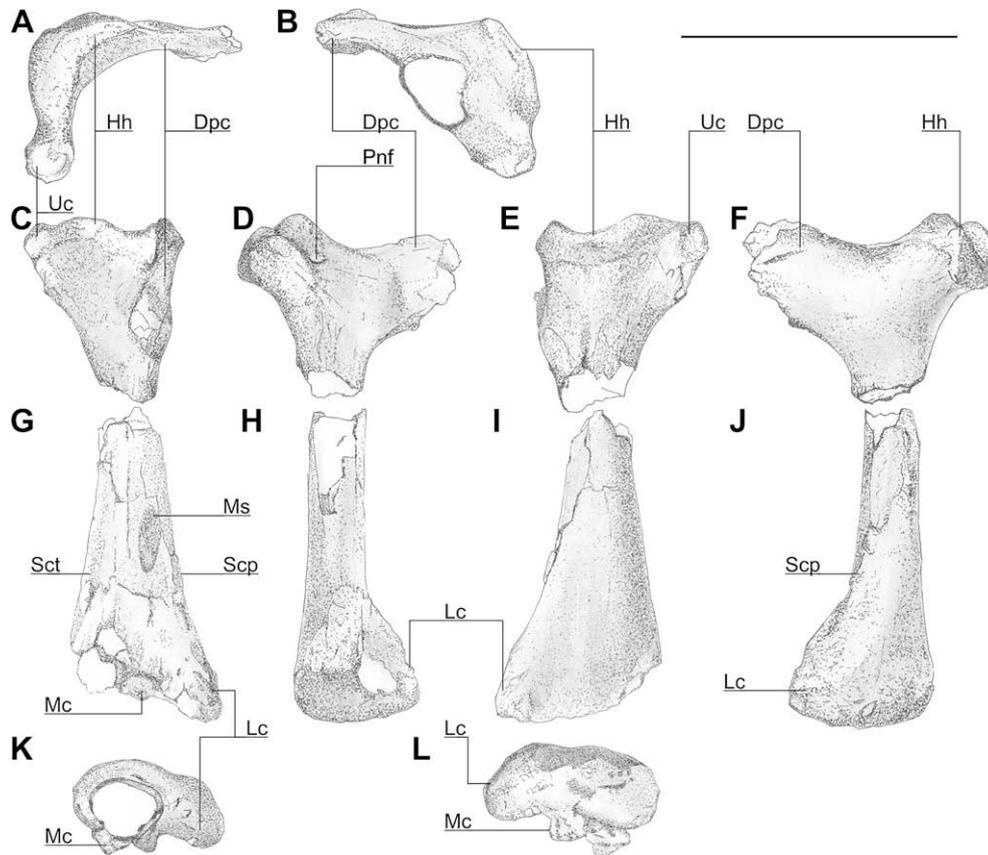
but that they were also pterosaurian (Owen, 1845). Mantell published a direct response to Owen in the following year (Mantell, 1846a) and, while agreeing that both pieces were from the same bone (Mantell claimed to have thought this before Owen suggested that each fragment represented a different bone), he did not agree that the bones were necessarily pterosaurian. Instead, Mantell repeatedly suggested that its identity remained mysterious (Mantell, 1846a,b, 1847) and that they could not be identified beyond belonging to ‘an animal capable of flight’ (Mantell, 1846b, p. 105). Strangely, Mantell stated in 1846 that he found the “*Palaeornis*” material twelve years prior to 1846 (i.e. 1834), but he stated in 1837 that the bones were first figured in 1827. Mantell appears to have held his views that BMNH 2353 and 2353a were avian until at least 1848 when he mentioned the otherwise-undocumented taxon “*Palaeornithis*” (Mantell, 1848): whether this name refers to “*Palaeornis*” is ambiguous, but the similarities between this name and “*Palaeornis*” are notable. The fact that Bronn (1848) found “*Palaeornis*” to be preoccupied in the same year suggests that Mantell could have been aware of the unavailability of the original generic name and wanted a suitably similar replacement. One year before his death, Mantell finally - and apparently begrudgingly - conceded that “*Palaeornis*” was pterosaurian, albeit a pterosaur specimen that “unquestionably differs from the arm-bone of any flying reptile hitherto observed” (Mantell, 1851, p. 191).

Even after the pterosaurian affinities of BMNH 2353 and 2353a were accepted, its nomenclature was subjected to further revisions. In his *Index Palaeontologicus*, Bronn (1848) noted that the name “*Palaeornis*” was preoccupied by the psittaciform *Palaeornis Vigors*,

1825 and placed the specimen in *Pterodactylus Clifti* (note the alternative spelling of the specific name), a binomial also used by Morris (1854) and Jukes (1862). When BMNH 2353 and 2353a were first discussed by Owen in 1845, he refrained from giving either specimen a name, but he apparently changed his mind by 1859 when, agreeing that the specimens belonged in *Pterodactylus*, he gave the specimens a new specific name, *sylvestris* (Owen, 1859). Not more than two years later, Owen created yet another specific name for BMNH 2353 and 2353a, *Pterodactylus ornis* (Owen, 1861). That Owen named the same ‘Wealden pterodactyle’ twice is in little doubt as both his 1859 and 1861 publications reference his same 1845 paper on the specimens. Later, Lydekker (1888) and Woodward and Sherborn (1890) tentatively placed BMNH 2353 and 2353a in *Ornithochirus*(?) [sic] rather than *Pterodactylus*. Lydekker (1888) was also the first to publish the specimen numbers, BMNH 2353 and 2353a. Newton (1888) was more confident than Lydekker in placing BMNH 2353 and 2353a in *Ornithocheirus*, dropping the question mark after the generic name to create *Ornithocheirus Clifti*. Zittel (1890) was the last author to cite the specimen as “*Palaeornis*”, and the specimen has since been referred to as *Ornithocheirus Clifti* or *Ornithocheirus clifti* (e.g. Hooley, 1914; Plieninger, 1929; Kuhn, 1967; Wellnhofer, 1978).

### 2.1. Systematic palaeontology

PTEROSAURIA Kaup, 1834  
 PTERODACTYLOIDEA Plieninger, 1901  
 LOPHOCRATIA Unwin, 2003



**Fig. 4.** Interpretive drawings of BMNH 2353 and 2353a; Lonchodectidae indet. A, BMNH 2353, proximal view; B, distal; C, anterior; D, ventral; E, posterior; F, dorsal; G, BMNH 2353a, anterior; H, ventral; I, posterior; J, dorsal; K, proximal; L, distal. Dpc, deltopectoral crest; Hh, humeral head; Lc, lateral condyle; Ms, muscle scar; Pnf, pneumatic foramen; Scp, supracondylar process; Sct, supracondylar tubercle; Uc, ulnar crest. Scale bar represents 50 mm.

#### Lonchodectidae Hooley, 1914

“Palaeornis” *cliftii* Mantell, 1844, nomen dubium

- 1827 Bird bone Mantell, p. 82; pl. viii.  
 1837 “Bone of Wader”, “Tibia?” Mantell, pl. xiii.  
 1844 *Palaeornis cliftii* Mantell p. 806.  
 1845 “Pterosaur bones” Owen, pp. 99–100.  
 1848 *Pterodactylus Clifti* Bronn, p. 871.  
 1854 *Pterodactylus Clifti* Morris, p. 353.  
 1859 *Pterodactylus sylvestris* Owen, pp. 15–16.  
 1861 *Pterodactylus ornis* Owen, p. 17.  
 1862 *Pterodactylus Cliftii* Jukes, p. 606.  
 1888 *Ornithochirus* (?) *clifti* Lydekker, p. 25.  
 1888 *Ornithocheirus Clifti* Newton, p. 526.  
 1890 *Ornithocheirus* (?) *clifti* Woodward and Sherborn, p. 254.  
 1890 *Palaeornis Clifti* Zittel, p. 797.  
 1914 *Ornithocheirus clifti* Hooley, p. 539.  
 1929 *Pterodactylus sylvestris* Plieninger.  
 1967 *Ornithocheirus* sp. Kuhn, pp. 42, 46.  
 1978 *Ornithocheirus clifti*, Wellnhofer, p. 58.

**Material.** BMNH 2353 and 2353a; proximal and distal components of an almost complete left humerus.

**Locality and stratigraphy.** From the Lower Cretaceous (Valanginian) Hastings Beds Group of the Weald Sub-basin (probably from the Upper Tunbridge Wells Formation), near Cuckfield, West Sussex, southeast England (Figs. 1 and 2).

**Preservation.** BMNH 2353 and 2353a are well preserved with no crushing or distortion. Both specimens are largely complete,

although the articular condyles of BMNH 2353a are missing. The two components do not articulate properly, suggesting that some of the diaphysis is missing between the two separate elements. However, the similar diaphyseal diameters at the broken margins of the two specimens suggests that only a small length of bone is missing. The compacta is worn or has broken away at some extremities and particularly so along the ventral surface of BMNH 2353a. These damaged areas reveal a sandy internal mould of the bone void. Several fine fractures extend along the dorsal diaphyseal surface towards the lateral condyle in BMNH 2353a.

**Description.** BMNH 2353 and 2353a (Figs. 3 and 4) form the proximal and distal portions, respectively, of a left humerus from a pterodactyloid pterosaur. They are separated by a transverse break across the diaphysis immediately adjacent to the distal margin of the deltopectoral crest, the sharpness of which suggests it occurred when the specimen was collected. The proximal and distal components do not articulate across the break but, with lengths of 32 mm (BMNH 2353) and 55 mm (BMMNH 2353a), the specimen is estimated length to have been c. 100 mm when complete. BMNH 2353 preserves the entire deltopectoral crest, humeral head and ulnar crest, while BMNH 2353a comprises most of the bone shaft and elements of the lateral condyle, but the medial condyle has almost-entirely broken away. The bone texture is smooth with few vascular canals and the extremities are well ossified, suggesting the bone originates from an osteologically mature individual (Bennett, 1993).

**BMNH 2353.** The proximal component has prominent ulnar and deltopectoral crests that form a rough ‘hatchet shape’ in anteroventral view. The humeral head has a saddle-shaped profile in

anterior view and wraps around onto the posterior humeral surface to create an expansive articular surface. On its posterior surface, this articulation is bracketed dorsally and ventrally by two well-defined muscle scars. The ventral scar is deeper than the dorsal and houses a small foramen. The anterior surface is smooth and concave and bears a deep foramen in its dorsal region. The ulnar crest is robust with a rounded ventral margin and several well-defined muscle scars on its posterior surface. The termination of this element is worn, but the remaining compacta has a rugose surface texture indicative of muscle attachment. Opposite the ulnar crest, the deltopectoral crest extends anteriorly with a slight proximal deflection relative to the humeral long axis. The lateral sides of the crest are parallel in dorsal view and, although the termination is incompletely preserved, the presence of the terminal expansion on the anteriormost ventral surface indicates that most of its length has been retained. The distal margin of the crest is slightly concave and muscle scars line its lateral margins: these scars depress the lateral margins to create a relatively bulbous crest midline. An additional muscle scar extends posteroproximally along the dorsal surface from the base of the deltopectoral crest to the humeral head. The break across the diaphysis reveals an approximately D-shaped diaphyseal cross-section with the anterior surface forming the longest and flattest margin. This surface has thin (0.5 mm) bone walls, while the curved posterior bone wall is thicker (1.4 mm) due to the presence of a tuberosity that extends across the fractured area.

**BMNH 2353a.** The diaphyseal cross-section of BMNH 2353a is more cylindrical than that of BMNH 2353 but the dorsal and ventral margins remain sub-angular. The anterior and posterior bone walls are thin at 0.9 mm but thicken to 1.2 mm along the dorsal surface. The diaphysis expands distally in a continuous but asymmetrical fashion with greater dorsal expansion than ventral. The 9 mm-long supracondylar process is positioned on the dorsal face of the diaphysis immediately before the considerably expanded lateral condyle. The anteroventral diaphyseal surface bears a supracondylar tubercle that wraps around the diaphysis distally. An additional 13 mm-long tubercle occurs on the anterior surface approximately half-way along the diaphysis.

The distal articular region of the humerus is incomplete with most of the lateral and medial condyles missing: the sharpness of the broken surfaces suggest that these portions were probably preserved but not collected. In distal profile, the bone assumes an oval cross-section and spongy bone can be seen in the exposed bone void. The distal end is strongly asymmetrical with the dorsal portion considerably more swollen than the ventral. The ventral-most extension of the lateral condyle is preserved and represents the only preserved portion of the elbow articulation.

## 2.2. On the affinities and status of “Palaeornis” cliftii

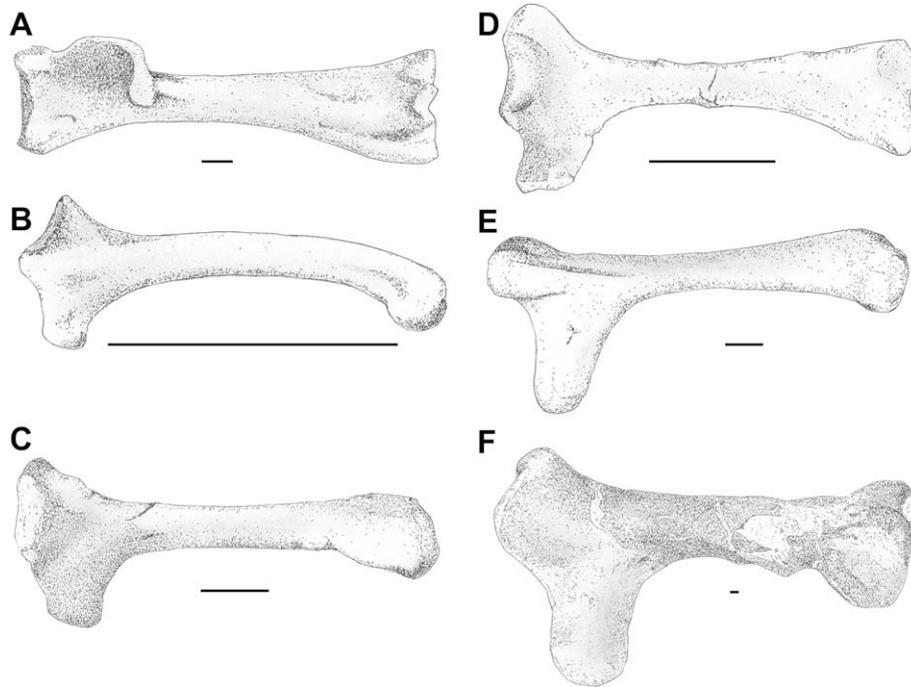
Owen's (1845) observations that BMNH 2353 and 2353a had pterosaurian affinities remain sound today with the bone wall thicknesses, straight humeral shaft and enlarged distal condyles comparing well with pterodactyloid humeri. The placement of the specimen by Lydekker (1888) and subsequent authors in *Ornithocheirus* is erroneous on two counts, however: not only is the *Ornithocheirus* holotype incomparable with BMNH 2353 and 2353a (Hookey, 1914), but the specimen compares extremely poorly against the derived morphology of ornithocheiroid humeri (Fig. 5A). These forms have distally displaced, warped deltopectoral crests that occupy 40 per cent of the humeral length and have proximal margins confluent with the humeral shaft, a diaphysis that expands in a continuous fashion distally when viewed in anterior or proximal view and a triangular distal profile (e.g. Hookey, 1914; Wellnhofer, 1985; Bennett, 1989, 2001). The deltopectoral

crest of BMNH 2353 is not distally displaced, has a proximal margin roughly perpendicular to the humeral long axis and does not curve ventrally across the anterior diaphyseal surface. Nor is there any indication that the distal end of BMNH 2353a would assume the triangular profile of ornithocheiroid humeri (Unwin, 2003): rather, it appears to have an oval or ‘D’ shaped cross section. Nyctosaurids bear a ‘hatchet’-shaped deltopectoral crest morphology that is distinct from those of other ornithocheiroids (Williston, 1902; Frey et al., 2006), but this is also quite unlike the condition seen in BMNH 2353. Thus, the morphologies of BMNH 2353 and 2353a are too distinct from those of ornithocheiroid humeri to warrant placement in this group. Given that the only other evidence of a non-ornithocheiroid pterosaur in Weald Sub-basin is a highly fragmentary jaw of controversial affinities (Unwin, 2001), a pterosaur bone from these deposits that is clearly removed from the Ornithocheiroidea is of some significance.

Ctenochasmatoid pterosaurs are known from older British Purbeck deposits (Howse and Milner, 1995) as well as deposits contemporary with the British Wealden in mainland Europe (Sánchez-Hernández et al., 2007). Thus, it would not be surprising to discover ctenochasmatoids in the English Wealden, but BMNH 2353 and 2353a are unlikely to represent these forms. Ctenochasmatoids have relatively small deltopectoral crests with distal margins confluent with the anterior margin of the diaphysis and often have bent humeral shafts (Fig. 5B; Wellnhofer, 1970; Fabre, 1976; Dong, 1982; Unwin, 2003). This morphology contrasts with those seen in the Sussex humerus, suggesting it does not have ctenochasmatoid affinities, either.

The morphology of BMNH 2353 and 2353a is more comparable with the humeral morphology of dsungaripteroids, lonchodectids and azhdarchoids (Fig. 5C–F). These forms share elongate, parallel-sided deltopectoral crests, oval-shaped distal ends and straight humeral shafts with BMNH 2353 and 2353a (e.g. Plieninger, 1901; Young, 1964, 1973; Lawson, 1975; Padian and Smith, 1992; Frey et al., 2003; Unwin, 2003). BMNH 2353 and 2353a cannot be placed in the Dsungaripteroidea, however: while BMNH 2353 shares a proximally-deflected deltopectoral crest with *Germanodactylus* (Wagner, 1851; Plieninger, 1901), its pneumatic foramen on the proximal anterior surface and the absence of a pneumatic foramen on its dorsal surface distinguish it from the humeri of *Dsungaripterus* and *Noriopterus* (Young, 1964; Lü et al., 2006). Moreover, BMNH 2353 and 2353a lack the thickened compacta reported to line dsungaripteroid long bones (Young, 1964; Bennett, 1989; Unwin and Heinrich, 1999; Unwin, 2003; Fastnacht, 2005). Note, however, that the distribution of thickened bone walls across dsungaripteroids is not entirely clear: it may not be present in all dsungaripteroids (Unwin, personal communication 2008) or, as demonstrated by the wing phalanges of *Dsungaripterus* (Young, 1964), continuous across the entire skeleton. Thus, while this character is of questionable use for diagnosing pterosaur bones, it acts in concert with the other discrepancies between the Wealden humerus and those of dsungaripteroids to suggest that BMNH 2353 and 2353a cannot be referred to the Dsungaripteroidea. Similarly, BMNH 2353 lacks the distally-displaced deltopectoral crest and swollen terminal expansion characteristic of azhdarchid humeri (Fig. 5F; Padian and Smith, 1992; Unwin and Lü, 1997), suggesting it is not a member of this group, either. Like some azhdarchids, however, BMNH 2353 does have a concave distal margin to its deltopectoral crest (Padian and Smith, 1992; Cai and Wei, 1994; Buffetaut et al., 2003).

The proximal humeral morphology seen in BMNH 2353 is better reflected in lonchodectids and non-azhdarchid azhdarchoids (Frey et al., 2003; Unwin, 2003; Lü and Ji, 2005; Unwin and Martill, 2007; Lü et al., 2008). These forms have large pneumatic foramina on their proximal anterior surfaces, but only lonchodectids have



**Fig. 5.** Pterodactyloid humeri compared. A, the ornithocheiroid *Coloborhynchus*; B, the ctenochasmatoid *Pterodactylus*; C, the lonchodectid *Lonchodectes*; D, the tapejarid *Tapejara*; E, the thalassodromid *Tupuxuara*; F, the azhdarchid *Quetzalcoatlus*. A, anterior view; B, C and F, dorsal; D, anteroventral; E, ventral. A and D, after Frey et al. (2003); B, after Wellnhofer (1978); C, after Seeley (1870); E, after Unwin (2003); F, after Wellnhofer (1991). Scale bars represent 20 mm.

deltopectoral crests with proximal margins confluent with those of the ulnar crests (Fig. 5C; Seeley, 1870; Unwin, 2003) like that of BMNH 2353. Chaoyangopterids and thalassodromids also appear to lack the atypically expanded lateral condyles seen in lonchodectids, tapejarids and BMNH 2353a (Unwin, 2003; Frey et al., 2003), suggesting the Wealden material cannot be referred to these groups. The proximity of the deltopectoral crest and swollen lateral condyle indicate that BMNH 2353 and 2353a represent a lonchodectid humerus. This adds credence to the lonchodectid identification of other Hastings Beds Group pterosaur material (Unwin et al., 2000; Unwin, 2001) and provides the first uncontroversial evidence of these pterosaurs in English Wealden strata.

### 2.3. Validity of “*Palaeornis*” *cliftii*

As noted by Mantell (1851), the morphology of BMNH 2353 and 2353a was undoubtedly distinct from other pterosaur humeri known at that time. Had this fact been seized by early pterosaur workers, they may have been justified in erecting a new taxon based on these remains. The considerably larger dataset available to modern pterosaur researchers reveals that while diagnostic at higher taxonomic levels, humeri are of little use in diagnosing pterosaur genera. Characteristics such as the continuity of the distal deltopectoral crest margin with the anterior diaphyseal face, diaphyseal slenderness and cross-sectional shape appear to reflect the age and size of individuals as well as their phylogenetic differences: (see Unwin, 2005, Fig. 7.7 for an example of ontogenetic variation in dsungaripteroid humeri). Thus, taxa based primarily on limb material (e.g. *Bennettazhia oregonensis* (Gilmore, 1928; Nesov, 1991) ‘*Santanadactylus spixi*’, ‘*Sanatandactylus pricei*’ (Wellnhofer, 1985)) have typically been considered *nomina dubia* by recent workers (Unwin, 2003). For this reason, the remains represented by BMNH 2353 and 2353a are considered inadequate to satisfactorily distinguish them from other lonchodectids. “*Palaeornis*” *cliftii* is therefore considered a *nomem dubium*.

### 3. New Wessex formation pterodactyloid

The lonchodectids reported from Wealden deposits of mainland Britain (Unwin et al., 2000) have yet to be unearthed from the Wealden Group of the Isle of Wight, rendering the pterosaur assemblage of this deposit dominated by ornithocheiroids. However, a new specimen, described here, clearly indicates that at least one other pterosaur group is present in these deposits. The specimen, a complete left humerus, currently resides in the collection of Mr Michael Green of Brighstone, Isle of Wight and, although describing a specimen without depositing the original in an appropriate institution is unorthodox, it is considered worthy of record here as it represents the first non-ornithocheiroid pterosaur from the Isle of Wight Wealden Group in over 130 years of collecting (see Howse et al., 2001). The specimen bears no autapomorphies that allow it to be used as the holotype of a new taxon and, in partial substitution for the original material, plaster replicas have been deposited in the Natural History Museum, London, Staatliches Museum für Naturkunde, Karlsruhe, and Dinosaur Isle Museum, Sandown, Isle of Wight (BMNH R 16497, SMNK PAL 9876, and IWCMS.2008.201, respectively). The casts were made from a GEDEO Siligum® silicon rubber moulding paste obtainable in most craft supply outlets and the original mould is kept in the School of Earth Sciences at the University of Portsmouth. All details of the specimen described below can be observed on these casts and access to the original specimen can be arranged through Mr. Michael Green. With no museum acquisition number for the specimen, the original material is referred to here as the ‘Wessex humerus’.

#### 3.1. Systematic palaeontology

PTEROSAURIA Kaup, 1834  
 PTERODACTYLOIDEA Plieninger, 1901  
 AZHDARCHOIDEA Nesov, 1984, *sensu* Unwin, 1992  
 NEOAZHDARCHIA Unwin, 2003

*Neoazhdarchia* indet.

**Material.** Isolated but complete left humerus (Figs. 6 and 7); plaster casts of original (SMNK PAL 9876, BMNH R16497, IWCMS.2008.201).

**Locality and stratigraphy.** The new specimen was discovered in situ in variegated mudstones of the Wessex Formation of the Isle of Wight Wealden Group (Figs. 1 and 2), on a foreshore exposure between Barnes High (NGR SZ 436805) and Hanover Point (NGR SZ 378837). Palynomorphs indicate that the Wessex Formation on this part of the coast is of Barremian age (Hughes and McDougall, 1990; Radley 2006b).

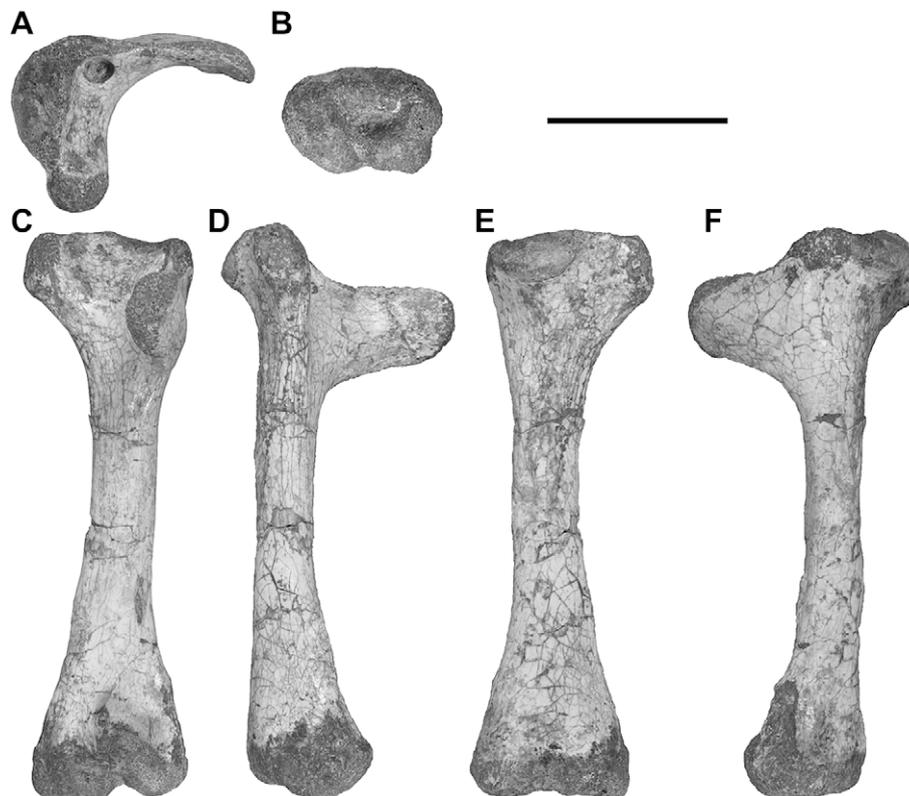
**Preservation.** The Wessex humerus was collected in three pieces and required only minor repair and washing to fully expose and reconstruct the bone. The bone is undistorted and excellently preserved in all three dimensions. The compacta displays numerous fine cracks and there is some slight pre-burial erosion of the bone margins proximally and distally. The bone void is filled with white calcite and brown limonite, which probably occurs as weathering product of original pyrite. The broken diaphysis of the specimen allowed observation of its cross-section prior to its reconstruction.

**Description.** The new specimen comprises a complete left humerus that has a maximum length of 157 mm. Both extremities have worn surfaces that reveal fine, densely-packed spongy bone tissues within the bone interior. The bone tissue has a smooth texture with little vascularisation, and the epiphyses are entirely ossified: the bone therefore meets the criteria proposed by Bennett (1993) to be considered osteologically mature.

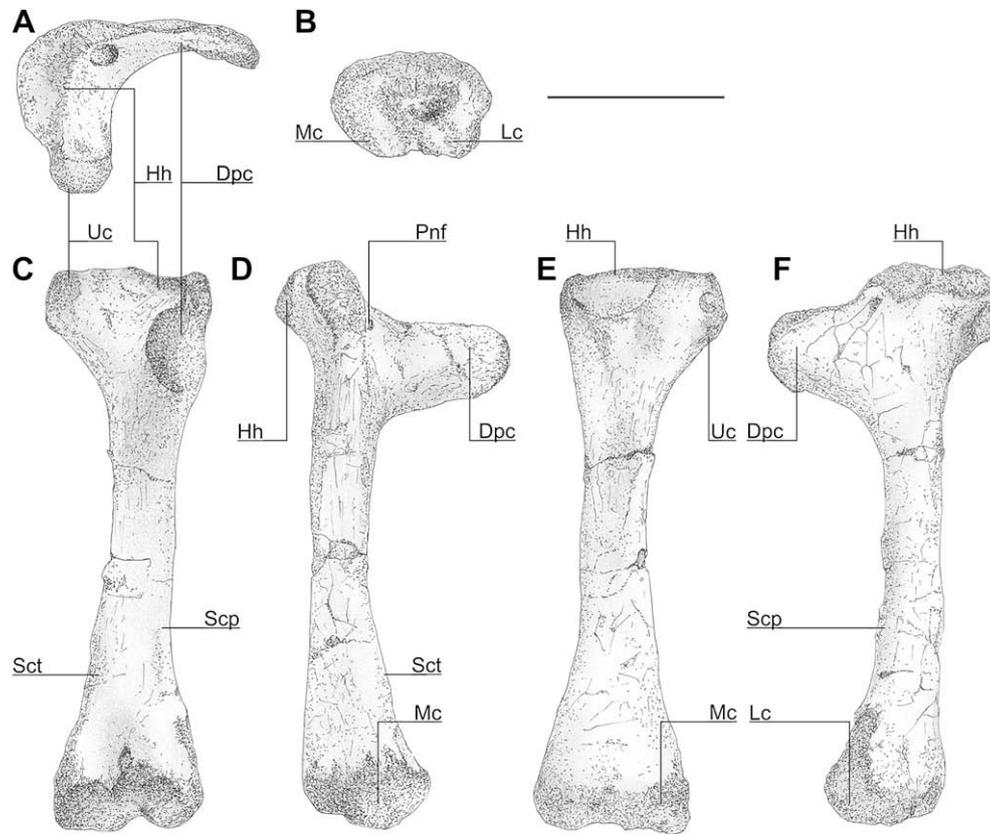
The humerus has a robust proximal region with a prominent humeral head and ulnar crest. The humeral head is broad and semi-circular in proximal view and saddle shaped in anterior view. The articular surface of this feature wraps around the humerus from the

proximal end onto the posterior face. The ulnar crest extends ventrally and terminates with a robust, squared profile when viewed anteriorly. A complex of muscle scars extend around the proximal humerus to divide the ulnar crest from the humeral head. Two foramina punctuate the dorsal and ventral scars of the anterior surface, with the dorsal foramen considerably larger than the ventral. The dorsal foramen appears to extend deeply into the bone shaft and probably had a pneumatic function. The deltopectoral crest is situated alongside this foramen and extends perpendicular to the humeral long axis. The lateral margins of the crest are sub-parallel in dorsal view but converge anteriorly in a rounded termination. A slight ventral curvature of the deltopectoral crest is exaggerated by the terminal expansion. Several broad muscle scars occur on the ventral surface of this crest, while the surface of the dorsal crest bears a proximal muscle scar with several more present in the region between the deltopectoral crest and humeral head.

The humeral shaft is straight and assumes a rounded 'D'-shaped cross-section almost immediately beyond the deltopectoral crest. A long muscle scar on the anterodorsal diaphyseal surface exaggerates the angularity of the dorsal margin, which bears thicker bone walls than the palmar, posterior and ventral surfaces. Bone wall thicknesses vary between 1–1.8 mm. The diaphysis extends with sub-parallel lateral margins for approximately one-third of the humeral length before expanding at the distal end. The base of this expansion is marked by the supracondylar process, a prominent, 13.5 mm long ridge of bone situated on the anterodorsal surface with an adjacent dorsal muscle scar. The supracondylar tubercle is situated almost directly opposite this on the anteroventral surface with a broad muscle scar extending posteriorly to cover much of the distal posteroventral face. Beyond the supracondylar process, the diaphysis expands to a broad, roughly symmetrical termination that has a deeply-sculpted anterior surface but comparatively smooth posterior. Both the lateral and medial condyles are warped



**Fig. 6.** The Wessex humerus, *Neoazhdarchia* indet. A, proximal view; B, distal; C, anterior; D, ventral; E, posterior; F, dorsal. Scale bar represents 50 mm.



**Fig. 7.** Interpretive drawings of the Wessex humerus, *Neozhdarchia* indet. A, proximal view; B, distal; C, anterior; D, ventral; E, posterior; F, dorsal. Abbreviations as in Fig. 4. Scale bar represents 50 mm.

so that their anterior extensions are ventral to their posterior, creating an anteroventrally-inclined intercondylar sulcus compared to the long axis of the bone. Epicondyles bracket these condyles to form the dorsalmost and ventralmost extensions of the distal region. The anterior surface has a deep concavity adjacent to the articular condyles that bears a shallow but poorly discernable pit in its ventral region. The presence of bone in this pit suggests it does not reflect the opening of a foramen and is more likely an attachment site for carpal and digit extensor muscles (see Bennett, 2003).

### 3.2. Affinities of the Wessex humerus

With a straight humeral shaft and developed medial condyle, the new specimen is quite unlike the humeri of basal pterosaurs (Wellnhofer, 1978; Unwin, 2003) and is better compared with those of pterodactyloids. Within the Pterodactyloidea, the Wessex humerus compares poorly with those of ornithocheiroids in lacking the distally placed, warped deltopectoral crest, robust diaphyses and triangular distal profile of these forms (Fig. 5A; Hooley, 1913; Wellnhofer, 1985; Bennett, 2001; Unwin, 2003). Similarly, the deltopectoral crest of the Wessex humerus is larger and erupts more prominently from the humeral shaft than those seen in ctenochasmatooids (Fig. 5B; Wellnhofer, 1970, 1978), and also lacks the curved humeral shaft of these forms. Thus, a ctenochasmatooid identity for the Wessex specimen is unlikely. Dsungaripteroid affinities are also doubtful: the presence of a pneumatic foramen on the proximal anterior surface, absence of a foramen on the corresponding dorsal surface, perpendicular extension of the deltopectoral crest and thin bone walls contrast with the humeral morphology of dsungaripteroid pterosaurs (Wagner, 1851;

Plieninger, 1901; Young, 1964; Bennett, 1994; Unwin, 2003; Lü et al., 2006), suggesting the new material cannot be placed in this group.

The perpendicular extension of the deltopectoral crest in the new specimen is comparable with that of lonchodectid and azhdarchoid humeri (Fig. 5C–F; Seeley, 1870; Plieninger, 1901; Young, 1964, 1973; Lawson, 1975; Padian and Smith, 1992; Frey et al., 2003; Unwin, 2003). The distal displacement of the deltopectoral crest in the new material distinguishes it from the humeri of lonchodectids, forms in which the proximal deltopectoral crest margin is approximately level with the corresponding margin of the ulnar crest (Seeley, 1870; Unwin, 2003; also see discussion of BMNH 2353 and 2353a above). The displacement of the deltopectoral crest in the Wessex material is not as pronounced as that seen in azhdarchoid humeri, however, and also lacks the relatively swollen terminal expansion characteristic of this clade (Padian and Smith, 1992; Unwin and Lü, 1997). All azhdarchoid and lonchodectid humeri possess similar pneumatic foramina on the anterior humeral surface to the Wessex humerus, but the distal end of the new material does not bear the dorsally-swollen lateral condyles demonstrated by lonchodectids or tapejarids (Frey et al., 2003; Unwin, 2003; also see above). Instead, the distal end is more like that of non-azhdarchoid neoazhdarchoids in bearing proximally-tapering dorsal and ventral margins with a squared-off termination. This attribute, combined with the marginal displacement of the deltopectoral crest, suggests that the Wessex humerus is most like those of non-azhdarchoid neoazhdarchoids. If so, this renders the new material as the first occurrence of a Wealden thalassodromid or chaoyangopterid. The humeri of the latter are presently only represented by crushed specimens from the Jiufotang Formation however, and are too poorly known at present to further clarify the identity of the Wessex humerus.

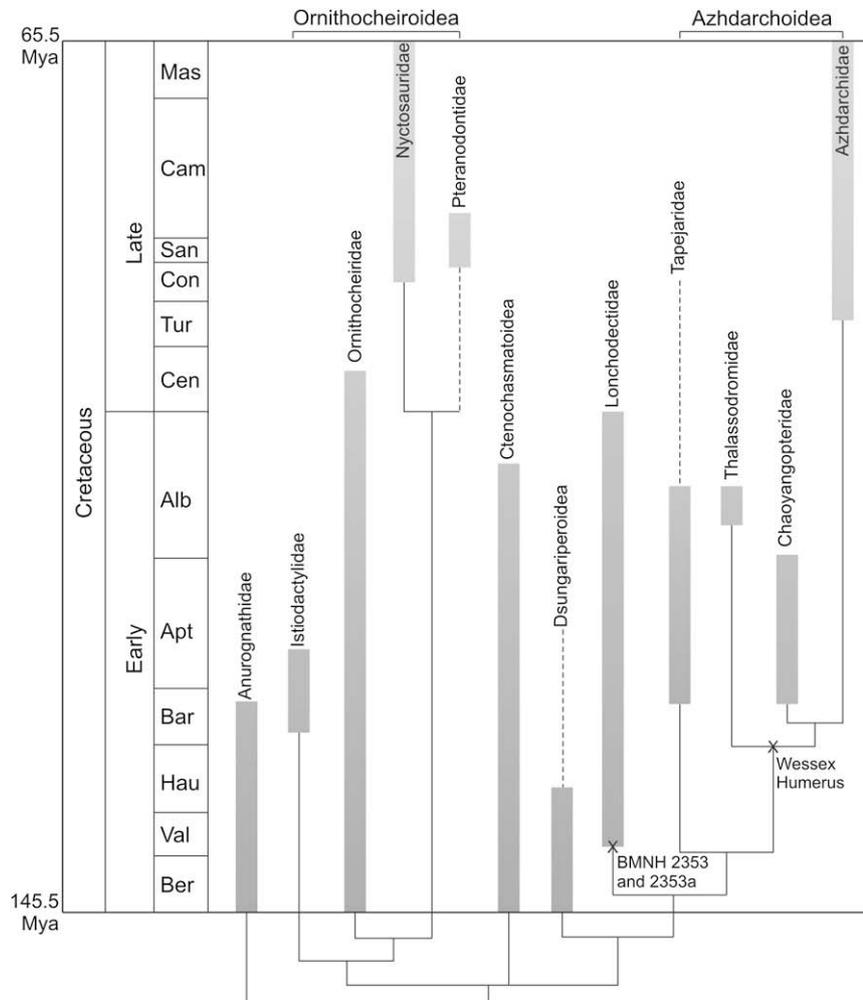


Fig. 8. Stratigraphic ranges of Cretaceous pterosaurs (modified from Lü et al., 2008). Mas, Maastrichtian; Cam, Campanian; San, Santonian; Con, Coniacian; Tur, Turonian; Cen, Cenomanian; Alb, Albian; Apt, Aptian; Bar, Barremian; Hau, Hauterivian; Val, Valanginian; Ber, Berriasian.

#### 4. Discussion

Only a handful of valid pterosaur taxa have been named from the British Wealden despite its large geographical expanse and temporal range. The Weald Sub-basin has yielded (?)*Lonchodectes sagittirostris* and *Coloborhynchus clavirostris* (Unwin et al., 2000), while Isle of Wight Wealden strata have yielded *Istiodactylus latidens* (Howse et al., 2001) and *Caulkicephalus trimicrodon* (Steel et al., 2005). With the controversial exception of (?)*Lonchodectes*, all these forms can be placed in the Ornithocheiroidea, making the confirmation of the Lonchodectidae and discovery of the Azhdarchoidea in the British Wealden significant contributions to our knowledge of Lower Cretaceous British pterosaur diversity. These discoveries are further complemented by new evidence that the Isle of Wight Wealden Group has higher pterosaur diversity than previously appreciated: microsieving plant debris horizons of the Wessex Formation has confirmed the presence of istiodactylids in this deposit (first mentioned by Sweetman in personal communication to Steel et al., 2005) and uncovered possible ctenochasmatoid teeth (Sweetman, personal communication 2007).

The significance of these specimens is heightened through their age. Lonchodectids are mainly known in Britain from the Cambridge Greensand and, although the age of the fossils in this formation has proved problematic, its pterosaur material has been confidently dated to the late Albian (Unwin, 2001). BMNH 2353 and

2353a confirm the presence of lonchodectids in the Valanginian and, along with the (?)*Lonchodectes sagittirostris* jaw, mark the oldest confirmed remains of this group (Fig. 8; Unwin, 2003). Similarly, the Wessex humerus from the Barremian Wessex Formation is the oldest neoazhdarchian material currently known (Fig. 8). The single report of an older neoazhdarchian is an azhdarchid cervical vertebra from Tithonian Tendaguru deposits of Tanzania (Sayão and Kellner, 2001), but these remains have since been re-assigned to Ctenochasmatoidea (Andres and Ji, 2008). Neoazhdarchians from other Lower Cretaceous deposits such as the Crato and Jiufotang Formations are of Aptian/Albian (Martill and Heimhofer, 2007) or Aptian age (Zhou et al., 2003), respectively. Additional Aptian material, reported to be an azhdarchid humerus by Murry et al. (1991), lacks the diagnostic characters of proximal azhdarchid humeri and is more likely to represent a non-azhdarchid neoazhdarchian. The discovery of a Barremian neoazhdarchian is unsurprising however, given the occurrence of the Neoazhdarchia sister-taxon, Tapejaridae, in the Barremian/Aptian Yixian Formation of China (Wang and Zhou, 2006).

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