Essay: THE WESSEX FORMATION

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BACKGROUND

The Cretaceous Period, which began 145.5 ma (Bui et al., 1995) was the final stage of the ''Age of Dinosaurs''. The Cretaceous Period saw some major worldwide events, such as; increased sea floor spreading rates along mid-ocean ridges and the highest marine transgressions of the post- Pangean world (The Mesozoic Era II, 2010). Movements within the Earth's mantle continued the break-up of the Pangea supercontinent (Fig.1) (Nudds & Selden, 2012). North America and Europe were divided, leading to the formation of the North Atlantic Ocean, while the southern and northern continents where further divided as the Tethys Ocean extended west (Nudds & Selden, 2012). This led to regional differences between the flora and fauna of the

northern and southern continents. During this period modern mammals first appeared in the fossil record (Bui et al., 1995), and birds, which had first appeared in the Late Jurassic, began to diversify (Terrestrial Life, n.d.). Flowering plants (Angiosperms) also appeared approximately 135 million years ago, and by the end of the Cretaceous were the most diverse group of terrestrial plants, their rapid diversification coinciding with the diversification of insects, an example of co-evolution (Terrestrial Life, n.d.). During the early Cretaceous, dinosaurs were still the dominating terrestrial animals; pterosaurs ruled the sky, ichthyosaurs and plesiosaurs were the top marine predators (Nudds & Selden, 2012). While all these entities were devastated during the Cretaceous-Tertiary mass extinction, during the cretaceous they continued to adapt, with new groups of dinosaurs, such as ceratopsians, pachycephalosaurs and hadrosaurs emerging (Bui et al., 1995) (Terrestrial Life, n.d.). Top Predators were replaced in ecosystems, such as the replacement of allosaurs, icthysaurs and pterosaurs by coelurosaurs, mosasaurs and pterodactyloids respectively (Nudds & Selden, 2012).
Fig 1: Position of the continents during the Early Cretaceous, 130Ma (Source; (The Mesozoic Era II, 2010)).

HISTORY OF DISCOVERY OF THE WESSEX FORMATION

The Wessex formation, the Wealden Group, located on the Isle of Wight, has a significant importance for vertebrate palaeontology, with bones found in the Wessex Formation being at the forefront of dinosaur research (Hooker & Sweetman, 2009). In 1829 William Buckland first described the pedal phalanx, of the dinosaur iguanodon, which was first scientifically described and named by Gideon Mantall in 1825. The bone was found at Yaverland, located on the south-east coast of the Isle of Wight (Hooker & Sweetman, 2009).

STRATIGRAPHIC SETTING AND TAPHONOMY OF THE WESSEX FORMATION

The Lower Cretaceous Wealden Group outcrops in two sections in the Isle of Wight. These sections are coastal, with a small exposure in Sandown Bay, on the south-eastern coast of the Isle of Wight, and another exposure along the southwestern shore of the Isle of Wight, which is larger, and more laterally extensive (Evans et al., 2004). In this area the Wealden Beds have been given group status, and are divided into two formations, the Wessex Formation, and the Vectis Formation (formerly known as Wealden Marls and Wealden Shales respectively) (Insole & Hutt, 1994). The Wessex Formation is thought to be Hauterivian-Barremian in age, with the lower section of the formation potentially being Valanginian in age (Hutt et al., 2001) (Insole & Hutt, 1994). The beds were dated through the use of biostratigraphical correlations, which were based on palynological and ostracod data. The Wessex formation is a red-bed sequence of interbedded, varicoloured, but predominately red non-marine mudstones and sandstones, with the occasional crevasse splay deposit, and plant debris beds (Evans et al., 2004) (Insole & Hutt, 1994). The Isle of Wight Wealden Group strata reaches a maximum outcrop thickness of 240m (Insole & Sweetman, 2010), however the maximum depth of the Isle of Wight Wealden Group strata, as shown by the Arreton 1 borehole, created for hydrocarbon exploration (Hopson, 2011) (Insole & Sweetman, 2010) (Insole & Hutt, 1994), with the top 180m of sediments comprising of the exposed Wessex Formation (Insole & Sweetman, 2010) (Evans et al., 2004). There a six facies associated with the Wessex formation (Insole & Sweetman, 2010), the first consisting of fining-up conglomerates, siltstones, mudstones and sandstones with a distinctive arrangement of sedimentary structures (Insole & Hutt, 1994).The second facies consists of heterolithic bodies of sediment, ranging from predominantly mudstone and siltstone, to over 50% fine grained sandstone (Insole & Hutt, 1994). The third facies consists of sequences infilling recognizable channels; the fill consists of either red mudstone or sand-mud interbeds. Facies association four comprises of small-scale fine grained sandstone and red mudstone alternations (Insole & Hutt, 1994). The fifth facies, which makes up the bulk of the Wessex Formation sequence, is characterized by massive red mudstones and siltstones, mottled with purple, green, yellow, brown and grey, forming complex patterns. Polygonal mud cracks and rootlet traces are common in this facies (Insole & Hutt, 1994). The final facies association, the plant debris beds, are relatively thin beds, mostly less than 1mm in thickness, however with some units reaching a maximum thickness of 2m (Insole & Hutt, 1994) (Evans et al., 2004). These beds comprise of green-grey mudstones (Evans et al., 2004), as well as flood-dominated accumulations of poorly sorted fragments of lignite and fusain within the clay matrix (Hutt et al., 2001). These lignite and fusain fragments, which are representative of charcoal and wood fragments, are often pyritized (Evans et al., 2004). The plant debris beds are fossiliferous and representative of flash floods washing debris, such as flora and fauna remains into depressions within the Wealden alluvial floodplain (Evans et al., 2004). Large branches and stems caught in these floods may have acted as a net, catching and concentrating vertebrate material. This accounts for some of the plant debris bed's abnormal features, such as the mixture of organisms from different habitats, the variability of preservation, and the discrepancy in grain size between the matrix and clasts (Insole & Hutt, 1994).

DESCRIPTION OF THE WESSEX FORMATION BIOTA

Flora: The flora contains few recognizable macrofossils, other than twigs, logs and the occasional cone (Insole & Sweetman, 2010) (Insole & Hutt, 1994). However there is an abundance of spores, and dispersed cuticles within the plant debris beds (Insole & Sweetman, 2010) (Insole & Hutt, 1994). Flora known within the plant debris beds includes pteridophytes, caytoniales, cycadophytes, gingkophytes, coniferophytes and angiosperms (Insole & Sweetman, 2010) (Insole & Hutt, 1994). Conifers and cycads are thought to have been major elements in the local vegetation, with a small proportion of these conifers being dominant, such as Pseudofrenelopsis parceramosa, which were large evergreen trees, potentially reaching heights of 10-15m (Insole & Hutt, 1994) (Insole & Sweetman, 2010). Infrared spectroscopy of amber, fossilized tree resin, found in the plant debris beds, supports a coniferous origin for the samples (Insole & Sweetman, 2010). It is thought that Wealden Group flood plains, or Early Cretaceous mid-latitude environments generally did not support coniferophyte-cycadophyte forests, instead they were similar to savannahs, covered in vegetation, with no closed canopy (Insole & Hutt, 1994). The abundance of fusain within the plant debris beds suggests that wildfires occurred, which may have prevented the development of dense gymnosperm growths (Insole & Sweetman, 2010) (Insole & Hutt, 1994). Megaspores are present in high numbers on some horizons, with some potentially representing aquatic plants, suggesting that several pools of standing water were colonised by these plants.

Macroinvertebrates: Macroinvertebrates are uncommon in the plant debris beds, however they are abundant in some other beds (Insole & Sweetman, 2010). Nippononaia fordi, Margaritifera valdensis, Unio elongate, and some other unioids are abundant (Insole & Sweetman, 2010). Comparisons with extant relatives, suggest that these bivalves were semi-infaunal, low-level suspension feeders, inhabiting shallow, perennial, well-oxygenated pools and lakes of low turbidity (Insole & Sweetman, 2010). Grazing gastropods are uncommon; however planorbids are both present and common within one of the plant debris beds (Insole & Sweetman, 2010). Viviparius and Physa have been recorded, with Viviparid gastropods being epifaunal, ciliary feeders that tended to habitate standing freshwater environments, with fine grain substrates (Insole & Sweetman, 2010). Physids and modern planorbids both dwell in slow moving to still vegetated ponds and lakes, with physids living in marginal zones, inhabiting the rooted vegetation (Insole & Sweetman, 2010). Arthropod remains are uncommon within the Wessex formation. Some amber has been found within the plant debris beds, and is fossiliferous, containing chironomids, as well as a wasp, a cockroach, a beetle and a spider (Insole & Sweetman, 2010). Ostracods have also been reported from a single calcareous sandstone horizon at Yaverland, Isle of Wight, and include species of Cypridia (Insole & Sweetman, 2010).
Eotyrannus lengi: Eotyrannus was a predatory theropod (Fig 2), and had serrated premaxillary teeth, and proportionally elongate tibiae and metatarsals (Hutt et al., 2001). A primitive Tyrannosauroidea, it had elongate neck vertebrae, with long, well developed arm forelimbs (Hutt et al., 2001). Eotyrannus also appeared to have exceptionally long hands, with one of the largest hands among non-avian theropods (Hutt et al., 2001). Eotyrannus is estimated to have measured approximately 4m in length, however the specimen is believed to be a juvenile, and thus an older specimen may have been longer (Hutt et al., 2001).

Figure 2: Eotyrannus lengi (Source: (Eotyrannus, n.d.))
Baryonyx walkeri: At a length of 9m, Baryonyx walkeri was a predatory spinosauroid (Fig 3) (Baryonyx, n.d.). A pescivore, Baryonyx walkeri had thin, long teeth and a long narrow snout (Baryonyx, n.d.). Baryonyx walkeri was adapted to catching and eating fish, hunting in the shallows (Baryonyx, n.d.). Baryonyx walkeri is thought to have lived around Wealden Lake in the Early Cretaceous, which provided plenty of prey (Baryonyx, n.d.).

Fig 3: Baryonyx Walkeri (Source: Charig & Milner, 1997)
Neovenator saleri:Neovenator salerii (Fig 4) is the first allosaurid theropod that was described in the Wealden of England (Estep et al., 1998). Discovered in 1978, at Brighstone Bay, Neovenator salerii stood at 2.5m with a length of approximately 7.5m (Neovenator, n.d.). Neovenator salerii had serrated teeth, and likely 3 digits on both its hands and feet (Neovenator, n.d.). Bi-pedal, Neovenator salerii was a carnivorous theropod, and is thought to have been an ambush predator, scavenging carrion when necessary (Neovenator, n.d.).

Figure 4: Neovenator salerii (Source: (Neovenator, n.d.))
Iguanodon bernissartensis and Iguanodon atherfieldensis: Iguanodon remains, first found in 1809, are common within the Wessex Formation (Iguanodon, n.d.). Two species have been found, the larger Iguanodon bernissartensis, which weighed up to 4 to 5 tons, was between 3.5 to 4 metres tall and grew to a length of 9-10 metres, possibly even reaching 13 metres (Iguanodon, n.d.). Iguanodon atherfieldensis (which has now been renamed to Mantellisaurus atherfieldensis), was smaller and grew to about 6 or 7 metres in length (Iguanodon, n.d.). Herbivores, they consumed tough plants, which are comparable to today's cycad and tree fern leaves (Iguanodon, n.d.).
Pterosauria: Pterosaurs are rare in both the Wessex Formation, and the Wealdan Group (Martill & Sweetman, 2010). Recent discoveries of pterosaur, along with re-evaluation of pterosaur material indicated a significantly higher diversity of pterosaurs however, than previously thought (Martill & Sweetman, 2010). The Wessex Formation is thought to contain one genus of Euomithocheridae (Caulkicephalus), a single undetermined ctenochasmatine, and three Istiodactylidae (Martill & Sweetman, 2010).
Crocodylia: Four families of Crocodile are represented in the Wessex Formation, Gonipholidae, Pholidosauridae, Bernissartidae and Atoposauridae (Sweetman, 2006).
Mammalia: Mammal remains are very rare within the Wessex Formation; however six taxa have been found (Sweetman, 2006). There are two multituberculates, with both being eobaatarids, premolars also suggest the presence of a zatherian or eutherian (Sweetman, 2006). There is also a dryolestoid, a gobiconodontid, and a spalacotheriid (Sweetman, 2006).
Other reptiles: Currently there have been 5 species of Anura, (frogs) found, 2 species of testudines (turtles) as well as 14 species of scleroglossa, a clade of lizards, which encompasses geckos and monitor lizards. There are also 3 species of Caudata (salamanders) and a single species of Albanerpetontidae, an extinct salamander-like lissamphibian (Insole & Sweetman, 2010) (Evans et al., 2004).

Other dinosaurs: Other dinosaurs that have been found at the Wessex Formation include: Ornithopisis hulkei, a small brachiosaurid sauropod, Eucamerotus foxi also a brachiosaurid, Valdosaurus canaliculatis an ornithopod, Ornithodesmus cluniculus and Yaverlandia bitholus, both theropods (Blows, 1995).
Dinosaur traces: First recorded by Beckles in 1851 (Insole & Hutt, 1994), footprints are relatively common both isolated, and associated with trackways (Insole & Hutt, 1994). Tridactyl prints are present, and are presumed to have been produced by the iguanodontids (Insole & Hutt, 1994).
Paleoichnology: Burrows are common at some levels of all facies associations, apart from the plant debris beds. Skolithos, Cylindricum, Ancorichnus, Muensteria and Planolites forms have been identified, and are typical of low-diversity Scoyenia ichnofacies, which indicate deposition within the shore zone of ephemeral lakes and in sluggish streams (Insole & Hutt, 1994) (Insole & Sweetman, 2010). Coprolites up to 100mm in diameter are found within the plant debris beds, large coprolites are uncommon, and are thought to represent faecal matter from dinosaurs and crocodilians. Smaller coprolites are abundant from mass screening residues, and are attributed to bony fishes. Coprolites less than 1mm axis length are attributed to termites, which suggest that termites were an important part of the Wessex Formation Ecosystem (Insole & Sweetman, 2010).

PALAEOECOLOGY OF THE WESSEX FORMATION BIOTA
During the Early Cretaceous, southern England lay between 30 and 35 degrees north (Insole & Sweetman, 2010). Evidence suggests that Early Cretaceous climates were more equable than modern climates, and thus isotherms moved poleward by around 15 degrees, in comparison to modern isotherms (Insole & Sweetman, 2010). This suggests that southern England experienced mean annual temperatures of approximately 20-25°C

during the early Cretaceous (Insole & Sweetman, 2010). Modern calcrete production is found in areas with a mean annual temperature of 16-20°C, and a low seasonal rainfall between 100-500mm per year (Insole & Sweetman, 2010). Sedimentological and palaeoecological evidence suggests that the Wessex Formation was deposited on a low relief alluvial flood plain, containing lakes and ponds, crossed by a moderate sized perennial meandering river system, independent of fluctuations of climate within the basin (Fig 5)(Insole & Hutt, 1994). Climatic and tectonic events would increase the bedload of the river, creating sandy point bars (Insole & Hutt, 1994). The plant debris beds, which make up 5% of the available succession, but yield more than 50% of the specimens (Insole & Hutt, 1994), are thought to have been formed by an exceptional combination of common events (Insole & Sweetman, 2010). Dry periods would lead to forests becoming susceptible to lightning strikes, causing fires (Insole & Sweetman, 2010). These forest fires would strip vegetation, increasing surface run off (Insole & Sweetman, 2010). High rainfall would produce flooding before the forest canopies and ground cover vegetation had a chance to recover and regenerate (Insole & Sweetman, 2010). These floodwaters would then pick up sediments and surface debris such as leaf litter, logs, and both decomposing animal carcasses, as well as a few live vertebrates, forming debris flows (Insole & Sweetman, 2010). These debris flows then ran into depressions within the alluvial plain depositing their load. This would allow anaerobic conditions to form, allowing the preservation of organic matter, and the production of pyrite (Insole & Sweetman, 2010). This explains why each of the plant debris beds are sedimentologically and paleontologically different (Insole & Sweetman, 2010). Most of the dinosaurs both lived and died in the flood plain, however the low productivity of vegetation within the floodplain would not have been capable of supporting a population of dinosaurs, such as sauropods, so it is likely that these were seasonal migrants (Insole & Hutt, 1994). Large therapods, such as Neovenator Salerii would have been the major predators, hunting all the taxa except the largest of sauropods (Insole & Hutt, 1994). Small theropods may have hunted other terrestrial vertebrates, such as the smaller ornithopods, facing competition from the crocodiles that inhabited the flood plain (Insole & Hutt, 1994).
Fig 5: Wessex Formation during the Early Cretaceous (Source: (Witton, 2013))

COMPARISONS WITH OTHER FOSSILIFEROUS DEBRIS FLOWS
Fossiliferous debris flows are rarely reported from the geological record, with those that are being incomparable to the plant debris beds of the Wessex Formation (Insole & Hutt, 1994). While the mode of deposition is completely different, the Permian pond bone beds, occurring in a red bed dominated floodplain sequence in Archer County, Texas, has been considered to be comparable (Insole & Hutt, 1994). These organic rich deposits, which accumulated within oxbow lakes and swamps, contain terrestrial and aquatic vertebrate remains (Insole & Hutt, 1994). These deposits also include fusain; however they are formed by the gradual accumulation of organic debris (Insole & Hutt, 1994)

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