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Palaeoenvironment and taphonomy of the *Hypsilophodon* Bed, Lower Cretaceous Wessex Formation, Isle of Wight

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Abstract: The *Hypsilophodon* Bed occurs at the top of the Wessex Formation (Early Cretaceous, Barremian) on the Isle of Wight, southern England. Numerous remains of the small ornithopod dinosaur *Hypsilophodon foxii* have been recovered from the bed since the mid-nineteenth century. Previous theories for these fossil occurrences have focused on catastrophic mass death events, including miring and flood-related mortality. However, only limited sedimentological and taphonomic analyses of the horizon and its fossil assemblage have been undertaken, hindering efforts to evaluate different theories about how the assemblage formed. Here, we report a sedimentological study of the bed to constrain its depositional environment, an examination of the matrix from *Hypsilophodon* fossils to identify where they were collected from within the bed, and a taphonomic investigation of *Hypsilophodon* specimens. Our results indicate a floodplain environment, which later became a marsh and then mudflats at the edge of a lagoon. *Hypsilophodon* fossils are spatially and stratigraphically distributed throughout the bed. The specimens are largely incomplete and unabraded, suggesting that most perished on, or near to, the floodplain and may have lain exposed for some time prior to burial. Overall, the evidence suggests that the fossil assemblage of the *Hypsilophodon* Bed formed as an accumulation of remains over time.

Supplementary material: Details of the *Hypsilophodon* specimens used in this study, coastal erosion calculations, images and descriptions of petrographic thin sections, images and details of microfossils and taphonomic data are available at https://doi.org/10.6084/m9.figshare.c.7439335

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Hypsilophodon is a small, bipedal, herbivorous, ornithopod dinosaur for which confirmed occurrences come exclusively from the *Hypsilophodon* Bed, a 1–2 m thick interval at the top of the Lower Cretaceous Wessex Formation of the Isle of Wight, southern England (Galton 1974). Known from specimens representing more than 20 individuals (with more in private collections), the anatomy of *Hypsilophodon* is well known (Galton 1974) and it has consequently become the archetypal basal ornithopod and an important taxon for studies of ornithopod phylogeny and evolution. However, much about the palaeobiology of the taxon remains unknown – for example, despite a large number of specimens of a variety of sizes being preserved, its growth and ontogeny have yet to be investigated and it remains unclear whether any of the preserved individuals are adults. One enduring mystery about *Hypsilophodon* is why the specimens have been found in such a spatially and temporally restricted setting (Galton 1974; Insole and Hutt 1994; Sweetman 2011; Coram *et al.* 2017).

Inconsistent definitions of the type of sediments that make up the *Hypsilophodon* Bed and the scarcity of taphonomic analysis of the *Hypsilophodon* fossils themselves have previously made it difficult to evaluate different theories about how the fossil assemblage of the *Hypsilophodon* Bed accumulated.

The aim of this paper is to assess the evidence for the mass mortality of herds of *Hypsilophodon* using taphonomic and sedimentological approaches. To achieve this, we examine the outcrop of the *Hypsilophodon* Bed and describe its constituent facies to allow an interpretation of its depositional environment. We also compare historical and present-day maps of the coastline to understand how much coastal erosion of the area has occurred since the first *Hypsilophodon* fossils were found. The matrix of the *Hypsilophodon* fossils in the Natural History Museum, London, UK (NHMUK) collections is examined to identify where in outcrop they were originally located. The taphonomy of *Hypsilophodon* fossils in the NHMUK collections is analysed in terms of specimen completeness and abrasion to gain insights into the processes that occurred between death and burial. These results will further our understanding of how the sediments and fossil assemblage of the *Hypsilophodon* Bed accumulated and may have implications for our understanding of the lifestyle of small ornithopod dinosaurs.

Geological setting

The Wealden Group of the Isle of Wight is an Early Cretaceous succession of sedimentary rocks known for hosting a diverse fossil assemblage, including, most famously, numerous species of dinosaur (Stewart 1978; Batten 2011). Cropping out on the SE and SW coasts of the Isle of Wight (Fig. 1), the group consists of the fluvial red bed sequence of the Wessex Formation and the overlying

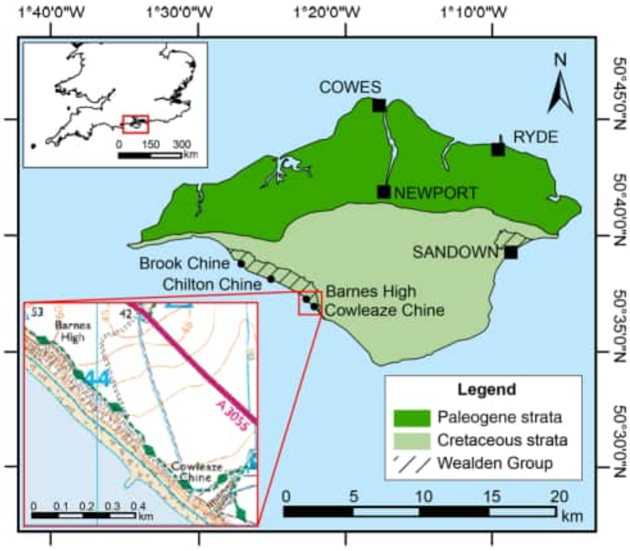

Fig. 1. Map showing the location of the Isle of Wight with summary geology, the location of the Wealden Group outcrop and the *Hypsilophodon* Bed. A detailed map of the coastline along which the *Hypsilophodon* Bed crops out in cliffs between Cowleaze Chine and Barnes High is also shown. Source: © Crown copyright and database rights 2022 Ordnance Survey (AC0000851941), Geological map data BGS © UKRI 2022.

grey mudstones of the lagoonal Vectis Formation (Fig. 2; Stewart 1978). The group was deposited within the Wessex sub-basin, one of several extensional basins that developed over southern England during the Mesozoic (Stoneley 1982). Falling sea-levels in the Tithonian caused the emergence of the basin, which, along with normal faulting related to crustal extension occurring in the Early Cretaceous, led to subsidence and the subsequent deposition of the thick successions of terrestrial sediments that comprise the Wessex Formation (Chadwick 1986). The amount of crustal extension and related normal faulting had decreased by the end of the Barremian and had been replaced by regional subsidence related to thermal relaxation (Chadwick 1986; Underhill and Stoneley 1998). At the same time, the relative sea-level was rising, causing an increasingly marine influence within the Wessex sub-basin, leading to the formation of the restricted lagoon in which the grey mudstones of the Vectis Formation were deposited, and, ultimately, a marine transgression in the Aptian (Chadwick 1986; Ruffell 1988).

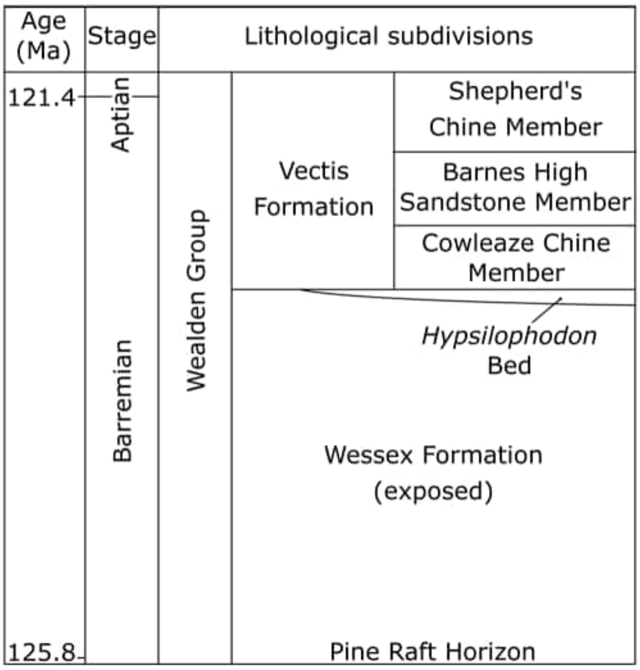

Fig. 2. Schematic stratigraphic section of the Isle of Wight Wealden Group showing the location of the *Hypsilophodon* Bed. The relative thickness of the units is not to scale. Source: after Radley and Barker (1998), with details from Allen and Wimbledon (1991).

The palynology, fossil wood carbon isotope data, radiometric dating of diagenetic calcite and palaeomagnetic data are all consistent in indicating a predominantly Barremian age for the exposed Wessex Formation strata, with the base of the exposed strata dating to the Hauterivian (Hughes and McDougall 1990; Allen and Wimbledon 1991; Robinson and Hesselbo 2004; Jacobs *et al.* 2023). The magnetostratigraphy suggests that the Barremian–Aptian boundary occurs in the upper part of the Vectis Formation (Kerth and Hailwood 1988). During the Barremian, the Isle of Wight was located between 35 and 40° N (Smith *et al.* 1981). Sedimentological, palaeontological and palaeobotanical evidence indicate a warm to hot climate, with evidence for periods of aridity, including desiccation cracks, calcrete formation and burned plant and insect remains (Stewart 1978; Insole and Hutt 1994; Watson and Alvin 1996; Allen *et al.* 1998). Numerical models also suggest a warm to hot climate, but indicate that rainfall was significant all year round, with the restricted availability of moisture in the hot season resulting from evaporation exceeding precipitation (Haywood *et al.* 2004). Evidence of intense storms are apparent throughout the Wealden Group, including debris flows within the Wessex Formation hypothesized to have been generated by intense rainfall and storm coquinas in the overlying Vectis Formation (Radley and Barker 1998, 2000; Sweetman and Insole 2010).

Hypsilophodon Bed

The *Hypsilophodon* Bed is located at the top of the Wessex Formation and crops out for roughly 1 km on the SW coast of the Isle of Wight, from beach level at Cowleaze Chine to the cliff top at Barnes High (Fig. 1), where it consists of 1–2 m of red mudstone and sandstone (Fig. 3; Hulke 1882; Reid and Strahan 1889). *Hypsilophodon* fossils were first found in 1849 when workmen discovered bones in a block of sandstone *c.* 100 m west of Cowleaze Chine. Initially, the bones were thought to belong to a juvenile *Iguanodon*; *Hypsilophodon foxii* was not formally described until 1869 when Huxley published a description of a specimen collected from the Isle of Wight by William Fox (Huxley 1870). Fox had collected several similar fossils from the same horizon. It has been estimated that the remains of more than 20 individuals are currently held in the collections of the NHMUK alone, with upper estimates of the total number of

Fig. 3. Annotated photograph of the top 1.5 m of the *Hypsilophodon* Bed and overlying Vectis Formation.

individuals recovered from the bed of *c.* 100, although new finds are now scarce (Coram *et al.* 2017).

Hypsilophodon fossils are often reported as being uniformly well-preserved, articulated and relatively complete, unusual in the Wessex Formation, where vertebrate fossils are typically fragmentary, isolated and most commonly form part of high-diversity assemblages within plant debris beds (Galton 1974; Insole and Hutt 1994; Sweetman and Insole 2010; Coram *et al.* 2017). Evidence exists for carcasses having been fully fleshed at the time of burial, such as the presence of ossified tendons, intercostal plates and grey reduction haloes in the matrix surrounding some bones, suggesting that the *Hypsilophodon* were rapidly buried at or soon after death (Hulke 1882; Galton 1974; Stewart 1978; Butler and Galton 2008; Sweetman 2011; Coram *et al.* 2017). The fossil assemblage is near-monospecific, with the only other vertebrate material reported from the bed comprising rare reptiles and fish (Hulke 1882; Galton 1974; Coram *et al.* 2017). Such features have led several researchers to suggest that the fossil assemblage of the *Hypsilophodon* Bed is the result of one or two catastrophic mass death events, whereby a group of closely associated individuals perished at the same location within a short space of time, involving either miring or flood-related mortality (Stewart 1978; Insole and Hutt 1994; Coram *et al.* 2017).

The involvement of herds of *Hypsilophodon* has been suggested based on the large numbers of fossils recovered, the close association of some individuals (at least one sandstone block is known to contain bones from three individuals) and the herding behaviour of some modern-day terrestrial animals (Galton 1974; Insole and Hutt 1994; Sweetman 2011; Coram *et al.* 2017). This interpretation has implications for the mode of life of *Hypsilophodon* and, by extension, other closely related basal ornithopods: it would indicate, for example, that basal ornithopods lived in multigenerational herds, implying the parental care of young, a feature that has previously only been demonstrated conclusively in ceratopsian dinosaurs and perhaps some hadrosaurs among Ornithischia (Horner 2000; Meng *et al.* 2004; Fastovsky *et al.* 2011). Understanding how and why monospecific concentrations of dinosaur fossils develop is crucial to our interpretations of dinosaur palaeobiology, yet suggestions that *Hypsilophodon* lived in herds have yet to be evidenced with detailed sedimentological or taphonomic data.

It is difficult to evaluate different hypotheses about how the fossil assemblage of the *Hypsilophodon* Bed formed for several reasons. First, the definitions of what the *Hypsilophodon* Bed is vary. Although all descriptions place it near to the top of the Wessex Formation between Cowleaze Chine and Barnes High, with most describing it as being between 1 and 2 m thick, few give a stratigraphic definition or description of the bed, and the few descriptions that do exist are not all consistent (Hulke 1882; Reid and Strahan 1889; Stewart 1978; Insole and Hutt 1994; Coram *et al.* 2017; Gale 2019). For example, Fox (letter from William Fox to Richard Owen, February 1870, cited in Blows 1983) described the bed as consisting of *c.* 1.5 m of light brown sandstone overlying clay, whereas Hulke (1882) depicted 1 m of mottled blue and red clay overlain by 1 m of grey sandstone and sandy clay. Reid and Strahan (1889) described 1 m of red–blue clay and sand located directly underneath the White Rock, which is a distinctive pale sandstone marking the base of the Vectis Formation at this location (Stewart 1978). Galton (1974) and Stewart (1978) both referred to mottled red mudstones with sandstones of variable thickness and lateral extent. Gale (2019) defined the *Hypsilophodon* Bed as a layer of silty clay with some conglomerate and sand occurring *c.* 2.5 m below the White Rock. The most detailed description is given by Coram *et al.* (2017), who denoted a 1 m thick layer of mudstone overlain by the White Rock and divided by a laterally variable sandstone extending for *c.* 600 m. To account for all previous definitions, we investigated the top 3 m of the Wessex Formation immediately below the White Rock.

Previous studies have included limited sedimentological detail with little micropalaeontological and palynological analysis. Palaeoenvironmental interpretations from previous work include a marsh and tidal mudflats interbedded with levee sands at the edge of a lagoon, and interbedded floodplain and crevasse splay deposits (Stewart 1978; Insole and Hutt 1994; Coram *et al.* 2017).

Another issue is the paucity of location information regarding the historical fossil finds and a scarcity of recent fossils finds, which make it difficult to identify where in the bed *Hypsilophodon* fossils are hosted. The majority of *Hypsilophodon* fossils in the NHMUK collections have no location information or note only '*Hypsilophodon* Bed'. Where further information is provided, most are said to come from either Cowleaze Chine or a location 100 m west of Cowleaze Chine, with only a few specimens recorded as coming from the western end of the bed (Fig. 1; Supplementary Material A; Galton 1974; Benton and Spencer 1995). Fewer still provide information on the stratigraphic location of fossils within the bed, although some insight can be gleaned from rare descriptions of the fossil matrix. For example, Fox (1870, cited in Blows 1983, p. 306) noted fossils coming from a 'mass of mud', whereas Hulke described fossils that he found in a 'sandy clay-stone' (Hulke 1874, p. 18). Other matrix descriptions include blocks of sandstone and soft grey clay (Galton 1974).

Another challenge in evaluating different hypotheses of formation is the lack of analysis of *Hypsilophodon* fossil preservation. Although it is commonly stated that the preservation is near-uniform and that skeletons are relatively complete, there is a lack of evidence to support these statements. Furthermore, Galton (1974) noted that although 20 *Hypsilophodon* specimens in the NHMUK collections are represented by some articulated material and that three of these specimens are close to complete, he also noted that there is much material consisting of isolated bones in poor states of preservation.

Methods

Sedimentology

Facies analysis and sample collection

Seven sedimentary logs were taken in 2021 and 2022 from the eastern end of the *Hypsilophodon* Bed, where it is exposed and accessible from beach level (Fig. 4). Overall, the location at which the logs are located is such that they will collectively record a continuous section from the base of the exposure (up to 3 m below the base of the White Rock) to 1 m above the White Rock, ensuring all the facies that may be considered as the *Hypsilophodon* Bed were examined.

Different facies were identified on the basis of changes in grain size, colour and/or sedimentary structures, and were assigned codes following Nichols (2009) (Fig. 4). Sediment samples were collected from each facies during logging for microfossils and petrographic thin section analyses.

Quantification of coastal erosion

To assess how much of the *Hypsilophodon* Bed has been lost to erosion since the first *Hypsilophodon* specimens were collected in the mid-nineteenth century, maps of the Isle of Wight from 1862 (the earliest available) and 2022 were downloaded from Digimap (digimap.edina.ac.uk). The cliff line between Cowleaze Chine and Barnes High was traced on each map using ArcMap v10.7. The distance between the two cliff lines was calculated using the Features to Vertices tool to find all the vertices of the 1862 cliff line, and subsequently using the Near tool to calculate the shortest distance between the 1862 cliff line vertices and the 2022 cliff line. The mean distance was taken as the average distance of cliff retreat. The area of land lost was found by drawing a polygon between the two cliff lines (Supplementary Material B).

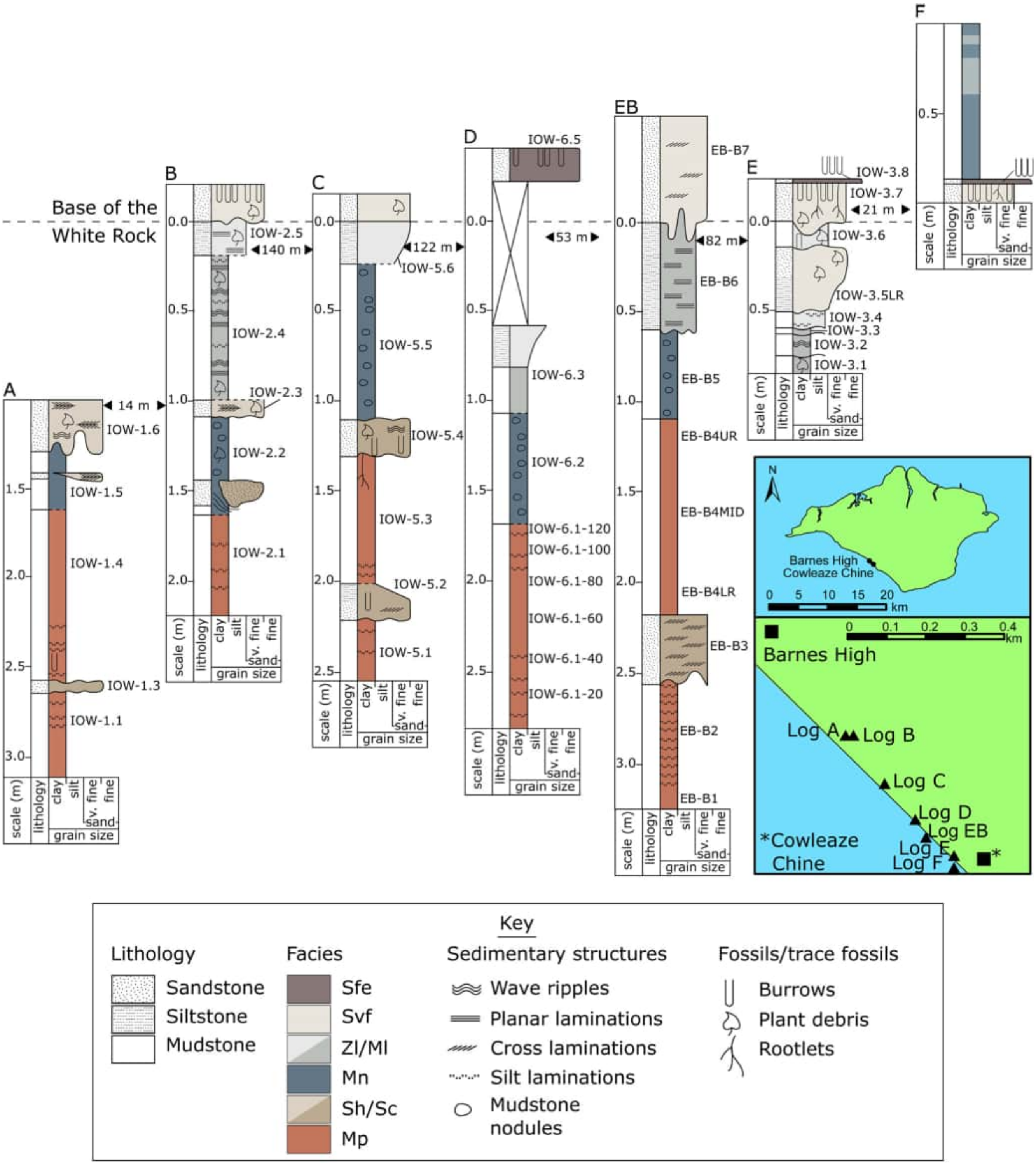

Fig. 4. Logs of the *Hypsilophodon* Bed with maps of the SW coast of the Isle of Wight showing their location. The logs summarize the lithology, grain size, sedimentary structures and fossils/trace fossils. The scales indicate the distance from the base of the White Rock. More details of each facies can be found in Table 2. The location and names of all the samples collected from the bed are noted to the right of each log, e.g. IOW-2.3. The locations of the logs are as follows. A, [SZ 44053 80433]; B, [SZ 44073 80433]; C, [SZ 44153 80310]; D, [SZ 44232 80218]; E, [SZ 44331 80126]; F, [SZ 44331 80095]; and EB, [SZ 44259 80172].

Hypsilophodon fossil matrix

The matrix was examined from 57 *Hypsilophodon foxii* specimens in the NHMUK collections to identify different matrix types. For each matrix type, specimens were identified that had sufficient matrix for removal and subsequent sedimentological analysis. Matrix was removed from four specimens (NHMUK PV R 192, PV R 200, PV R 2474 and UNREG, an unregistered specimen collected by Dr P.L. Robinson, University College London (Galton 1974); Supplementary Material A), with removal undertaken at the NHMUK.

Petrographic thin sections

Seven petrographic thin sections of sandstones from the *Hypsilophodon* Bed outcrop (samples IOW-1.3, IOW-1.6, IOW-

5.5, IOW-3.7 and IOW-3.8; see Fig. 4 for sample locations) and *Hypsilophodon* fossil matrices (NHMUK PV R 192 and NHMUK PV R 200) were made at the NHMUK. The thin sections were polished to a standard thickness (30 µm) and left unstained; see Supplementary Material C for images and descriptions of all the thin sections.

Micropalaeontological analysis and palynology

A total of 37 sediment samples were examined for microfossils, which included all samples collected from the *Hypsilophodon* Bed, apart from those from the red mudstones because our initial examinations indicated that this facies is barren of microfossils. Four *Hypsilophodon* fossil matrix samples (NHMUK PV R 192, PV R 200, PV R 2474 and UNREG, unregistered specimens collected by Dr P.L. Robinson, University College London (Galton 1974); Supplementary Material A) were also examined; see Supplementary Material D for the detailed methodology, scanning electron microscopy images of recovered microfossils, identification and palaeoenvironmental implications.

A total of four samples from the White Rock and grey sediments below the White Rock (IOW-3.1, IOW-3.6, IOW-3.7 and IOW-6.2) were examined for palynomorphs. A 10 g mass of each sample was processed for palynological content using hydrochloric–hydrofluoric acid digestion to remove the mineral content, leaving an organic residue that was then sieved at 10 µm. No oxidation of the organic residue was required; see Supplementary Material E for full details of the palynomorph assemblages.

Taphonomy

The following taphonomic methods were undertaken on *Hypsilophodon* specimens held at the NHMUK (see Supplementary Material A for details of the specimens examined; the specimens examined differ slightly between each method). Articulation was not quantified due to the high number of specimens that had either been fully prepared or were found in unconsolidated matrix and are therefore no longer representative of the original state of articulation.

Specimen completeness

Specimen completeness was quantified for 53 *Hypsilophodon* specimens (see Supplementary Material A for details of which specimens were examined). To quantify the completeness of the *Hypsilophodon* skeletons, skeletal completeness was scored from 0 to 1 as in Cashmore and Butler (2019), where 1 represents an entire region being present, 0.5 represents half of the region being present and 0 represents the absence of a region. Skeletal completeness was scored by region (skull, vertebrae and ribs, pectoral girdle and forelimbs, pectoral girdle and hindlimbs) rather than by element due to the deformed, damaged or obscured nature of many of the *Hypsilophodon* specimens. To quantify the skeletal completeness for entire specimens, the regional completeness scores were multiplied by the proportional size of each skeletal region and then summed. The skeletal proportions were calculated from the two-dimensional area of each skeletal region of a *Hypsilophodon* skeletal reconstruction.

Abrasion

Abrasion of bones belonging to 52 *Hypsilophodon* specimens (see Supplementary Material A for details of which specimens were examined) were categorized according to the criteria detailed in Table 1 (Ryan *et al.* 2001). The maximum abrasion stage of the constituent bones was recorded for each specimen.

Table 1. Criteria for categorizing bones into different stages of abrasion (after Ryan et al. 2001)

Stage	Stage of abrasion
0	Fossil surface is pristine with no abrasion
1	Fossil surface is polished, with rounding of broken edges
2	Fossil surface is well-polished, although the original texture is still evident; both broken and unbroken edges are well-rounded; processes are rounded, but still recognizable
3	Fossil surface is well-polished, with all edges very well-rounded; processes are still evident as protrusions, but only where they are attached to the bone

Results

Sedimentology

Facies analysis

A total of eight facies were recorded from the *Hypsilophodon* Bed outcrop, including red mottled mudstones, rippled sandstones (with and without herringbone cross-stratification), nodular black–red mudstones, organic-rich laminated clay and silt, white–grey silty very fine sandstone and iron-cemented fine sandstone. The facies are interpreted as being deposited in either fluvial floodplain or marginal lagoonal settings. All sedimentary logs are shown in Figure 4. Table 2 is a facies table giving detailed descriptions and process interpretations of each facies; images of each facies are shown in Figure 5a–h.

Quantification of coastal erosion

The mean coastal erosion along the *Hypsilophodon* Bed between 1862 and 2022 was 73 m (minimum 50 m, maximum 96 m), with a total area of land lost of *c.* 62 000 m^2 (Fig. 6; Supplementary Material B).

Hypsilophodon fossil matrix

Examination of the fossil matrix from 57 *Hypsilophodon* specimens (see Supplementary Material A for details of which specimens were examined) revealed the presence of four distinct matrix types (Fig. 7).

1. *Matrix type A.* A red silty mudstone with millimetre- to centimetre-scale grey mottling. Grey reduction haloes are sometimes present around fossils.
2. *Matrix type B.* Grey to orange silt to silty fine sand. Grains are well-sorted, sub-angular to subrounded and comprise >95% quartz. May or may not contain angular matrix-supported clasts of red clay, 2–100 mm in diameter, up to 40% density.
3. *Matrix type C.* Pale grey, well-cemented fine sandstone. Grains are well-sorted, sub-angular to subrounded and comprise >95% quartz. Considerably harder and more consolidated than the other matrix types and contains no obvious mud or clay.
4. *Matrix type D.* Irregular and angular porous black encrustations or loose nodules.

Of the 57 specimens examined, 56% had no matrix due to the bones being fully prepared or due to the fissile nature of the matrix. Matrix type B was most common, being found in 28% of specimens, with matrix type A being found in 12%. Matrix types C and D were rare and found only in one specimen each (Supplementary Material A).

Table 2. Facies scheme for the *Hypsilophodon* Bed. Facies presented in the order in which they occur, beginning with the base of the bed

Facies	Code (following Nichols 2009)	Colour for logs	Description	Image	Process interpretation
Red mottled mudstone	Mp	🟥	Red silty clay with millimetre-scale vertical grey and sometimes purple mottling. Pale grey millimetre-scale silt laminae and burrows up to 2 cm wide present. Desiccation cracks 2–3 cm wide and up to 5 cm deep may be present. Interbedded with facies Sc. Units are generally metre-scale and laterally continuous. Bottom contact is obscured; top contact gradational with Mn	Figure 5a	Very fine grain size suggests deposition from low-energy conditions. Millimetre-scale vertical mottles interpreted as rootlets. Rootlets, colour mottling and desiccation cracks suggest that pedogenesis of sediment occurred after deposition, with previous work interpreting the red mottled mudstones of the Wessex Formation as vertisols (Wright *et al.* 2000). Red colour suggests an oxidized subaerial setting. Silt laminae form due to coarser material input by relatively high-energy events
Silty sandstone with/without climbing ripples	Sc	🟫	Grey–brown silty very fine sandstones with unidirectional and/or climbing ripples defined by very fine-grained plant debris or clay. Grains sub-angular, well-sorted and consisting of >95% quartz with 1% plant debris grains and rare 1 mm mica flakes. Calcite cement and clay are present between grains. Contain variable densities of centimetre-scale red mudstone clasts. May be burrowed. Units are generally centimetre- to decimetre-scale and laterally discontinuous (varies from tens of metres to tens of centimetres). Bottom contacts are erosive with Mp; top contacts are sharp and planar/symmetrically rippled or gradational with facies Mp or Mn	Figure 5b	Erosive base and relatively coarse grain size compared with surrounding sediments suggests deposition by a flow of relatively high velocity. Climbing ripples indicate waning unidirectional flow and increased deposition (Chaudhuri 2005). Red clay clasts suggest that material was incorporated from the surrounding floodplain. Climbing ripples indicate rapid deposition of sediment (Ashley *et al.* 1982). Symmetrically rippled tops suggest reworking in shallow water by waves (Stewart 1978)
Silty sandstones with herringbone cross-stratification	Sh	⬜	Grey–brown silty very fine sandstones with unidirectional and/or climbing ripples defined by very fine-grained plant debris or clay. Grains sub-angular, well-sorted and consist of >95% quartz with 1% plant debris grains and rare 1 mm mica flakes. Calcite cement and clay present between grains. As facies Sc, but in places herringbone cross-stratification defined by grey clay is present. May be burrowed. Units are generally centimetre- to decimetre-scale and laterally discontinuous (varies from tens of metres to tens of centimetres). Bottom contacts are erosive or highly undulating with facies Mn or Zl, with relief varying by up to 15 cm in some cases. Top contacts are sharp and planar or gradational with facies Mn and Zl	Figure 5c	Erosive base and relatively coarse grain size compared with surrounding sediments suggests deposition by a flow of relatively high velocity. Herringbone cross-stratification suggests a tidal influence (Rust 1977). Where the base is highly undulating, it is likely infilling depressions on the floodplain, such as the dinosaur footprints that are noted to be common in this area, particularly at the base of the White Rock (Radley *et al.* 1998; Gale 2019)
Nodular black–red silty mudstones	Mn	🟦	Red–black silty mudstone consisting of rounded nodules (1–4 cm diameter, average 2 cm) of red silty clay with millimetre-scale grey mottling. Nodules weather to black on the outside, giving the facies a black appearance in outcrop. Some nodules are pervasively black and some contain small, irregular, hard black nodules up to 1 cm in diameter. Interbedded with facies Sh, which, in some cases, appears to infill depressions that were likely formed as single dinosaur footprints. Units are generally decimetre-scale and laterally continuous. Bottom contacts gradational with facies Mp. Top contacts are gradational with facies Ml	Figure 5d	Silty clay grain size suggests deposition in a low-energy environment. The similarity between the interior of nodules and facies Mp and the gradational relationship between the two suggests that this facies was originally deposited as Mp
Organic-rich laminated clay	Ml	▨	Grey silty clay with millimetre-scale laminae and/or symmetrical ripples defined by abundant, very fine-grained black plant debris. Undulating pale grey silt laminae are present and increase in frequency with time, giving an overall coarsening-upwards trend into facies Zl. Laminae are often deformed by depressions interpreted as multiple	Figure 5e	Silty clay grain size suggests deposition in a low-energy environment. The grey coloration and abundance of organic matter indicate an anoxic environment. Symmetrical ripples indicate deposition in a shallow body of water and the action of waves (Tanner 1967). Silt laminae indicate increases in the energy of the environment at

(continued)

Table 2. *Continued*

Facies	Code (following Nichols 2009)	Colour for logs	Description	Image	Process interpretation
		▨	generations of dinosaur footprints. In places up to 85% of the surface area is covered by orange–brown staining. Interbedded with facies Sh. Isolated dinosaur footprints with layered infill are sometimes present. Unit is generally decimetre-scale and laterally continuous. Bottom contacts are gradational with Mn, top contacts are gradational with Svf or sharp and undulating where the contact is deformed by dinosaur footprints		times and are interpreted as wavy bedding, typically considered to form in tidally influenced environments (Reineck and Singh 1980). Laminae indicate little to no invertebrate bioturbation or vegetation in the sediment. Multiple generations of infilled dinosaur footprints indicate that the area was frequented by dinosaurs and that the waters were shallow or at times emergent (Radley *et al.* 1998)
Organic-rich laminated silt	Zl	▨	As facies Ml, but coarser grained (grey clayey silt)	Figure 5f	Coarser grained material (silt) indicates an overall increase in the energy of the environment
White–grey silty very fine sandstone	Svf	▨	White to yellow grey silty very fine sandstone. Grains moderately sorted, subrounded and consist of >95% quartz with <1% black plant debris grains. Calcite cement present. Abundant vertical burrows (5–15 mm wide) and rootlets present. Silt may define some laminae, but appearance largely massive due to intense bioturbation. Unit is decimetre- to metre-scale and extremely laterally continuous. Bottom contact commonly infills multiple generations of dinosaur footprints in layers, but is gradational with facies Zl when not deformed. Top contacts are sharp and planar with Sfe	Figure 5g	The pale colour of the sands suggests a reducing environment. The layered infill of dinosaur footprints implies that the sediment was initially delivered in pulses. Burrows suggest that the sands were at one time submerged, but oxygenated, whereas rootlets indicate they were also vegetated at some point in time (Radley *et al.* 1998)
Iron-cemented fine sandstone	Sfe	▨	Dark red–grey well-cemented fine sandstone. Intensely burrowed with preservation of burrow casts throughout. Unit is centimetre-scale in thickness (average 2 cm) and laterally continuous across the outcrop. Bottom contact is sharp and planar with Svf, top contact is sharp and planar with the grey muds of the Vectis Formation	Figure 5h	Red coloration and the hard, well-cemented nature suggest that the sand is iron-cemented. Coupled with the restricted thickness and intense bioturbation, this suggests a period of restricted sedimentation (Allulee and Holland 2005)

Taphonomy

Specimen completeness

The majority of the specimens are highly incomplete, with 85% of the 53 examined returning a completeness score <0.1 (Fig. 8a) – that is, <10% of the skeleton represented. Of the more complete specimens, six scored between 0.1 and 0.2. NHMUK PV R 196 was the most complete specimen at 0.684, with NHMUK PV R 5829 being the second most complete at 0.385 (Supplementary Material F).

Abrasion

The overwhelming majority of the 52 *Hypsilophodon* specimens examined (79%) displayed no evidence of abrasion of their constituent bones. A total of 13% of the specimens had some bones that displayed stage 1 abrasion, whereas 4% of the specimens exhibited abrasion stage 2 and 4% of the specimens exhibited abrasion stage 3 (Fig. 8b). Of the two specimens that displayed stage 3 abrasion (NHMUK PV R 147 and NHMUK PV R 636), both are represented by isolated bones only (Supplementary Material G).

Palaeoenvironmental interpretation

Although previous interpretations of the depositional environment of the *Hypsilophodon* Bed have been made, most are brief and focus solely on the red mudstones and interbedded sandstones. Stewart (1978) interpreted it as marshes and tidal mudflats at the edge of a lagoon, where levees were reworked in shallow water. Insole and Hutt (1994) and Coram *et al.* (2017) both suggested that the bed was deposited as interbedded floodplain and crevasse splay deposits. Detailed sedimentary logs (Fig. 4) and the analyses of sediment samples undertaken in this work agree overall with the interpretation of the *Hypsilophodon* Bed as a floodplain environment consisting of interbedded palaeosols and crevasse splay deposits, but also provide new insights into the changing environment of the bed.

The lower parts of the succession consist of red mottled mudstones (facies Mp) interbedded with silty sandstones with climbing ripples (facies Sc) (Table 2; Fig. 5). We interpret facies Mp as suspended material deposited by ponded water on the floodplain following overbank flood events. The red mottled colour, evidence of rootlets and desiccation cracks suggest that the sediment later underwent pedogenesis, with soils forming on a well-oxidized and well-drained river floodplain (Stewart 1978; Wright *et al.* 2000). Wright *et al.* (2000) interpreted the red mottled mudstones of the Wessex Formation, such as facies Mp, as vertisols. The thin (5–30 cm) laterally discontinuous (varying from tens of metres to tens of centimetres in lateral extent) sandstones of facies Sc commonly present with erosional bases and climbing ripples indicative of rapid deposition and waning flow and are interpreted as crevasse splays deposited during overbank flood events (Burns *et al.* 2017). Symmetrically rippled tops in some instances suggest the temporary ponding of water, which allowed reworking of the sediments by wave action (Stewart 1978). The large number of facies Sc units observed at various stratigraphic levels suggest that the floodplain

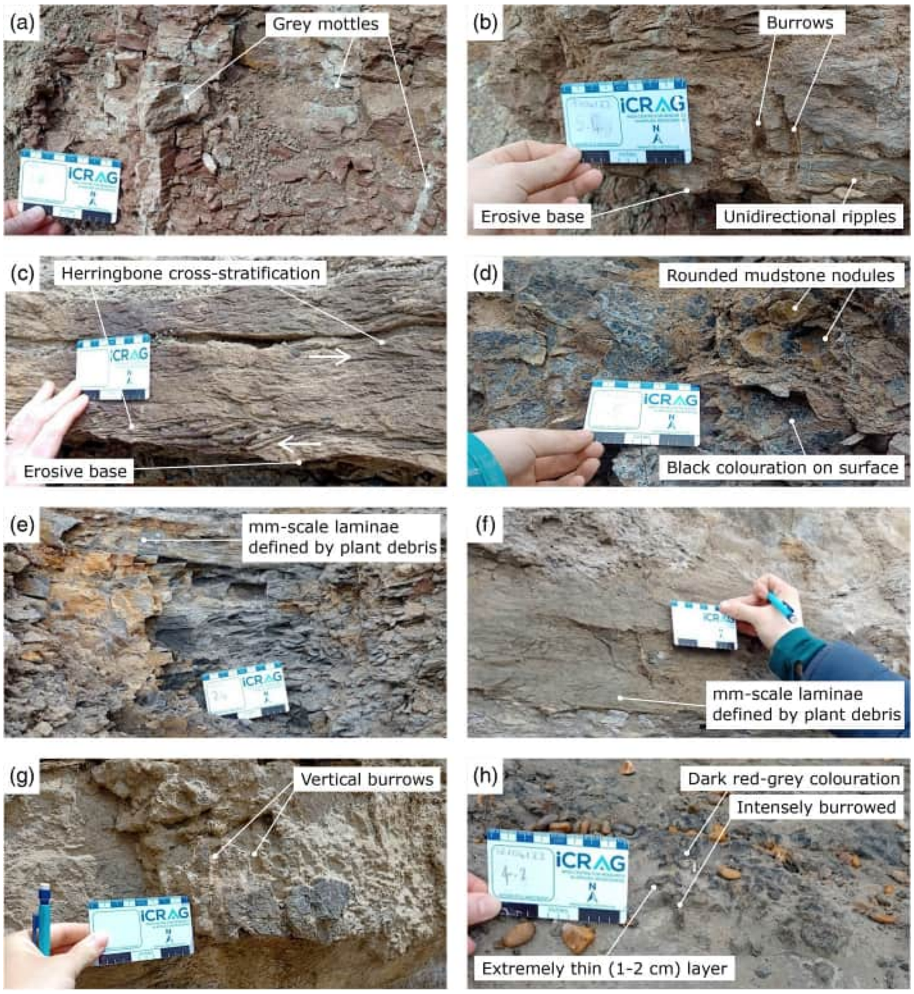

Fig. 5. Images of facies in the *Hypsilophodon* Bed. (**a**) Red palaeosols (Mp). Red silty clay with grey mottling and millimetre-scale silt laminae. (**b**) Silty sandstones with/without climbing ripples (Sc). Thin laterally discontinuous units of grey–brown silty very fine sandstones with erosive bases and unidirectional and/or climbing ripples. (**c**) Silty sandstones with herringbone cross-stratification (Sh). Thin, laterally discontinuous units of grey–brown silty very fine sandstone with unidirectional and/or climbing ripples with herringbone cross-stratification in places. White arrows indicate the direction of flow. (**d**) Nodular black–red silty mudstone (Mn). Red–black silty mudstone consisting of rounded nodules of red silty clay. (**e**) Organic-rich laminated clay (Ml). Grey silty clay with millimetre-scale laminae and/or symmetrical ripples defined by very fine-grained plant debris. (**f**) Organic-rich laminated silt (Zl). Grey clayey silt with millimetre-scale laminae and/or symmetrical ripples defined by very fine-grained plant debris. (**g**) White–grey silty very fine sandstone (Svf). White to yellow grey silty very fine sandstones with abundant vertical burrows and rootlets. Photograph shows burrows. (**h**) Iron-cemented fine sandstone (Sfe). Extremely thin unit of dark red–grey well-cemented fine sandstone with intense burrowing. See Table 2 for full facies descriptions. Subdivisions on scale bars are 1 cm.

was subject to numerous overbank flood events during its deposition. Facies Mp with interbedded facies Sc extends downwards uninterrupted until the Chine Farm Sandstone *c.* 10 m below. However, due to uncertainty surrounding the exact stratigraphic location of many of the fossil finds, largely due to a number of finds from fallen blocks on the beach, how much of this succession hosts *Hypsilophodon* fossils and thus may be considered as the *Hypsilophodon* Bed is not known.

Gradationally overlying facies Mp is 0.3–0.85 m of nodular black–red silty mudstone (facies Mn), which can be traced for the entire kilometre-long outcrop. Closer examination of the nodules shows them to be up to 4 cm in diameter, with a black outer and a mottled red mudstone inner (Fig. S2c), similar in appearance to facies Mp, although some nodules are pervasively black. The gradational relationship between facies Mn and facies Mp and the similarity of the nodule interiors to facies Mp suggests that facies Mn originally formed as a red mudstone. A number of *Chara* oogonia were recovered from facies Mn, along with rare *Theriosynoecum* and *Cypridea* ostracods, suggesting that the floodplain was submerged for extended periods under fresh to brackish conditions (Wilkinson 2011; Herbst *et al.* 2018; Supplementary Material D). As charophytes were not found in all the sediment samples from facies Mn, the submerged conditions may have been localized and confined to ponds on the waterlogged floodplain. It is hypothesized that the black coloration and nodular appearance of the facies is related to waterlogging, although the exact cause is unclear. One possibility is that the nodules represent the early stages of siderite nodule formation because siderite concretions are known to form within marshes (Pye 1984). Given the large lateral extent of facies change, a regional cause of waterlogging is proposed, likely related to relative sea-level rise and the landward advance of the Vectis lagoon (Radley and Barker 2000).

Overlying facies Mn is 0.25–1.0 m of organic-rich laminated clay (facies Ml), a grey clay layer that is laterally continuous for the entire lateral extent of the outcrop. Facies Ml contains abundant organic matter and silt laminae, which define symmetrical ripples in places and increase in frequency upwards. The very fine grain size, grey coloration and the presence of symmetrical ripples throughout the facies suggest that it was deposited in a low-energy body of shallow water influenced by waves. Silt laminae within the clay are interpreted as wavy bedding, typically associated with tidally influenced environments (Reineck and Singh 1980). The upwards increase in the frequency of silt laminae leads to an overall coarsening trend into organic-rich laminated siltstone (facies Zl), perhaps reflecting trends of increased storm activity over time, as observed in the overlying Vectis Formation, or marking increased proximity to the sea or lagoon (Radley and Barker 1998, 2000; Daidu *et al.* 2013).

Rare *Theriosynoecum* ostracods and a *Paracypris* ostracod have been recovered from samples in this facies, suggesting freshwater to brackish conditions and brackish to marine conditions, respectively (Wilkinson 2011; Supplementary Material D). The palynological examination of material collected from facies Sh found pollen and spore assemblages dominated by fern and other trilete spores, with low numbers of coniferous inaperturate and bisaccate pollen (Supplementary Material E). No marine palynomorph was found, suggesting that the *Paracypris* ostracod was likely not *in situ* and was instead transported to the region from a nearby marine environment. We argue that facies Ml and Zl represent tidally influenced mud and mixed flats at the edge of the Vectis lagoon,

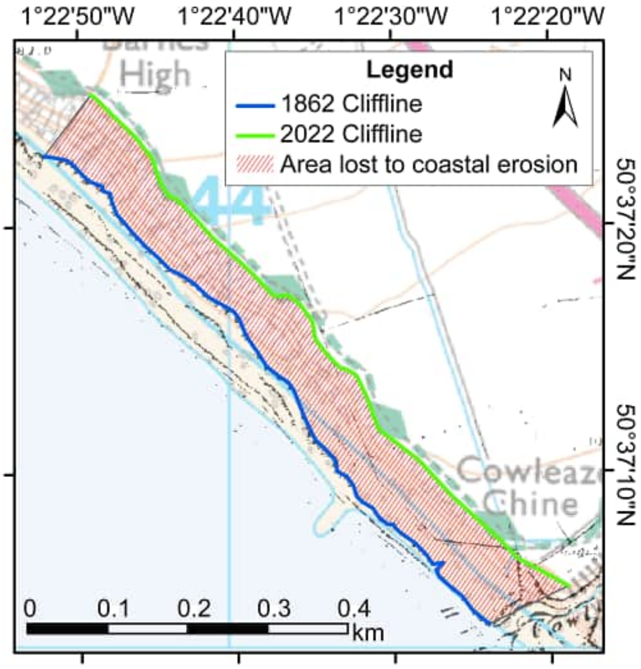

Fig. 6. An 1862 map overlain on a 2022 map of the SW Isle of Wight coastline. Clifftops from both maps have been traced over the full extent of the *Hypsilophodon* Bed outcrop (Barnes High to Cowleaze Chine) with the area lost shaded in red. Source: © Crown Copyright and Landmark Information Group Limited 2022. All rights reserved (1862). © Crown copyright and database rights 2022 Ordnance Survey (AC0000851941).

marking increased proximity to the lagoon as the relative sea-level continued to rise (Semeniuk 2005; Desjardins *et al.* 2012).

Interbedded within facies Mn, Ml and Zl are decimetre-scale (20–30 cm thick), laterally discontinuous (varying from tens of centimetres to tens of metres) units of silty sandstone with herringbone cross-stratification (facies Sh). Facies Sh is very similar to the crevasse splay deposits of facies Sc, but was deposited under waterlogged or subaqueous conditions and, in some cases, displays herringbone cross-stratification, again suggesting a tidal influence (Rust 1977).

Facies Zl passes gradationally into a white–grey silty to very fine sandstone (facies Svf), where the contact is undisturbed, but commonly sharp and irregular due to abundant depressions in the upper surface of facies Zl, which have previously been interpreted as dinosaur footprints, suggesting that the flats were frequented by dinosaurs (Radley *et al.* 1998; Gale 2019). Some footprints up to 1 m wide are likely to have been formed by sauropods (Gale 2019).

The distinctive pale grey silty sands of facies Svf, traceable across the entire 1 km long outcrop and known at this locality as the White Rock, form a useful marker bed for the base of the Vectis Formation. The thickness of Svf varies from 0.25 m to >1 m as a result of the infilling of dinosaur footprints in the underlying strata. The infill is layered, suggesting that sediment was delivered to the area in pulses. Facies Svf is extensively burrowed, which has removed much of the primary structure, giving a massive appearance. The burrows are up to 1.5 cm in diameter and have a lumpy outer appearance. Whether or not these burrows represent the ichnogenera *Ophiomorpha* or *Beaconites* has been a source of debate, with the current consensus being that they are *Beaconites* (Stewart 1978; Goldring and Pollard 1995). A lack of marine palynomorphs found in sediment samples from this horizon suggests a predominantly freshwater or brackish environment (Supplementary Material E). Numerous rootlets are observed within facies Svf, indicating that it was at one stage vegetated. Our interpretation is consistent with previous work, which suggested that facies Svf represents a marginal lagoon sand flat that was at one time exposed and covered with vegetation (Stewart 1978; Radley *et al.* 1998; Desjardins *et al.* 2012).

A thin unit (1–15 cm thick) of intensely burrowed, iron-cemented (Fig. S2e) fine sandstone (facies Sfe) is found overlying facies Svf, forming a sharp contact between the white sands and the overlying grey muds of the Vectis Formation. Iron cementation develops when a low accumulation rate allows sediment to spend a greater time within the geochemically active water–sediment interface, with

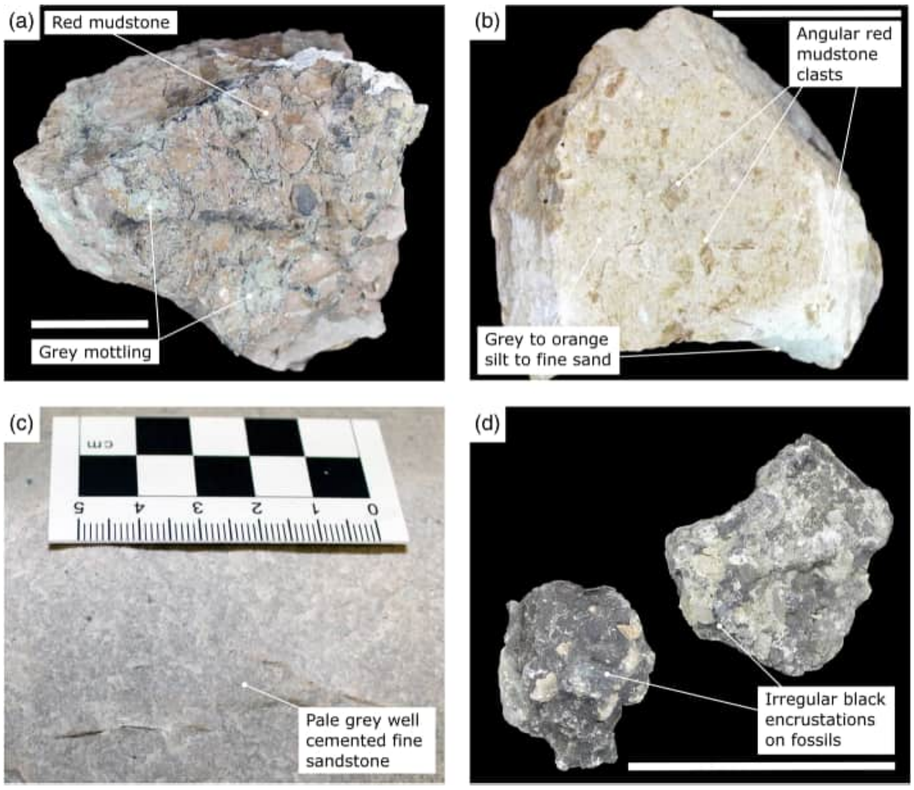

Fig. 7. Images of the four matrix types identified from the *Hypsilophodon* specimens in the Natural History Museum, London, UK collections. White lines represent 5 cm. (**a**) Matrix type A (red silty mudstone). (**b**) Matrix type B (grey to orange silt to fine silty sand). (**c**) Matrix type C (pale grey well-cemented sandstone). (**d**) Matrix type D (irregular and porous black encrustations or nodules).

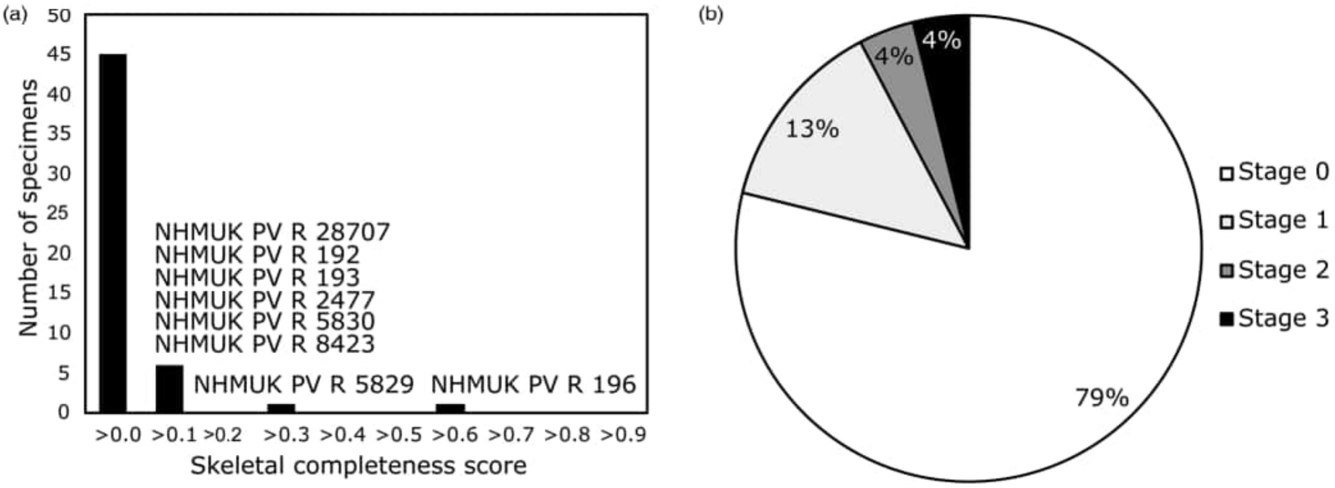

Fig. 8. Taphonomic data for *Hypsilophodon* specimens in the Natural History Museum, London, UK (NHMUK) collections. (**a**) Skeletal completeness for 53 NHMUK *Hypsilophodon* specimens with the specimen names given for the eight most complete specimens. (**b**) Average abrasion stages of fossils from 52 NHMUK *Hypsilophodon* specimens. Stage 0, fossils unabraded; stage 1, fossils show slight signs of abrasion and surface polishing; stage 2, fossils are well-polished, but with original textures still evident; and stage 3, fossils are well-polished with all edges well-rounded. See Table 1 for full criteria and Supplementary Material A for details of which specimens were examined.

intense burrowing resulting from organisms repeatedly burrowing into the same layer of sediment (Allulee and Holland 2005). The sands are interpreted as a flooding surface, where the rate of increase in accommodation outstrips that of the sediment supply, resulting in a decrease or hiatus in sedimentation (Allulee and Holland 2005). The presence of facies Sfe suggests that a relatively rapid increase in relative sea-level occurred after the White Rock was deposited, eventually resulting in the Vectis lagoon being established across the area.

The depositional environment of the *Hypsilophodon* Bed is interpreted as a well-oxidized and well-drained fluvial floodplain subject to numerous localized fluvial flood events (Fig. 9). Over time, and likely related to a concurrent rise in relative sea-level, the floodplain became permanently waterlogged, forming a marsh and then muddy tidal flats at the edge of a lagoon. Dinosaurs frequented the flats, leaving behind footprints that were later infilled by pulses of sediment, forming a sandflat at the edge of the lagoon. The overlying Svf and Sfe facies are not part of the *Hypsilophodon* Bed, but provide an insight into the nature of the transition between the Wessex and Vectis formations. Following the deposition of the White Rock, sea-level rose relatively rapidly, leading to the development of an iron-cemented and intensely burrowed sandstone layer as the Vectis lagoon was established across the area.

Taphonomic interpretation

Stratigraphic and spatial distribution of fossils

Examination of the fossil matrix from specimens in the NHMUK collections identified the presence of four distinct matrix types. Matrix type A is similar in appearance to the red mudstones of facies Mp (Fig. 5a) and accordingly it is assumed that fossils with matrix type A were originally hosted within facies Mp. Matrix type B is the most common matrix type and is similar in appearance to the flood-deposited sands of facies Sc and Sh (Fig. 5b, c). Similarity between the two facies is supported by thin sections of samples from facies Sc and Sh and from NHMUK PV R 192 and NHMUK PV R 200 (Supplementary Material C, Fig. S2a, b, f and g). Matrix type C does not resemble any lithology encountered in the *Hypsilophodon* Bed, but may have been deposited as a splay sandstone, like facies Sc and Sh, given its fine sand grain size. Matrix type D, found as encrustations of irregular and angular black material and a pot of black nodules from which teeth have been picked, is similar in appearance to the small irregular black nodules found within facies Mn (Fig. 5d).

The similarity of matrix types A, B and D to facies Mp, Sc and/or Sh and Mn, respectively, suggests that *Hypsilophodon* fossils are hosted within at least three different facies. With regards to facies Mn, it is not possible to ascertain whether the fossils were buried before or after the floodplain formed a marsh due to permanent waterlogging, but does indicate the occurrence of *Hypsilophodon* at higher stratigraphic levels than those within facies Mp. The occurrence of fossils within different facies does not necessarily mean that they are stratigraphically distributed if there is also a spatial distribution of the fossils because different facies can be deposited at the same time in different places. However, the discovery of fossils with multiple matrix types from localities noted as close to Cowleaze Chine (e.g. the unregistered Robinson specimens, NHMUK PV R 2466–PV R 2467 and NHMUK PV R 28707) supports the conclusion that at least some of the fossils are stratigraphically distributed through the vertical extent of the bed.

The absence of any lithology resembling matrix type C within today's *Hypsilophodon* Bed outcrop is unusual, especially because the location of the find is given as 100 m west of Cowleaze Chine, an area that was covered by the sedimentary logs in this work. One explanation may be that the bed from which the specimen originated has eroded away since the mid-nineteenth century, given the lateral discontinuity of other sandstone units in the region and the average cliff retreat of 73 m experienced by the locality since that time (Fig. 6).

Some *Hypsilophodon* remains are known to be closely associated based on the occurrence of multiple individuals occurring within a single slab of rock (e.g. NHMUK PV R 192); however, there is also evidence that others were widely spatially distributed (Galton 1974). Although the majority of *Hypsilophodon* fossils with locality information are reported to have come from, or near to, the eastern end of the bed by Cowleaze Chine, a small number (NHMUK PV R 197, PV R 189 and PV R 190) are also reported to have come from the western end of the bed by Barnes High (Fig. 1). Furthermore, considering that most specimens have no location information or are solely labelled *Hypsilophodon* Bed, it is possible that other specimens originated from the western end of the bed (Galton 1974).

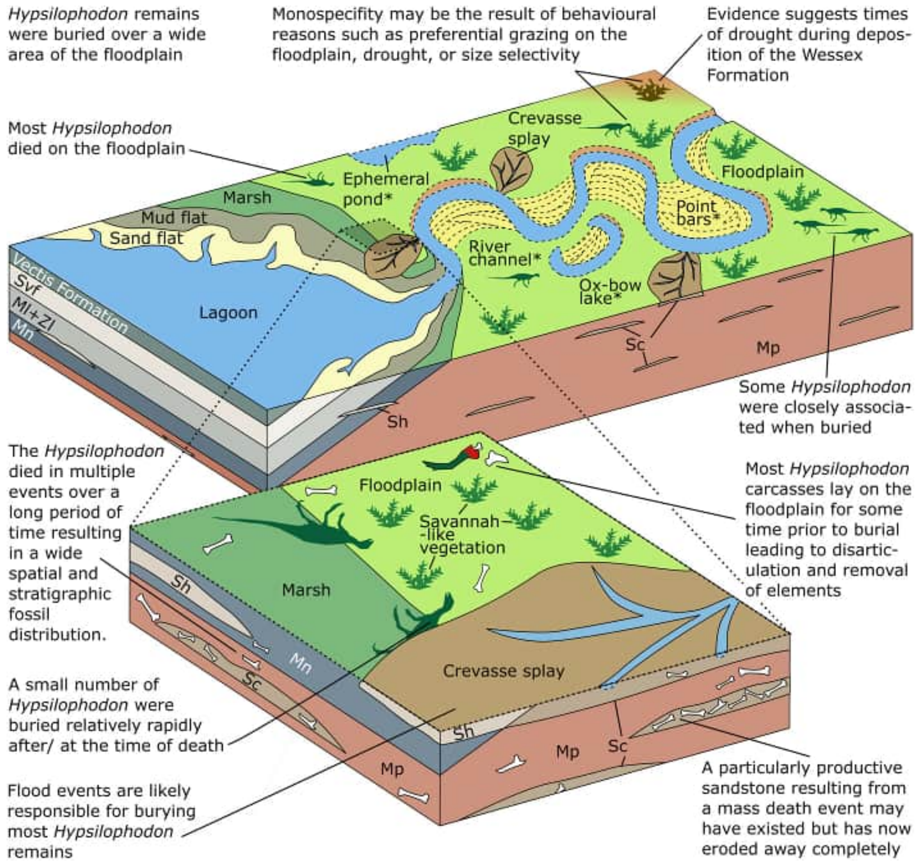

Fig. 9. Annotated facies model of a palaeoenvironmental interpretation of the *Hypsilophodon* Bed with an interpretative model showing how the fossil assemblage of the *Hypsilophodon* Bed may have formed. The figure is an interpretive representation of the palaeoenvironment and fossil assemblage formation mechanism and therefore the relative sizes of the sedimentary structures and other features are not to scale. Facies codes and colours are detailed in Table 2. Mp, red palaeosols; Sc, silty sandstone with/without climbing ripples; Sh, silty sandstones with herringbone cross-stratification; Mn, nodular black–red silty mudstones; Ml and Zl, organic-rich laminated clay and silt; Svf, white–grey silty very fine sandstone. * Features outlined by dashes have not been directly observed in the *Hypsilophodon* Bed outcrop, but are known to be present in the wider Wessex Formation (e.g. Stewart 1978). Consequently, they are not featured in the facies sketches on the side of the model.

Other evidence for the spatial distribution of fossils comes from the high rate of cliff retreat experienced by the region. On average, the cliffs in the area have retreated by 73 m since the first *Hypsilophodon* fossils were found (Fig. 6). Some specimens in the NHMUK were collected in the 1960s, with reports of rare fossils still being found in the bed today. Given the extent of cliff retreat in the interim, it is highly unlikely that these remains were closely associated with specimens recovered in the mid- to late nineteenth century.

Completeness

Examination of *Hypsilophodon* specimens in the NHMUK collections confirmed the presence of large numbers of fossils. There are >55 specimens with distinct accession numbers within the NHMUK collections, although this number must be treated with some caution due to the difficulties associated with fossil collection and accession – for example, it cannot be ruled out that, in some cases, different specimens may represent bones from a single individual. The minimum number of individuals represented was 17.

We found that the *Hypsilophodon* specimens in the NHMUK collections were highly incomplete, with much material represented by isolated bones. The predominantly low completeness can be interpreted in multiple ways. It may suggest that the burial of most of the remains was not instantaneous, with time for the bones to be removed by various processes, including transport by floodwaters, decomposition and scavenging. However, low completeness may not necessarily reflect that specimens were incomplete when buried; low completeness may also be the result of, or be exaggerated by, various processes, including the removal of bones during natural exhumation or weathering, or incomplete collection, and it is possible that a number of the isolated bones that have been collected have come from much more complete skeletons (Hungerbühler 1998).

Although articulation cannot be quantified, it is noted that much of the material in the NHMUK collections is, although largely incomplete, articulated to some degree. Relatively high levels of articulation and completeness are often found associated with floodplain environments because remains are typically only preserved where burial is relatively rapid. Such a trend was noted in the wider Wessex Formation by Insole and Hutt (1994).

Abrasion

We found that almost all the specimens show no sign of abrasion, suggesting that most of the *Hypsilophodon* have experienced little to no transport and thus died on or near to the floodplain (Fig. 8b). An alternative possibility is that the *Hypsilophodon* died within the river channel and that some fluvial transport of the carcasses occurred soon after death, which left little evidence on the bones. For example, Behrensmeyer (1990) demonstrated how bone may be resistant to abrasion when fresh and not broken. Alternatively, the carcasses could still have been fleshed during early transport, protecting the bones from abrasion. In either scenario, some mechanism, such as overbank flooding, would have been needed to move the carcasses out of the fluvial channel and on to the floodplain, given the interpreted palaeoenvironment of the *Hypsilophodon* Bed. Fossils with matrix type B are evidence that some *Hypsilophodon* remains are associated with overbank flood events. However, in the case of bones with matrix type A, the lack of coarse-grained sediment makes such a scenario less likely because there is no evidence of a high-energy overbank flood event to move the carcasses or bones onto the floodplain. We therefore argue it is more likely that most of the *Hypsilophodon* died on the floodplain and were later buried by sediments during overbank flood events, rather than perishing in the river channel and later being transported from the channel onto the floodplain.

Given the low level of abrasion of many of the bones, it is unlikely that the removal of elements during transport was responsible for the incompleteness of many of the *Hypsilophodon*. Alternatively, the carcasses may have lain on the floodplain for some time before burial, where decomposition and the removal of some elements by floodwaters, scavenging and/or trampling may all have acted to remove elements from the exposed remains. A lack of evidence of scavenging, such as tooth marks on bones, has previously been taken as evidence against such a scenario, although Fiorillo (1991) found that tooth-marked bones are a highly unusual feature in dinosaur assemblages (found in 0–4.0% of dinosaur assemblages, in contrast with up to 37.5% of mammalian assemblages). The observed lack of tooth marks on bones in the *Hypsilophodon* Bed may therefore not necessarily rule out the scavenging of remains on the floodplain. The uniformly low abrasion of the bones indicates that most of the *Hypsilophodon* remains were not extensively reworked, suggesting that reworking is unlikely to be responsible for all the observed stratigraphic distribution of fossils (Ryan *et al.* 2001).

Discussion

Origin of the fossil assemblage

If the accumulation of *Hypsilophodon* fossils in the *Hypsilophodon* Bed was due to one or two catastrophic mass death events, as has previously been suggested, then we would expect to find a predominantly monospecific assemblage, with uniform taphonomic signatures and a restricted spatial and stratigraphic extent of fossils (Ryan *et al.* 2001; Ősi *et al.* 2019; Hübner *et al.* 2021). Alternatively, if the specimens accumulated over an extended period of time, then the resulting assemblage would be expected to have a wider diversity of species, with a wide stratigraphic and spatial distribution and a variety of levels of completeness, articulation and preservation reflecting different causes of death, transport and/or time spent exposed on the floodplain before burial (Insole and Hutt 1994; Coram *et al.* 2017).

Sedimentological examination of the outcrop and fossil matrix indicates that the *Hypsilophodon* fossils were hosted in several different facies, including Mp, Sc and Mn, which are interpreted as well-drained floodplain mudstones, flood-deposited sandstones and marsh mudstones, respectively. It is unlikely that the reworking or deposition of different facies that are spatially and temporally disconnected can account for all the spatial or stratigraphic distribution. Consequently, the overall fossil distribution is more consistent with an accumulation hypothesis than a catastrophic mass death hypothesis. However, the concentration of finds with matrix type B (theorized to be hosted within facies Sc) found from, or near to, Cowleaze Chine and the close association of some remains raises the possibility that a particularly productive sandstone bed may have existed in the region of Cowleaze Chine, which could represent a mass death event occurring within the overall accumulation. Extensive cliff retreat since the mid-nineteenth century may have led to this bed eroding away completely, which would also explain the disparity in find frequency between the nineteenth century and the present day.

Taphonomic study shows that the majority of *Hypsilophodon* specimens in the NHMUK collections are highly incomplete, with many represented by isolated bones only. Very few bones show any sign of abrasion, suggesting that most of the *Hypsilophodon* underwent little transport or reworking. Given the lack of evidence for the extensive transport or reworking of bones, the remains may have lain exposed on the floodplain for some time to attain the high levels of incompleteness observed through processes including decomposition, scavenging and/or trampling, although it must also be considered that processes during exhumation and the collection of specimens could also have led to incompleteness. The level of uniformity in abrasion and the low completeness of the fossils could suggest that the *Hypsilophodon* underwent similar processes between death and burial and, as such, may be taken as evidence for catastrophic mass death events. However, the presence of notable exceptions, such as the two relatively complete specimens NHMUK PV R 5829 and NHMUK PV R 196, indicates that not all the specimens followed the same route from death to burial, with some bones being rapidly buried almost instantly, while others may have lain on the floodplain for some time. Because only a few specimens are known to be closely associated, it must also be considered that the uniformity between carcasses may be the result of the environment of death preserving the remains in a similar way.

Considering the taphonomic and sedimentological evidence together, the assemblage of the *Hypsilophodon* Bed is consistent with an overall accumulation origin, whereby the majority of *Hypsilophodon* died on or near to the floodplain and may then have lain exposed on the floodplain for some time before burial during flood events (Fig. 9). Some individuals were buried more rapidly, in some cases while still fully fleshed, while others lay exposed for greater lengths of time.

Cause of death

It is not possible to conclusively state the cause of death of the *Hypsilophodon* based on the sedimentological and taphonomic evidence, although some possibilities can be ruled out. An absence of burned wood or bone within the sediments of the *Hypsilophodon* Bed means fire can be ruled out, whereas a lack of associated volcanic ash or bentonite clay layers indicates volcanism was not involved (Sander 1987; Gates 2005).

Given the palaeoenvironmental interpretation of the *Hypsilophodon* Bed as a fluvial floodplain, both flood-related mortality and miring in soft floodplain muds or quicksand, as suggested by previous work, are possible causes of death (Stewart 1978; Insole and Hutt 1994). The presence of matrix types B and C, and matrix types A and D, are consistent with, although not diagnostic of, flood-related mortality and miring in mud, respectively.

Drought may also have played a part in the death of some of the *Hypsilophodon*, as in the *Coelophysis* quarry of Ghost Ranch, New Mexico (Schwartz and Gillette 1994). Drought leads to fossil assemblages with high preservation potential, but often leaves no obvious trace in the sedimentology, particularly in its early stages. According to Shipman (1975), during phase one of drought, lower than usual rainfall impacts the growth of new vegetation and causes temporary water bodies to dry up, increasing mortality among vulnerable animals, but leaving little evidence in the rock record. Individuals weakened by thirst or starvation are also more likely to succumb to death by other causes. A heightened risk of flash flooding immediately post-drought as a consequence of the increased runoff from the dry ground increases the chances of preserving any animals that perished in the drought (Shipman 1975). Sedimentological and palaeobotanical evidence from the wider Wessex Formation suggest that periods of drought occurred during its deposition (Allen *et al.* 1998).

However, in most instances, the evidence suggests that some time has elapsed between the death and burial of an animal and, without direct evidence, the cause of death can only be hypothesized. As such, it is likely that a range of causes of death existed, including flood-related mortality, miring and drought, but also other causes, such as predation or disease.

Monospecificity

If the *Hypsilophodon* Bed does represent an overall accumulation of remains over a long period of time, as opposed to a small number of catastrophic mass death events, the monospecificity of the bed is unusual. One possible explanation could be behavioural – for example, the floodplain may have been frequented by

Hypsilophodon, perhaps due to the existence of a certain type of vegetation that was preferential for grazing. Consequently, they are much more likely to be preserved on the floodplain than other dinosaurs or vertebrates, which only passed through the area. Drought may also explain the observed monospecificity because animals more dependent on water converge close to water sources (Shipman 1975). Another reason for the monospecificity of the *Hypsilophodon* Bed may be size selectivity. The presence of large footprints attributed to sauropods within the *Hypsilophodon* Bed suggest that larger dinosaurs were also present in the area (Gale 2019). Perhaps their limbs were too long or too strong for them to perish in floods or become stuck in the floodplain muds, unlike the much smaller *Hypsilophodon*.

Conclusions

We investigated the *Hypsilophodon* Bed by examining the top 3 m of the Wessex Formation, directly below the White Rock, where it outcrops between Cowleaze Chine and Barnes High on the SW coast of the Isle of Wight. The bed consists of mottled red mudstones, nodular black mudstones and laminated grey clays and siltstones interbedded with thin, laterally discontinuous sandstone units. The palaeoenvironment of the bed is interpreted as a well-drained fluvial floodplain, subject to numerous overbank flood events, which subsequently became a marsh and mudflat at the edge of a lagoon due to relative sea-level rise. Examination of historical reports and the fossil matrix suggests that the *Hypsilophodon* fossils were stratigraphically and spatially distributed throughout the bed.

The *Hypsilophodon* specimens in the NHMUK collections are highly incomplete, with many represented by isolated bones alone, although there is significant variability, with some relatively complete specimens also being found. The high incompleteness of the collected material suggests that the *Hypsilophodon* remains were similarly incomplete when buried, indicating the disarticulation and scattering of remains prior to burial – however, it cannot be ruled out that the removal of bones during natural exhumation and/or incomplete collection may also be responsible for some amount of specimen incompleteness. Most of the specimens show little sign of abrasion, suggesting little to no transport of the remains. Consequently, many carcasses may have lain exposed for some time on the floodplain, resulting in their observed incompleteness, although rare instances of highly complete specimens suggest that some of the *Hypsilophodon* were buried very rapidly.

Combined with the stratigraphic and spatial distribution of fossils, the varied taphonomic signatures and evidence for delayed burial are consistent with an accumulation origin for the fossil assemblage of the *Hypsilophodon* Bed. However, it is possible that particularly productive layers representing mass death events may have occurred within the overall accumulation, although these have most likely been eroded away since they were first discovered in the mid-nineteenth century as a result of extensive coastal erosion. The cause of death is difficult to ascertain, but it is likely that there were multiple causes. Although the monospecificity of the bed is unusual for an accumulated assemblage, behavioural reasons, drought and size selectivity may explain the low diversity of the fossil assemblage.

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