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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-azhdarchid neoazhdarchian and, being from Barremian deposits, represents the earliest known occurrence of such a pterosaur.

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 ctenochasmatoids along with ornithocheirids and istiodactylids (Jursack and Popa, 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, ctenochasmatoids 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-ornithocheirid 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 neoazhdarchian 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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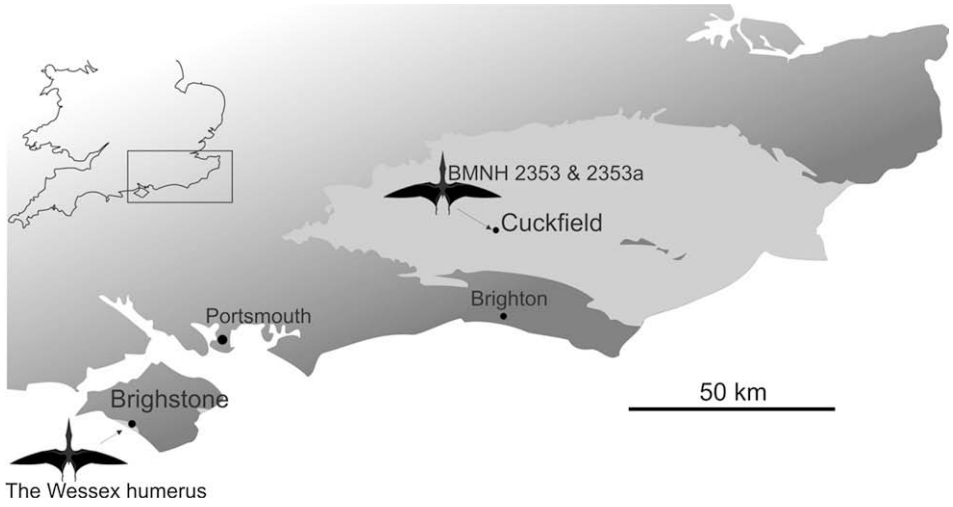

Fig. 1. Distribution of Wealden strata across southeast England (grey shading), and approximate localities of the pterosaur specimens described here. Wealden deposits of Dorset omitted for clarity.

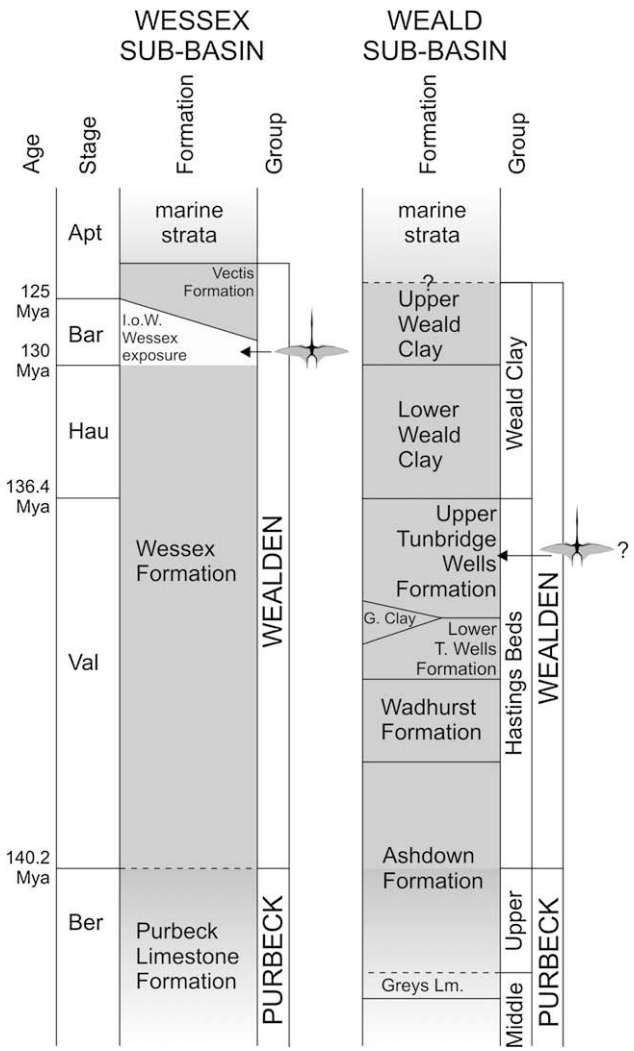

Fig. 2. Simplified stratigraphy of the Weald and Wessex Sub-basins based on Radley (2006a). Pterosaur silhouettes show approximate location of their source strata. Apt, Aptian; Bar, Barremian; Hau, Hautervian; Val, Valanginian; Ber, Berriasian.

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-pteroodactyloid 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 tarsometarsus 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,