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## THE TETRAPOD MICROBIOTA OF THE WESSEX FORMATION (LOWER CRETACEOUS, BARREMIAN) OF THE ISLE OF WIGHT, UK.

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**Abstract:** Although remains of small vertebrates in the (Barremian) Wessex Formation of the Isle of Wight, southern England, are rare and fragmentary bulk screening techniques have resulted in the recovery of a diverse terrestrial microvertebrate fauna including lissamphibians, archosaurs, lepidosaurs, and mammals. Most taxa are generically distinct from those occurring in other European Early Cretaceous deposits, but in general aspect the faunas are similar. Palaeoenvironmental differences appear to have affected the balance of taxa present but the faunas are dominated by an essentially relictual assemblage of small theropod and ornithischian dinosaurs, crocodylians, scincomorph and anguimorph lizards, frogs of discoglossid grade, salamanders and albanerpetontids. Many elements of this fauna are also encountered in the Early Cretaceous of central and eastern Asia, northern Gondwana and North America. It is becoming increasingly apparent that despite evidence for the existence of marine barriers separating these areas, faunal interchange occurred. The Wessex Formation microbiota lends further support to this concept and the occurrence of a gobiconodontid and a spalacolestine spalacotheriid in particular are consistent with other evidence supporting east/west, west/east dispersals.

**Key words:** Cretaceous, dispersal, faunal interchange, microvertebrate, palaeobiogeography.

UNTIL recently the tetrapod microfauna of the Early Cretaceous (Barremian) Wessex Formation of the Isle of Wight, southern England was largely unknown, reflecting difficulties associated with its recovery. Bulk screening techniques have now resulted in the isolation of remains representing a diverse fauna. This includes small theropod and ornithischian dinosaurs, crocodylians, pterosaurs, scincomorph and anguimorph lizards, turtles, frogs, salamanders, an albanerpetontid and mammals.

The Wessex Formation was deposited on a near coast, low gradient, floodplain by a meandering river system flowing from west to east within a narrow, fault bounded valley (Underhill 2002). The bulk of the succession comprises varicoloured, massive, overbank mudstones that are largely unfossiliferous. The remainder of the succession comprises sandstones, intraformational conglomerates, crevasse splay deposits and plant debris beds (Stewart 1978). The latter represent storm-water generated debris flows derived from a landscape that was in many cases denuded of vegetation following wildfire events. Although making up only about one percent of the succession, the plant debris beds have yielded the majority of macro and microvertebrate remains.

The climate was seasonal. Xerophytic elements of the flora suggest that the climate was arid, at least for part of the year, but climate modelling indicates that significant precipitation occurred throughout the year, apparent seasonal aridity resulting from high summertime temperatures at the time of which evaporation exceeded precipitation (Haywood *et al.* 2004). Despite seasonally harsh climatic conditions the Wessex Formation floodplain provided considerable habitat diversity and this is reflected in the terrestrial vertebrate fauna.

## THE WESSEX FORMATION TERRESTRIAL BIOTA

The dinosaur fauna, comprising more than twenty taxa, is without parallel elsewhere in Europe (Martill and Naish 2001). Considering also its age and palaeogeographical location, the Wessex Formation dinosaur assemblage is of considerable significance in the context of Early Cretaceous dinosaur faunas worldwide. Screening for microvertebrates demonstrates that a number of taxa unknown from macro skeletal remains are also present. These include two or three small ornithischians and a several

small theropods, some of which, including a troodontid, may already be known from fragmentary skeletal remains. Distinctive teeth have also allowed recognition of a large velociraptorine dromaeosaur (Sweetman 2004).

Remains of other small tetrapods are dominated by the teeth of crocodylians. At least four families are represented; Goniophoridae, Pholidosauridae, Bernissartidae and Atoposauridae but it is not possible using isolated teeth to make any estimate of the total number of species. However, one moderately large species not currently recognized from macro skeletal remains is present. This possessed a dentition including teeth with strongly denticulate carinae.

The second most abundant small tetrapod remains are those of an albanerpetontid and at some horizons albanerpetontid bones, particularly dentary fragments, occur in very large numbers. A combination of characters relating to the dentary, maxilla, premaxilla and fused frontals allow identification of a new taxon (Sweetman in prep.). Other lissamphibians include at least three salamanders based on atlas morphology and at least three frogs based on ilia, all of which appear to be of discoglossid grade.

At least two anguimorph and seven scincomorph lizards are present in the assemblage, although remains of the former are uncommon. One of the anguimorphs, based on vertebral structure, may have been limbless or with very reduced limbs (S. E. Evans pers. comm. 2003). In contrast, scincomorphs are relatively abundant and diverse. Seven taxa have been identified on the basis of tooth tip morphology and the common occurrence of lizard osteoderms demonstrates that some of these were paramacellodids.

Remains of pterosaurs and turtles are rare but labiolingually compressed, spatulate teeth characteristic of the pterosaur *Istiodactylus*, otherwise known only from the upper Barremian to lower Aptian Vectis Formation, have been recovered from two horizons. One of these came from the base of the exposed Wessex Formation thereby extending the range of this taxon by several million years. Other isolated pterosaur teeth are indeterminate but probably pertain to ornithocheirids. Turtle carapace fragments representing two taxa are occasionally encountered as are osteoderms of the solemydid *Helochelydra*.

Mammal remains are extremely rare in the Wessex Formation but six taxa have now been recovered. These include: two multituberculates both of which are eobaatarids,

neither of which can be referred to the mainland UK Wealden genus *Loxaulax*; a zatherian or possibly eutherian currently represented by premolars only; a dryolestoid; a gobiconodontid (Sweetman in press *a*); and a spalacolestine spalacotheriid (Sweetman in press *b*); the latter two are significant from a palaeobiogeographical perspective and the spalacolestine is of considerable significance in terms of the evolutionary history of Spalacotheriidae.

*Early Cretaceous terrestrial faunas and palaeobiogeography.*

The Wessex Formation terrestrial microbiota is, in general aspect, similar to that occurring elsewhere in the Early Cretaceous of North America, Laurasia and northern Gondwana. Palaeoenvironmental differences, and to some extent palaeogeographical isolation, appear to have affected the balance of taxa present but the faunas are dominated by an essentially relictual assemblage of small theropod and ornithischian dinosaurs, crocodylians, and scincomorph and anguimorph lizards. Variably present are albanerpetontids, frogs, salamanders choristodires, rhynchocephalians, mammals and birds. As new discoveries are made it is becoming increasingly apparent that, despite evidence for the existence of marine barriers separating these areas, faunal interchange between them did occur, albeit perhaps sporadically, during the Late Jurassic and Early Cretaceous. Two of the mammals in the Wessex Formation lend further support to this concept.

Isolated gobiconodontid teeth have now been recovered from the Barremian of both Spain (Cuenca-Bescós and Canudo 2003) and Britain (Sweetman in press *a*). Outside of Europe gobiconodontids are encountered in the Early Cretaceous (?Berriasian) of North Africa (Sigogneau-Russell 2003), the Early Cretaceous of central and eastern Asia (e.g. Rougier *et al.* 2001 and references therein), and the Aptian-Albian of North America (Jenkins and Schaff 1988). The diversity of gobiconodontids encountered in central and eastern Asia suggests that the Gobiconodontidae may have originated and diverged in that area (Cuenca-Bescós and Canudo 2003). The currently known distribution of Gobiconodontidae appears therefore to represent dispersal events originating in central Asia and involving a westward dispersal to northern Gondwana and

western Europe during the Late Jurassic and/or Early Cretaceous and a somewhat later eastward dispersal to western North America. However, lack of gobiconodontid remains from strata deposited to the east of the epicontinental sea which divided North America in the Cretaceous may well represent a collecting artefact reflecting the small number of Early Cretaceous mammal-bearing sites so far known from this area.

The occurrence of a spalacolestine spalacotheriid in the Wessex Formation represents the earliest record of the subfamily (Sweetman in press *b*), its closest temporal relatives being the highly specialized Aptian spalacolestine *Heishanlestes* Hu *et al.*, 2005 from the Aptian Shapai Formation of north-eastern China and *Spalacotheroides birdwelli* Patterson, 1955 from the Aptian - Albian Antlers Formation of Texas, USA. Its occurrence therefore is also of significance when considering faunal interchange in the Early Cretaceous. The well documented North American radiation of Spalacolestinae during Aptian - Campanian times led Cifelli and Madsen (1999) to propose a European ancestor for Spalacolestinae, spalacolestines being known from North America only at that time. In view of this apparent confinement, Averianov and Archibald (2003) proposed a Late Cretaceous, North American ancestor for the mid-Asian, Turonian - ?Santonian ?spalacolestine spalacotheriid *Shalbaatar*. However, this now appears inconsistent with the recently reported occurrence of a specialized spalacolestine in the Aptian of north-eastern China (Hu *et al.* 2005). The occurrence of both is however consistent with a European ancestor now supported by the occurrence of a British, Barremian spalacolestine. European ancestry for the Spalacolestinae is also consistent with other evidence for both west-east and east-west dispersal between Europe and Asia during the Late Jurassic and Early Cretaceous, e.g. the occurrence of hypsilophodontid and iguanodontid dinosaurs in the basal Cretaceous of Japan (Manabe and Hasegawa 1995; Evans *et al.* 1998) in the case of the former and the occurrence of a gobiconodontid in the basal Cretaceous of northern Gondwana (Sigogneau-Russell 2003) in the case of the latter. However, at present data are limited and all palaeobiogeographical models must be treated with caution.

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