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A Middle Devensian woolly rhinoceros (*Coelodonta antiquitatis*) from Whitemoor Haye Quarry, Staffordshire (UK): palaeoenvironmental context and significance

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ABSTRACT: This paper reports the discovery of a rare partial skeleton of a woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach, 1799) and associated fauna from a low Pleistocene terrace of the River Tame at Whitemoor Haye, Staffordshire, UK. A study of the sedimentary deposits around the rhino skeleton and associated organic-rich clasts containing pollen, plant and arthropod remains suggests that the animal was rapidly buried on a braided river floodplain surrounded by a predominantly treeless, herb-rich grassland. Highlights of the study include the oldest British chironomid record published to date and novel analysis of the palaeoflow regime using caddisfly remains. For the first time, comparative calculations of coleopteran and chironomid palaeotemperatures have been made on the same samples, suggesting a mean July temperature of 8–11 °C and a mean December temperature of between −22 and −16 °C. Radiocarbon age estimates on skeletal material, supported by optically stimulated luminescence ages from surrounding sediments, indicate that the rhino lived around 41–43 k cal a BP. The combined geochronological, stratigraphic and palaeoenvironmental evidence places the assemblage firmly within the Middle Devensian (Marine Oxygen Isotope Stage 3). This would agree with other regional evidence for the timing of aggradation for the lowest terrace of the Trent and its tributary systems. Copyright © 2012 John Wiley & Sons, Ltd.

KEYWORDS: Devensian; Invertebrates; Palaeoenvironments; River Trent; Woolly rhinoceros.

Introduction

In 2002, the partial skeleton of an exceptionally well-preserved woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach, 1799) came to light in a single machine bucket scoop at Whitemoor Haye sand and gravel quarry (SK 173 127) in the valley of the River Tame, Staffordshire, UK (Fig. 1). The bones were in excellent condition and represent the best example of a woolly rhinoceros found in Britain this century and one of the most important finds of a Pleistocene fossil mammal skeleton made in the UK in the last 100 years (Fig. 2). The stratigraphic position of the Holme Pierrepont terrace, which is relatively low within the Trent 'terrace' staircase (Fig. 3), is consistent with a Late Pleistocene age for the remains. During rescue excavations, additional remains of fossil mammals (including other rhinos) were discovered at the site, together with well-preserved beetles, aquatic invertebrates, pollen and plant macrofossils, thereby allowing the palaeoenvironment occupied by this extinct mega-herbivore to be reconstructed within a well-constrained geochronological framework based on radiocarbon and optically stimulated luminescence (OSL) dates.

The River Tame is one of the major tributaries of the Trent catchment, draining the area to the east of Birmingham before entering the Trent near Alrewas in Staffordshire. Historically, Quaternary research along the Tame Valley has been limited, with the majority of studies concerning Pleistocene fluvial history and environmental change undertaken on the terrace sediments of the Trent and its tributaries downstream of Burton-on-Trent, including palaeodrainage courses denoted by spreads of sand and gravel across present-day Lincolnshire (e.g. Clayton, 1953; Brandon and Sumbler, 1988, 1991; Howard et al., 2007, 2011; White *et al.*, 2007, 2010; Bridgland *et al.*, 2012). Vertebrate assemblages reported include Ipswichian remains from the terrace deposits of the River Derwent near Derby (Bemrose and Deeley, 1896; Jones and Stanley, 1974) and a pre-Ipswichian fauna from the Balderton Sand and Gravel near Newark on Trent (Lister and Brandon, 1991; Schreve, 2007). In contrast to the well-documented palaeontological evidence from the Thames valley (Bridgland, 1994; Schreve, 2001), this part of the Trent has been notably poor in terms of fossil vertebrates, owing to the acidity of the underlying Permo-Triassic bedrock. With the exception of the Derby site mentioned above, all other vertebrate localities are underlain by the calcareous Jurassic lithologies further to the east. The Whitemoor Haye site is therefore unusual and represented an exceptional opportunity to reconstruct the palaeoenvironmental and faunal history of an open-air Late Pleistocene site in the western part of the English Midlands.

Geological context

The quarry is situated on a low terrace of the River Tame, approximately 2 km upstream from the contemporary confluence with the Trent and 32 km NNE of Birmingham. Exposures of sand and gravel indicate a bipartite sequence

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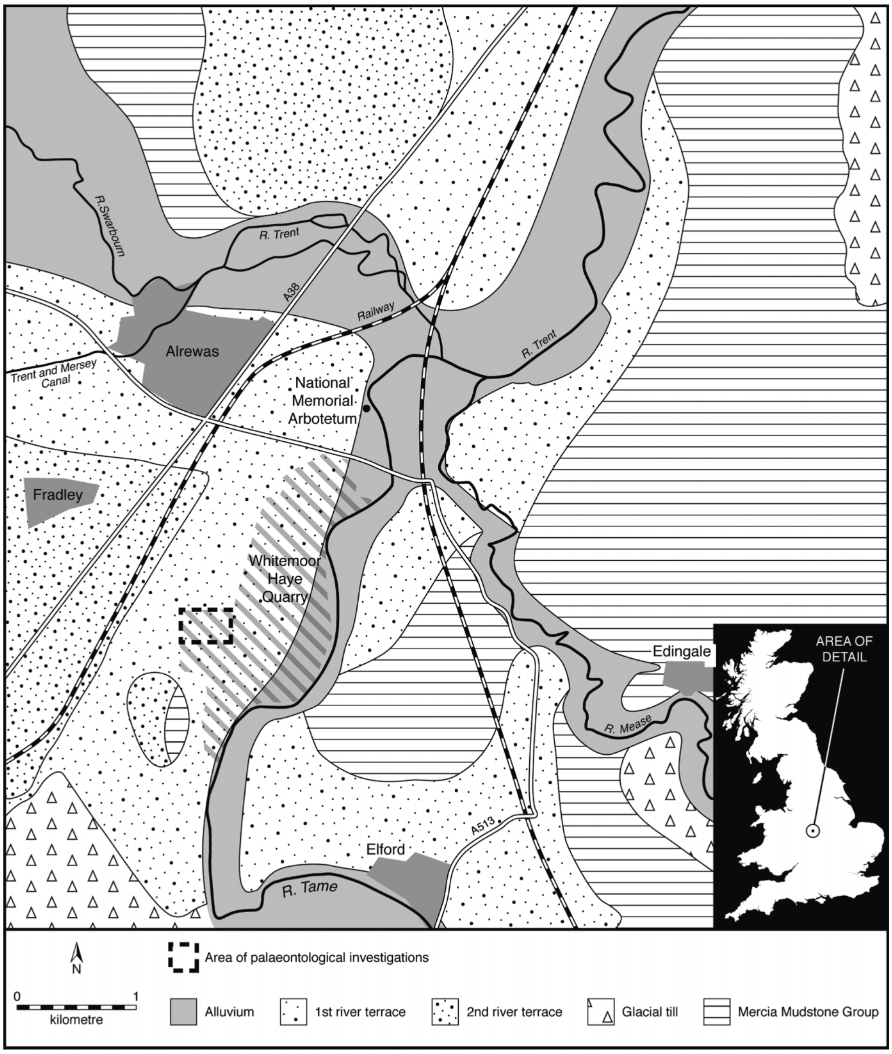

Figure 1. Location and solid–superficial geology of the Whitemoor Haye area. Based on BGS sheet 140 (Burton on Trent) and 154 (Lichfield). These sheets have not been revised in terms of modern terminology for the Trent Valley as illustrated on Fig. 3 (for a review see Howard *et al.*, 2007). The 1st Terrace of the Tame–Trent confluence is the lateral equivalent of the Holme Pierrepont Sand and Gravel and the majority of the 2nd Terrace (also recorded as the Older River Gravel on Sheet 154) is probably equivalent to the Beeston Sand and Gravel, although correlation of parts of this deposit with earlier terrace units cannot be discounted on the basis of current research knowledge.

of deposits comprising an upper unit of massive to poorly bedded gravels (3–4 m thick), underlain by a lower unit of well-bedded sands (*c.* 2 m thick). This bipartite sequence rests on the undulating rockhead surface of the Mercia Mudstone Group [red mudstones, marls and siliceous siltstone bands (skerries) of Triassic age], which is demonstrably lower in the central part of the current quarry area, probably due to fluvial scour and channelling. The woolly rhinoceros skeleton was discovered by machine excavation close to the contact of the lower sand unit with the bedrock in the Phase 4 area of the quarry (Fig. 4).

Figure 2. The rhinoceros skeleton shortly after its discovery. This figure is available in colour online at wileyonlinelibrary.com.

The lower unit (here termed the Lower Sands) predominantly comprises a sequence of well-sorted sands occupying a series of stacked channels in a braided river system, with some thin interbedded units of massive gravel (comprising local Triassic ‘Bunter Pebble Bed’ quartzite and quartz, now part of the Sherwood Sandstone Group). Internally, these sand-filled channels exhibited well-developed bedding structures including both planar and trough cross-bedding and ripple lamination. Internal structure was commonly picked out by fragments of coal deposited along foresets (Fig. 5). Individual trough foresets were up to *c.* 0.5 m high with planar foresets up to 0.3 m high. Multiple reactivations and erosion of individual channel bedforms and changes in bedform type (i.e. trough to

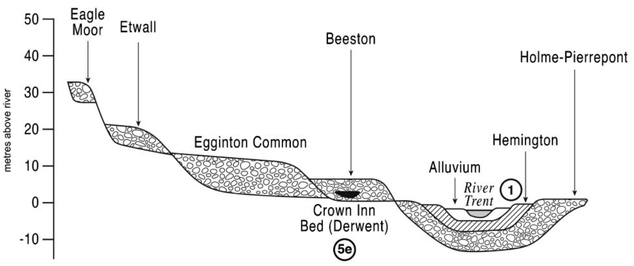

Figure 3. Schematic cross-section through the middle Trent terrace staircase with inferred correlation of interglacial deposits with the marine oxygen isotope record (numbers in circles), modified from Bridgland *et al.* (2012).

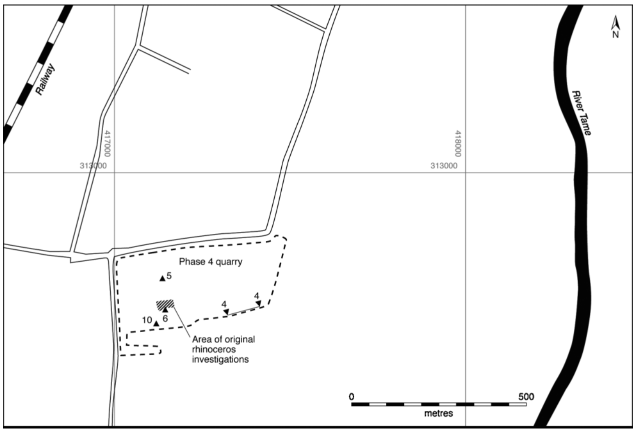

Figure 4. Detail of Phase 4 of the quarry, with the area of the original investigation marked (centred on the rhinoceros skeleton) and other sections mentioned in the text numbered and indicated by a black triangle.

ripple bedded) suggested frequent changes in flow velocity and discharge. Measurement of palaeocurrent (from foresets and imbrication) indicated no uniform flow direction, but variation between 210 and 310° (south-west to north-west) suggests that although these terrace sediments are in the confluence zone, they were deposited by the tributary River Tame. Examples of frozen sediment (denoted by sharp deformed contacts) entrained within these sandy channels suggest that the River Tame was probably operating under a periglacial climatic regime (Bryant 1982a, b). Thin organic-rich clays (0.01–0.1 m thick) with macroscopic plants remains were observed within the basal metre of the Lower Sands. These formed small lenses within the sands or more continuous drapes over pre-existing bedforms and suggested areas and periods of lower energy flow across the floodplain, probably across bar surfaces and within abandoned braid-channels away from the main channel belt. Where organic material was preserved, in parts it had the appearance in the field of a humic gley soil (S. Limbrey, pers. comm.). Such soil development would imply subaerial conditions prevailed for a prolonged period allowing a plant community to become established.

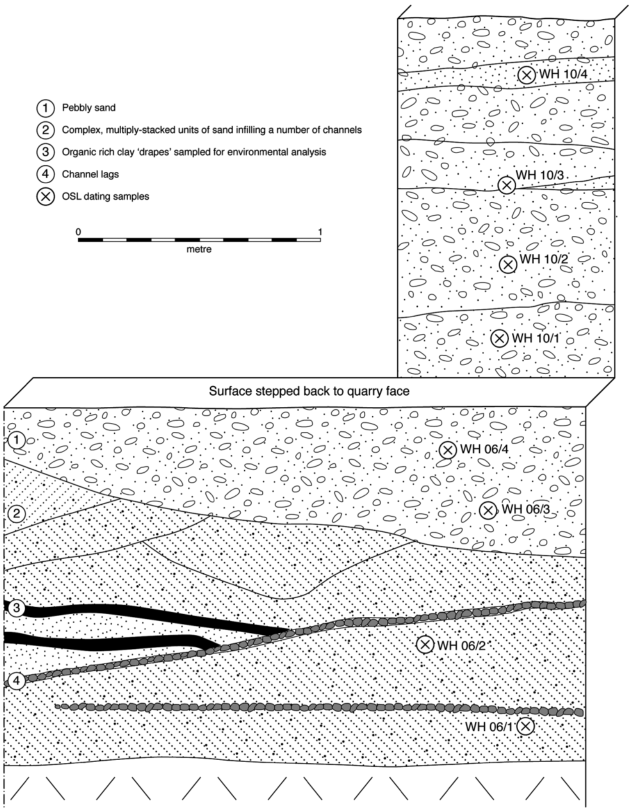

Figure 5. Schematic section through the Lower Sands of Section 6 and Upper Gravels of Section 10, with location of OSL sampling points (WH06/1-4 and WH10/1-4) indicated.

pH samples taken from Section 6 (Fig. 5), close to the principal rhino location, lay within the range 5.1–5.6 (moderately acidic) in the Lower Sands but fell to extremely acid levels of pH 3.0–3.8 in the clay drapes. A sample of sand from within the nasal cavity of the rhinoceros skull gave a pH of 3.6. This would suggest that the skeleton lay at the level of the clay drapes within the sands, rather than at the interface with the bedrock. Preservation of bone and tooth even for short periods under such acid conditions requires a protective process. The bones are stained reddish-brown, indicating impregnation with iron oxides and/or other iron compounds. Some isolated bones found elsewhere on site (see below) are well mineralized and black, suggesting uptake of iron sulphide. The undulating surface of the Mercia Mudstone would have provided opportunities for localized ponding and stagnation of water and organic debris, leading to a near-neutral pH. This would have produced the necessary reducing environment for mobilization of iron and the mechanism for its uptake in bone, thereby assisting in preservation (S. Limbrey, pers. comm.).

Although no evidence of cold-climate periglacial structures such as ice wedge pseudomorphs (Harry and Gozdzik, 1988) was noted within the Lower Sands immediately around the main concentration of vertebrate remains, a thin organic channel beneath the overlying coarse gravels in Section 4 (Fig. 6) displayed evidence for a 'frozen' contact with the Lower Sands and ice-related deformation. Elsewhere, dislocated frozen blocks of sand and gravel, still containing evidence of bedding structures, were noted within the Lower Sand (I. Candy, pers. comm.), and may have been incorporated into these sandy channels by the undercutting of frozen channel banks by fluvial processes. Ventifacts, a common feature of periglacial environments, were also observed across the quarry floor. A second small organic channel (*c.* 2 m wide) was observed in Section 5 (Fig. 7), incised into the base of the Mercia Mudstone and close to the main concentration of rhinoceros bones.

The Lower Sands were overlain by 3–4 m of massive to poorly sorted, coarse, clast-supported gravels ('Upper Gravels') (Fig. 5 upper part; Fig. 6). Lithologically, the gravels comprised locally derived quartzite and quartz (of 'Bunter' origin). These gravels were interspersed by thin (0.2–0.4 m) units of sand either overlying the gravels or forming small (slough) channels. Internally, the sands varied between structureless, rippled or cross-bedded. Palaeocurrent direction measured from foresets or imbricated clasts indicated a wide spread of palaeoflows, akin to those of the Lower Sands. No organic-rich beds were noted within the Upper Gravels. The top 1 m was clay-enriched and included matrix-supported pebbles of quartzite and friable sandstone, suggesting weathering of this upper surface. The base of the 'weathered' zone appeared coincident with a level of sediment deformation in the form of V-shaped depressions (Fig. 6), each approximately 1 m wide and 1.5 m deep. These depressions were infilled with sands and pea gravel and had weathered contacts with the surrounding Upper Gravels. These deformation features could not be traced between sections or identified upon the stripped surface of the quarry and are therefore not considered to represent ice wedge casts (Harry and Gozdzik, 1988; Worsley, 1996). However, they are

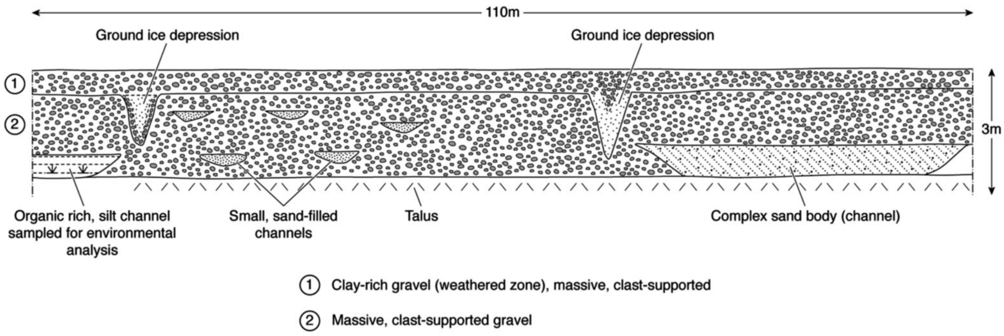

Figure 6. Schematic section through the Upper Gravels in Section 4.

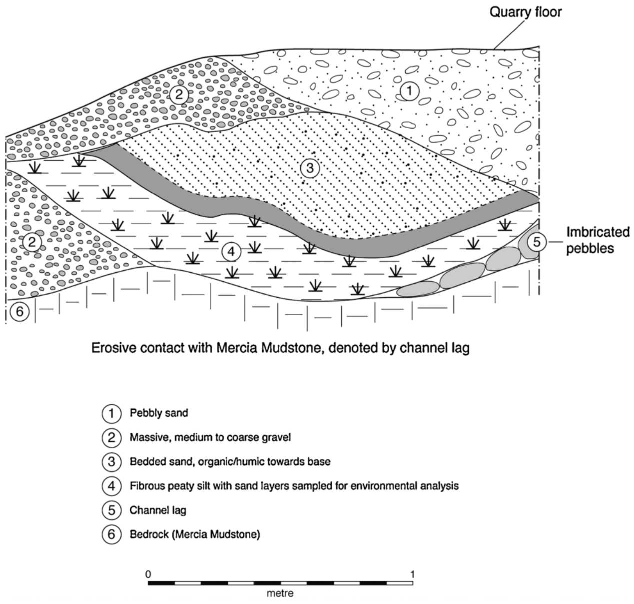

Figure 7. Schematic section through the channel deposits in Section 5.

considered to be of periglacial origin, associated with ground ice under permafrost conditions.

On the basis of observed evidence, it can be demonstrated that the Upper Gravels were also deposited under braided river conditions (Bryant, 1982a, b), although the coarser sediment of this unit suggests increased discharge, perhaps reflecting the onset of harsher climatic conditions, a suggestion corroborated by the periglacial evidence.

Vertebrate remains

The fluviatile sands and gravels yielded a fossil mammal assemblage attributable to the Middle Devensian [Marine Oxygen Isotope Stage (MIS) 3, *c.* 60–25 ka BP), the most significant find being the well-preserved anterior part of a skeleton of woolly rhinoceros (*C. antiquitatis*). Woolly rhinoceros material is relatively common at sites of this age across Britain (see Jacobi *et al.*, 2009) but it is rarely so well preserved and is usually heavily gnawed by the dominant predator, the spotted hyaena *Crocuta crocuta* Erxleben. Although the skeletal material was not seen *in situ* in the ground, the fact that it was recovered from a single machine bucket scoop and is composed predominantly of associated elements (Fig. 8) strongly suggests that these were originally in articulated (or near-articulated) position. The discovery of associated skeletal parts is unusual in Pleistocene deposits of any age but particularly so in the West Midlands, where vertebrate remains are encountered only infrequently because of the bedrock conditions described earlier. The only other remains of woolly rhinoceros of comparable completeness were found in Dream Cave, near Wirksworth in Derbyshire (Buckland, 1823) but this skeleton has unfortunately long since disappeared. The mammalian species list from Whitemoor Haye is shown in Supporting Information, Table S1, together with numbers of identified specimens and minimum numbers of individuals.

Thirty-three separate elements were identified from the partial rhinoceros skeleton (supporting Table S1). These include a complete cranium (Fig. 9A,B) and lower jaw (Fig. 10), some of the vertebrae and ribs, a single scapula and the major parts of the anterior limbs. The material is superbly preserved, although some bones showed minor damage from machine excavation, for example the left jugal of the cranium. Although major parts of the posterior skeleton (pelvis and hind limbs) were not found, the last lumbar vertebra and the last rib on the right side were later recovered from the same area as the front part. This would suggest that either the posterior part had been removed by quarrying at an earlier stage and had been destroyed, or that the posterior part had become dispersed by fluvial activity in antiquity. The recovery of two almost perfect ribs, seemingly part of the articulated skeleton, 100–150 m to the north-west of the rhinoceros site, may support the latter hypothesis. A number of features of the partial skeleton all point to the very rapid burial of a (probably frozen) carcass. These include the excellent preservation of the bone surface, the presence of the fragile stylohyoid bones and nasal turbinates, the occurrence of dental calculus (normally removed by post-depositional

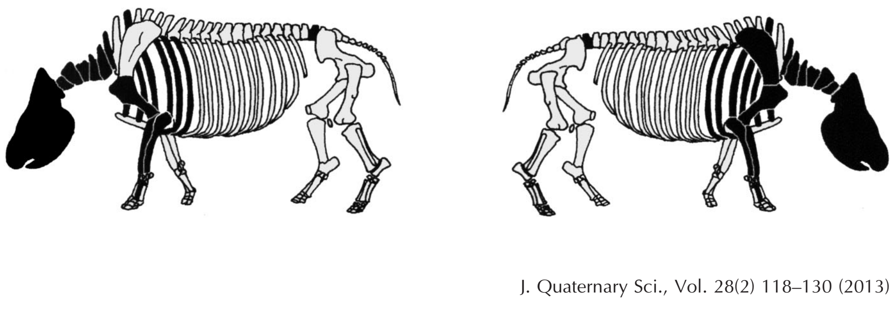

Figure 8. Left and right sides of diagrammatic rhinoceros skeleton, showing anatomical position of recorded elements in black.

Figure 9. (A) Lateral view of cranium of woolly rhinoceros (from anterior skeleton); (B) dorsal view of same. Scale in cm. This figure is available in colour online at wileyonlinelibrary.com.

transport) and the preservation of plant remains in the fossae of the upper dentition (Fig. 11). It is therefore suggested that the posterior part of the carcass became re-exposed after deposition and was subsequently dispersed by the braided river, whereas the anterior part remained undisturbed.

Based upon additional material collected, the remains of at least four adult woolly rhinoceroses are preserved at the site (the most abundant species within the vertebrate assemblage). Aside from the partial skeleton, the three other individuals were all identified on the basis of partial crania (see supporting Table S1), in varying states of completeness. The remainder of the faunal assemblage reveals a range of preservational states, including quite badly abraded material that has clearly been fluvially transported. After woolly rhinoceros, a minimum number of two individuals of reindeer (*Rangifer tarandus*), including one female, is present, together with two individuals of mammoth (*Mammuthus primigenius*) (one juvenile) and a single individual each of horse (*Equus ferus*), bison (*Bison priscus*) and wolf (*Canis lupus*).

In terms of the first rhinoceros' ontogenetic age, it exhibits a nearly complete nasal septum (Fig. 9A), a feature that gradually ossifies during senescence in order to strengthen the skull and support the very large nasal horn. Borsuk-Bialynicka (1973) provided a scheme for identifying the biological age of woolly rhinoceros using the state of ossification of cranial sutures, level of tooth wear and degree of ossification of the nasal septum. Following this scheme, the specimen from Whitemoor Haye has a fully erupted dentition with an upper third molar that is entering wear; the palatomaxillary suture is not fully ossified; the nasal bones conform to group 'C' (Borsuk-Bialynicka's final developmental stage) (Fig. 9B); and the nasal septum falls into category 'D' (ossification almost complete). These characteristics indicate that this individual was an 'old-adult', the penultimate age class in Borsuk-Bialynicka's scheme. However, the degree of ossification of the nasal septum suggests that this specimen is a young representative of this age class. Based upon comparison with the longevity of the extant white rhinoceros (*Ceratotherium simum* [Burchell]) (Hillman-Smith *et al*., 1986), which has a similar morphology and grazing diet to the woolly rhinoceros, the Whitemoor Haye specimen was probably between 14 and 20 years old at time of death.

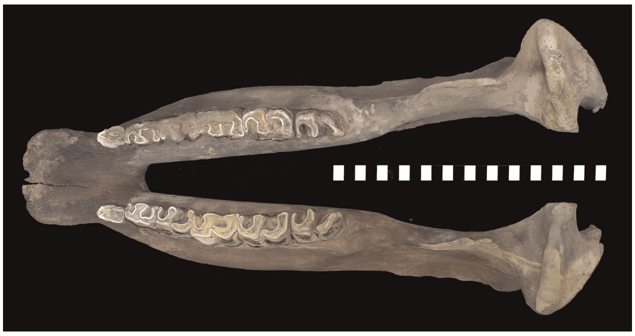

Figure 10. Lower jaw of woolly rhinoceros (from anterior skeleton). Scale in cm. This figure is available in colour online at wileyonlinelibrary.com.

Invertebrate remains

Samples for arthropod analysis were taken from three localities, Sections 4, 5 and 6 (Figs. 5–7). Sections 4 and 5 were taken from the two small palaeochannel deposits and were bulked up from multiple samples. At Section 6 (Fig. 5, in the vicinity of the rhinoceros skeleton), samples 6, 7 and 8 were recovered from discrete organic clasts within the clay drapes and clay balls within the Lower Sands. The samples, all approximately 40 L in volume, were processed according to Coope (1968, 1986), Kenward *et al*. (1980) and Greenwood *et al*. (2003) and sorted from the resulting floating fraction (sieved down to 90 μm for the chironomids, which were extracted from the beetle floats) using a ×10–40 binocular microscope. Identifications were made by direct comparison of the fossils and modern specimens using a surface illuminating microscope with magnifications up to ×200. All the samples of organic sediments yielded abundant well-preserved insect remains, as well as crustaceans. Most numerous and diverse of the insects were Coleoptera, but Chironomidae and Trichoptera were also examined in detail. Other orders present, not described in detail here, include Hymenoptera, Hemiptera, Megaloptera and Arachnida.

Supporting Table S2 lists the beetle species recovered (all now archived in the Lapworth Geological Museum, University of Birmingham). The nomenclature and taxonomic order is according to that of Lucht (1987). Altogether, 156 coleopteran taxa were recognized, of which 118 could be determined to species or species group. There is no significant difference

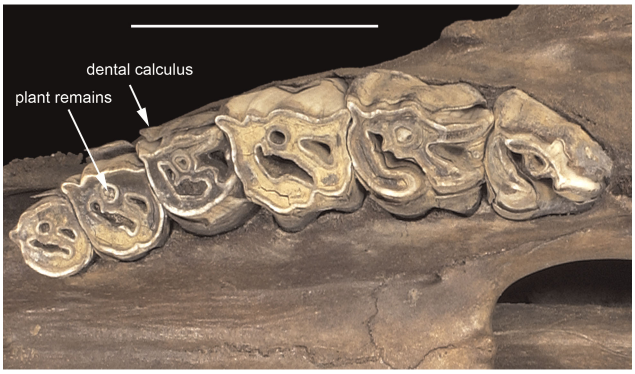

Figure 11. Detail of the right upper dentition of the rhinoceros, showing embedded plant remains within the dental fossae and the presence of dental calculus. White scale bar = 10 cm. This figure is available in colour online at wileyonlinelibrary.com.

between the beetle assemblages from all three sections and they appear to represent debris swept off the adjacent land surface either by wind or by flood-water and deposited in local sedimentary traps on the floodplain. Chironomid remains from Sections 4 and 5 are listed in supporting Table S3, with identification and ecological assessment following Brooks *et al.* (2007). Twenty-six chironomid taxa were identified from 97 specimens. Caddis fly remains are listed in supporting Table S4 according to the nomenclature and taxonomic order of Barnard (1985). A total of 17 taxa from six families were found. Again, the distribution of taxa across all samples shows little variation and as such the data set is considered as a single assemblage.

Pollen and plant macrofossils

A bulk sample from Section 6 (Fig. 5) was taken from the thin organic-rich clay drapes at the base of the Lower Sands. A subsample of 200 cm^3 was disaggregated in cold water and then wet-sieved through a nest of sieves, the finest mesh size being 150 μm. Macroscopic plant remains were picked from the resulting residues under a low-power binocular microscope and identification of the fossils was accomplished by comparison with modern reference material. The nomenclature follows Tutin *et al.* (1964–1993) and the assemblage is listed in supporting Table S5. The sample from Section 6 yielded a low-diversity assemblage with only 17 plant taxa recorded, supplemented by a seed of Caryophyllaceae and a moss fragment from Section 4, and a seed of *Taraxacum* sp. from Section 5, which were recovered during processing for pollen (see below).

Because of the fragmentary nature of the organic lenses, it was only possible to take spot samples for pollen analysis, two of which are reported here from Sections and 5 (Figs 6 and 7). Samples were processed using a modified version of the standard method (see Moore *et al.*, 1991); about 1-cm^3 subsamples were dispersed in dilute NaOH and filtered through a 70-μm mesh to remove coarser material. The finer organic part of the sample was concentrated by swirl separation on a shallow dish. Fine material was removed by filtration on a 10-μm mesh. The material was acetolysed to remove cellulose, stained with safranin and mounted on microscope slides in glycerol jelly. Counting was undertaken with a Leitz Dialux microscope with material compared with a personal pollen reference collection and standard texts such as Faegri and Iversen (1989) and Andrew (1984). The nomenclature and order of the taxa follow Bennett (1994) and Kent (1992), respectively (see Table 6). The pollen counts were low, although this is not unexpected given the restricted size of the organic clasts sampled. The spectra from each sample are similar and they are therefore combined for discussion (see below).

Palaeoclimatic reconstruction

The beetle remains are strongly indicative of severely cold and continental climates akin to central Asia today. Of the 118 coleopteran species determined, 44 are now exotic to Britain with some found living today only in northern Siberia or in the high plateaux of central Asia. Cold-adapted species include *Amara alpina*, *Diacheila arctica*, *Aphodius holdereri*, *Bembidion hyperboraeorum*, *Ochthebius kaninensis* and a range of others indicated by an asterisk (*) in supporting Table S2, now widespread across northern or central Asia. Two circumpolar species of *Helophorus* (*H. oblongus* and *H. splendidus*) occur in northern Siberia as far west as the Ob Gulf, but have yet to be found in arctic Europe (Angus, 1992), whereas *Tachinus instabilis* is widespread in northern Canada and Alaska as well as arctic Siberia. An undetermined species of *Aphodius* (subgenus *Volinus*), characterized by an unusual aedeagus, is not a European species but resembles several exclusively central Asiatic species. The Whitemoor Haye coleopteran assemblage included 53 species of carnivorous and general scavenging beetles that may be used to make a quantitative estimate of the palaeoclimate using the Mutual Climatic Range (MCR) method (Atkinson *et al.*, 1987). Species used in this calculation are indicated by MCR in supporting Table S2. These species gave the following values:

T_{max} (mean monthly July temperature): 8–11 °C

T_{min} (mean monthly January–February temperature): −22 to −16 °C

These figures should be viewed as conservative estimates only because actual mean monthly temperatures were probably at the lower end of both these summer and winter ranges (see Coope *et al.*, 1998). The MCR estimates indicate that any precipitation during the colder part of the year would have fallen as snow and would have accumulated until the following spring thaw, when high-energy flood waters would have dominated the hydrological regime.

The chironomid assemblage contains a mixture of taxa characteristic of temperate, mesotrophic to eutrophic lakes (in particular *Chironomus anthracinus*-type, 21% of the fauna) but also taxa preferring lower temperatures and less eutrophic conditions, including *Stictochironomus rosenschoeldi*-type, *Micropsectra insignilobus*-type and *Corynocera ambigua*. In addition, cold stenothermic taxa make up 13% of the fauna, such as *Micropsectra radialis*-type, *Orthocladius* type S and *Hydrobaenus conformis*-type. These taxa are typically restricted to arctic or high alpine, oligotrophic waters. A chironomid-based, weighted averaging-partial least squares two-component, mean July air temperature inference model (Birks, 1995) was employed to reconstruct mean July air temperature; this represents the first time that beetle- and chironomid-derived summer temperatures have been produced from the same samples. The model has a root mean squared error of prediction of 1.01 °C and a coefficient of variation (r^2) of 0.91, and is based on a modern Norwegian calibration set of 154 lakes covering a mean July air temperature range of 3.5–16.0 °C (Brooks and Birks, 2001; Self *et al.*, 2011). This yielded a July temperature estimate of 10.8 ± 1.1 °C, thus similar to the summer palaeotemperature reconstruction based on beetle MCR and implying that the ecologies of both groups have probably not changed since this period. The mix of chironomid taxa with a wide range of thermal and trophic preferences is unusual. In a modern calibration set of 157 Norwegian lakes, *Chironomus anthracinus*-type and *Micropsectra radialis*-type occur together in only four lakes, which have a range of mean July air temperatures from 9.5 to 11.2 °C. The fossil assemblage has no close analogues in the modern dataset and has a high squared chord dissimilarity of more than 20% of the empirical distribution of dissimilarity coefficients. The indication from the beetle assemblage that the climate was more continental than today is also supported by chironomid analysis. Estimates from a chironomid-based continentality inference model developed by Self *et al.* (2011), based on a modern calibration set of 149 lakes from Norway and European Russia, suggest that the continentality index was 30, similar to that found today in the eastern Baltic, eastern Europe and European Russia. Summer temperatures inferred from a Russian chironomid-based inference model (Self *et al.*, 2011) are estimated at 13.3 ± 1.0 °C. This higher temperature estimate reflects the higher temperature optima required by chironomid species to complete their life cycles in the short highly continental Russian summer. Nevertheless, the fossil assemblage has no close modern analogues in the modern Russian calibration set and squared chord dissimilarity is more than 20% of the empirical distribution of dissimilarity coefficients. A temperature reconstruction was also produced using a modern calibration set based on the Norwegian dataset combined with a Swiss dataset (Heiri *et al.*, 2011). This model estimated the mean July air temperature at 11.3 ± 1.3 °C, which is close to the estimate based on the Norwegian model. The fossil assemblage has no close analogues in the modern Norwegian–Swiss calibration set but is about 15% of the empirical distribution of dissimilarity coefficients. The caddisflies provide little evidence of palaeoclimatic conditions at this time but of potential palaeoclimatic interest is an unidentified species of *Stenophylax* whose nearest match appears to be an un-named Icelandic specimen.

A single example of a crustacean, the tadpole shrimp *Lepidurus arcticus*, was recorded from Section 4. Today, it has a circumpolar distribution in the Arctic where it is usually found in temporary pools, occurring no closer to Britain than the Norwegian mountains. It has been recorded as a fossil from numerous sites in Britain where it is always associated with cold-adapted beetle species (Taylor and Coope, 1985). Cold climatic conditions are echoed by the plant macrofossils, which are all from taxa today that can survive close to the Arctic circle (Hultén, 1950; Meusel and Jäger, 1965, 1978; Jalas and Suominen, 1972; Hultén and Fries, 1986).

Palaeoenvironmental reconstruction

MIS 3 (the Middle Devensian in Britain) represents the warmest part of the last cold stage and is characterized by rapid (often millennial-scale) climatic oscillations. Interpreting the impact of rapid climatic fluctuations on the landscape, vegetation and fauna remains challenging and has been hindered by the dual constraints of poor chronology and resolution, particularly in open (i.e. non-cave) sites. Nevertheless, the highly diverse mosaic environment of this period, generally termed 'mammoth steppe' (Guthrie, 1990), was capable of supporting extremely large herbivore biomass. The large mammals indicate the predominance of open ground conditions with abundant grazing and a cold climate. The presence of *C. antiquitatis* itself is diagnostic of the presence of grasses and low-growing herbaceous vegetation, as woolly rhinoceroses possessed a low-slung head carriage and a hypsodont dentition with thick enamel and dental cement that is typical of grazing animals. Woolly rhinoceroses were furthermore adapted to dry climates with minimal snowfall, as their large size, combined with relatively short legs and the lack of splayed hooves or pads on the feet, made it impossible for them to cope with deep snow (Kahlke, 1999). A similar picture of open vegetation is revealed by the pollen assemblage, with grasses and sedges most numerous, a range of herbs and tree and shrub pollen very limited (mostly *Betula* with a trace of *Pinus*, although *Quercus* was noted in Section 5).

The invertebrate assemblages, in particular the beetles, are ecologically diverse and include species of aquatic, riparian and also drier habitats (see supporting Table S7). The presence of both running and permanent standing or slow-flowing water at the site is indicated by all invertebrate groups. Aquatic beetle taxa are present that are associated with well-oxygenated running water, such as streams with hard substrates of sand and gravel and some submerged vegetation. However, riffle beetles (Elminthidae) that are often abundant in shallow streams in temperate environments are conspicuously absent. Species of still-water environments are varied and abundant. Of particular interest is the abundance of *Helophorus glacialis*, which is stenothermic and largely confined to pools at the margins of melting snow patches where the temperature of the water is close to freezing (Hansen, 1987). Most of the chironomid taxa present in the assemblage typically occur in standing waters but *Eukiefferiella* (2.1% abundance) primarily inhabits flowing water. The resting eggs (ephippia) of *Chydorus* sp. and *Camptocercus* sp., which live amongst aquatic weeds, were fairly common in the samples and water flea, *Daphnia* cf *pulex*, a species of small shallow (often temporary) ponds, was present in modest quantities.

The four aquatic plant taxa recorded denote deposition in relatively shallow still or slow-flowing water, probably less than 1.5 m deep. This relatively shallow water may account for the lack of modern analogues for the fossil chironomid assemblage in the modern datasets, as many of these lakes are deeper than this. Preston (1995) noted that *Potamogeton friesii* prefers calcareous water that is often eutrophic, and likewise *Myriophyllum spicatum* favours alkaline water conditions with a mesotrophic to eutrophic nutrient status. The presence of *Ranunculus* subgenus *Batrachian* achenes indicates that the water surface was locally covered by patches of water buttercup.

A diversity of flow conditions is upheld by the composition of the caddisfly assemblage (see supporting Table S4), as the larvae have distinct habitat preferences and the different species are associated with most types of water-body, from ephemeral pools to large lowland rivers (Greenwood *et al.*, 2003). A metric (PalaeoLIFE), based on that developed for contemporary streams (LIFE – 'Lotic-invertebrate Index for Flow Evaluation') by Extence *et al.* (1999), has been developed for hind-casting palaeochannel flow environment and has been successfully applied to Trichoptera, Coleoptera and Chironomidae (Greenwood *et al.*, 2006; Howard *et al.*, 2009, 2010). All freshwater macroinvertebrate taxa are assigned to one of six flow groups, ranging from Group I taxa (primarily associated with rapid flows, typically $>100\,\mathrm{cm\,s^{-1}}$) to Group VI taxa (associated with drying or drought-impacted sites). Applying the metric gives a value for each assemblage of between 12 (all members of the community being Group I) and 1 (all members of the community being Group VI). The taxonomic diversity of each fossil community and the categorization of each taxon into a known flow group then allow the reconstruction of palaeoflow conditions. At Whitemoor Haye, the PalaeoLIFE scores using the caddisfly data range from 6.88 to 7.22, with the number of taxa in each flow group shown in supporting Tables S4 and 8A.

To compare the flow regime inferred from the caddisflies with that from the beetles, a parallel exercise was carried out using the aquatic beetles only (supporting Table S8B). This shows a remarkably similar grouping of flow indicators provided by the two insect orders. Based upon their flow characteristics, there appear to be two assemblages within the caddisfly and coleopteran assemblages from Whitemoor Haye: taxa associated with moderate to fast flows ($20–100\,\mathrm{cm\,s^{-1}}$) from Flow Groups I/II ($n = 8/15$) and taxa from Flow Groups IV/V associated with standing water ($n = 7/15$). Most individuals (63%) are from Flow Group II. Although there is very little variation in the distribution of taxa between samples, it is significant that the filter-feeding taxa are only present from Section 5 (*Hydropsyche pellucidula*) and Section 6 (*Brachycentrus subnubilus*), giving a clear indication of moderate- to fast-flowing channels at those locations. However, *Eccilisopteryx* sp., a taxon of fast flowing water, is equally present at all sites. The presence in all samples of the larvae of the alderfly *Sialis lutaria* is indicative of Flow Group V, associated with ponds, lakes and sluggish river and stream habitats where there is an abundance of silt.

The terrestrial invertebrate assemblages, in particular the various Carabidae, highlight the presence of bare ground where the substrate is sandy or stony but localized marshy habitats and the availability of rotting vegetation are also indicated by the beetles and by the cranefly *Dicranomyia*, which lives amongst decaying vegetation or mosses on the margins of aquatic environments feeding on decaying plant material or algae. However, the absence of waterside and damp ground plant taxa indicates that marginal reed-swamp did not exist at the channel edge. Drier habitats with little vegetation and tundra grasslands are suggested by the occurrence of various xerophilous beetle species, while *Agonum ericeti* is found on both moist bogs and dry ground, such as hummocks of *Calluna* and *Vaccinium*, preferring very acid soils with a pH of 3.6–4.6 (Lindroth, 1986). The precise location of the source plants in relation to the site of deposition is difficult to determine, because in an open, treeless landscape, some of the leaves may have been blown considerable distances before deposition. However, the presence of open tundra is clearly indicated by the occurrence of dwarf arctic–alpine plants. Only two fragments of *Betula nana* were recovered, possibly suggesting that dwarf birch was not abundant in the source vegetation, although macroscopic remains of this species are rarely abundant in British Pleistocene sediments (West, 2000). The dominant dwarf tree taxon is *Salix herbacea*, indicating open habitats with fresh and basic soils (West, 2000), often subject to solifluction, and particularly associated with late snow patches. *Dryas octopetala* was probably found growing within this dwarf wood.

The Carabidae and the presence of Poaceae, *Linum perenne*, *Potentilla anserina*, *Viola* subgenus *Melanium* and *Taraxacum officinale* point to dry and disturbed ground with exposed bare soil in places. Erosion of the underlying deposits may also have been the source of the pre-Pleistocene megaspores noted. The disturbance may have been formed by bank collapse at the channel margins or by the trampling activities of large mammals, their presence echoed by the large numbers of dung beetles, particularly from Section 5. Although locally calcareous in places, evidence of soil salinity is possibly provided by *Potentilla anserina* and *Silene maritima*. The underlying Mercia Mudstone contains gypsum beds locally but the salinity may also reflect high levels of evaporation and moisture depletion during periods of permafrost (see Gibbard, 1985).

Phytophagous (especially monophagous) beetle species provide further insights into the composition of the local flora (see supporting Table S7), revealing the presence of *Potamogeton*, *Myriophyllum*, *Equisetum*, *Ranunculus repens* and mosses, amongst others. Notably, the assemblage includes no beetle taxa that are dependent on trees and the presence of *Salix*-feeding beetles and *Cacopsylla palmeni* (Hodkinson and Bird, 1998) are probably associated with the dwarf arctic–alpine willows apparent in the plant macrofossil assemblages. Several of the chironomid taxa in the fauna (*Glyptotendipes pallens*-type, *Polypedilum nubeculosum*-type and *Cricotopus* spp.) are associated with aquatic macrophytes (Brodersen *et al.*, 2001; Langdon *et al.*, 2010).

Inferred age of the deposits

The composition of the vertebrate assemblage from Whitemoor Haye fits well with the Pin Hole Mammal Assemblage-Zone of Currant and Jacobi (2001), typical of the Middle Devensian in Britain and correlated through radiocarbon dating of key faunal elements with MIS 3 of the marine oxygen isotope record. The Middle Devensian is characterized by substantially higher species diversity than the early part of the last glaciation (Currant and Jacobi, 2001), in particular witnessing the return to Britain of several key species such as woolly rhinoceros, woolly mammoth, horse and spotted hyaena, in addition to the reappearance of Neanderthals after a protracted absence. *Coelodonta* itself first appeared in Britain in the late Middle Pleistocene (Schreve, 1997) and disappeared from there *c.* 35 ka BP (OxCal 4.1 recalibration of Jacobi *et al.*, 2009; Stuart and Lister, 2012), coincident with the onset of Greenland Interstadial (GI) 7. In continental Europe, the Last Glacial Maximum caused a marked contraction of the woolly rhinoceros' range and although the Lateglacial saw the widespread presence of *C. antiquitatis* in Siberia, this animal failed to return to western and southern Europe during this period (Stuart and Lister, 2007, 2012). In north-eastern Siberia, woolly rhinoceros survived through much of GI-1e (Bølling) and GI-1d and probably went extinct at or close to the onset of GI-1c (Allerød) *c.* 13.9 ka BP, its final disappearance broadly coincident with the climatic warming of the Lateglacial Interstadial. The replacement of herbaceous vegetation by shrubs and trees at the beginning of the Allerød (Stuart and Lister, 2007, 2012), and, crucially, the likely increase in precipitation (especially snowfall) resulting in wetter ground, would have both proved disadvantageous to woolly rhinoceros (Guthrie, 1990; Sher, 1997).

The dental morphology of the Whitemoor Haye individual is typical of a Middle Devensian specimen. The upper cheek teeth exhibit the characteristic medifossette of *Coelodonta*, and the upper third molar (M3) is of the typical triangular shape with no pronounced metaloph. Dental metrics (such as buccal–lingual measurements across the M3 protoloph and metaloph) and postcranial measurements (such as proximal breadth and total length of the 3rd metacarpal) indicate that the Whitemoor Haye specimen is very typical for the Late Pleistocene and falls well towards the median of both British and European specimens of last cold stage age (Crocker, 2010).

The Whitemoor Haye invertebrate assemblages contain no species of biostratigraphical significance, although the beetle assemblage is very similar to others recovered from full glacial deposits in Britain (e.g. Coope, 1968; Briggs *et al.*, 1985) that have been attributed on the basis of stratigraphical context and associated radiocarbon dates to the Middle Devensian (Coope, 2002).

Geochronology

Three samples of the partial woolly rhinoceros skeleton were submitted to the Oxford Radiocarbon Accelerator Unit. Details of the chemical pre-treatment, target preparation and accelerator mass spectrometry (AMS) measurement details are given in Bronk Ramsey *et al.* (2002, 2004a, b). The radiocarbon dates are as follows:

OxA-15843 WMH 01 lumbar vertebra δ^{13}C –18.96‰ 43 350 ± 500 BP

OxA-15844 WMH 02 humerus midshaft δ^{13}C –19.26‰ 42 850 ± 450 BP

OxA-15845 WMH 03 zygomatic arch δ^{13}C –19.57‰ 41 690 ± 400 BP

The dates are presented in supporting Table S9, alongside other dates on selected woolly rhinoceros remains from Britain (from Jacobi *et al.*, 2009) and plotted in Fig. 12 against the NGRIP palaeoclimate record (NGRIP members, 2004). The three dates indicate a Middle Devensian age estimate for the Whitemoor Haye skeleton and are consistent with the inferences drawn from the biostratigraphy and from the position of the site within the Holme Pierrepont terrace of the Trent. The ages correlate with GI-12, one of the longest and warmest phases of the last cold stage.

OSL dating was also applied to the sedimentary deposits. Eight sediment samples for quartz optical dating were collected within

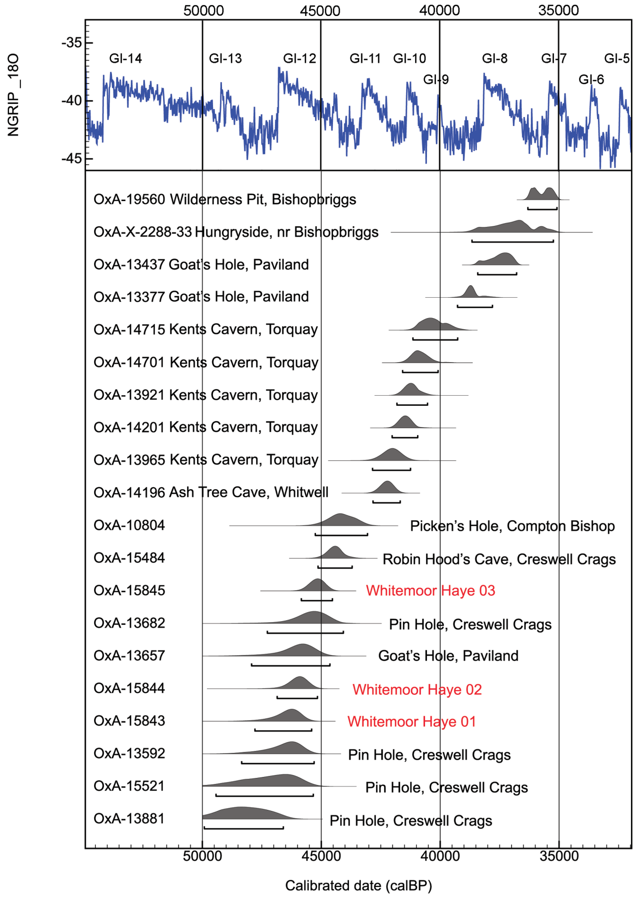

Figure 12. Age models for the AMS radiocarbon ages on woolly rhinoceros bones from Whitemoor Haye, together with selected other British specimens, shown against the NGRIP δ^{18}O curve (OxCal v4.1.7 Bronk Ramsey (2010); r: 5 Atmospheric data from Reimer *et al.*, 2009) for the period 60–32 ka. Further details of the determinations can be found in supporting Table S9. The probability distributions for each radiocarbon sample are shown with a range beneath representing the age ranges at 95.4% probability. This figure is available in colour online at wileyonlinelibrary.com.

opaque plastic tubing forced into Section 10 (see Fig. 5) 0.13–1.17 m beneath the excavation surface for the Upper Gravels (OSL WH 10/1 through to OSL WH 10/4), and 0.34–1.51 m below the excavation surface in Section 6 for the Lower Sands (OSL WH 6/1 through to WH 6/4). The impermeable nature of the underlying Mercia Mudstone and low level of the terrace required the quarry to be pumped, suggesting a saturated moisture content history. The dates are given in supporting Table S10. Two samples within the Lower Sands (GL03023 and GL03024) failed the repeat regenerative-dose test prescribed by Murray and Wintle (2000; exceeding ± 10% of unity). Fig. 13 illustrates the distribution of optical ages from equivalent stratigraphic units. Collectively there is a divergence in dose rate (D_r) values and convergence in ages for the Lower Sands (excluding sample GL03023 with the poorest repeat ratio), but less convergence in the age estimates for the Upper Gravels. The convergence in ages from differing dose rates within the Lower Sands and their stratigraphic consistency relative to the Upper Gravel age estimates is encouraging. The geometric mean age of the Lower Sands is (excluding GL03023 and GL03024) 38 ± 4 ka, coeval with radiocarbon age estimates.

Synthesis

Sedimentological evidence from Whitemoor Haye indicates deposition within a braided river environment under periglacial climatic conditions. This has important implications for understanding the taphonomy of the fossil mammalian assemblage, in particular the sequence of events that led to the burial of the woolly rhinoceros carcass. The partially articulated skeleton (and other associated faunal material), which appears to be intimately associated with the Lower Sands, may have entered the channel under a range of different scenarios. Either the animal may have become stuck and died within a ‘quicksand’ at the edge of a channel whilst feeding (miring being a typical cause of death for megaherbivores even today), or the animal may have been cut off on part of the floodplain and died as a result of increased stream flow in the valley bottom (e.g. floods associated with spring snowmelt), or the bones may be locally reworked from other parts of the floodplain environment.

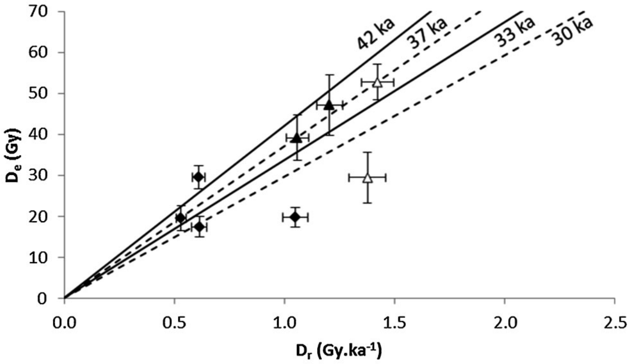

Figure 13. D_e/D_r plot of optical dating results from the Upper Gravels (diamonds) and Lower Sands (triangles). The solid black lines define the geometric mean age range for the Lower Sands (excluding samples GL03023 and GL03024; unfilled symbols), the dashed lines that of the Upper Gravels.

The excellent preservation and partial articulation of the bone material implies that reworking from other parts of the floodplain is the least likely scenario for the Whitemoor Haye rhinoceros skeletal material. The periglacial nature of the climate suggests that any carcasses deposited on the floodplain would have been quickly frozen and buried. Whilst freezing may have helped preserve some of the material in a semi-articulated form, it may also have allowed fluvial processes to scour away parts of the body. Parts of the carcass could equally have been removed by scavengers, although there is no direct evidence of gnawing. As noted previously, vertebrate remains are extremely rare in this part of the Midlands and it is likely that pH and local geological conditions played a key role here in facilitating the preservation of this important specimen.

There is little evidence of season of deposition, with the tentative exception of a shed female reindeer antler. Unusually amongst the Cervidae, both male and female reindeer bear antlers, with males shedding their antlers after the rut, in late October to November, and females shedding their antlers about 1 week after calving in spring. The limited evidence is thus consistent with reindeer passing through the area, possibly as part of a seasonal migration, in spring time and would also chime with the inferred time of death of the first rhinoceros.

The beetles and chironomids indicate that prevailing climatic conditions were extremely cold, with the former suggesting continentality akin to central Asia and the presence of species currently inhabiting arctic tundra and high-altitude mountainous regions. The combined palaeoenvironmental evidence from arthropods, plant macrofossils and pollen indicates a river floodplain with a series of broad, shallow channels, surrounded by open vegetation dominated by grasses, sedges and an arctic–alpine assemblage of dwarf shrubs. Areas of bare and disturbed ground were present adjacent to the variably flowing water source, together with pools at the margins of melting snow patches.

Radiocarbon dating of three separate elements of the rhinoceros skeleton yielded age estimates of between 43 and 41 k cal a BP placing the faunal remains firmly within the Middle Devensian (MIS 3) and correlated with GI-12. OSL dating of sands surrounding the rhinoceros skeleton suggested a coeval age of 34–42 ka. The combined palaeoenvironmental, bio- and lithostratigraphic evidence appear consistent with the Middle Devensian age derived from the radiocarbon dates and OSL age estimates. While climatic conditions during this part of GI-12 were clearly very cold, as highlighted by the invertebrate evidence described above, they must also have been dry, given the precipitation intolerance of *C. antiquitatis*. It is interesting to speculate that although woolly rhinoceroses were present in Britain in interstadials GI-12 to GI-8 inclusive, their disappearance from Britain coincides with GI-7, indicating that this interstadial may have been of different, less suitable nature, perhaps with elevated precipitation in this most westerly and oceanic part of the species' range. As indicated by Stuart and Lister (2012), the full picture of woolly rhinoceros presence or absence is likely to be very complex and heavily influenced by local factors in different areas, including variations in temperature, vegetation and precipitation, especially snow cover.

Within the catchment, the Whitemoor Haye organic deposits appear stratigraphically and chronologically similar to those recorded by Coope and Sands (1966) further upstream in the Tame Valley at Minworth and Whitacre Heath. Coope and Sands (1966) believed that these organic units were part of a continuous bed affected by periglacial processes, occurring in a peaty sand at the interface of the sand and gravel and Mercia Mudstone bedrock. It is therefore probable that the sediments at Whitemoor Haye and those recorded elsewhere within the Tame Valley form part of a wider, potentially mappable lithostratigraphic unit. Radiocarbon dating of the organic material from these two sites yielded age estimates of 32 160 ± 1780–1450 ^{14}C a BP. Within the broader West Midlands region, fossiliferous detrital peats and organic clays of broadly comparable Middle Devensian age have been recorded within cryoturbated basal terrace gravels of the River Salwarpe, a Severn tributary at Upton Warren, Worcestershire (Coope *et al.*, 1961), Four Ashes, Staffordshire (Morgan, 1973), Avon Terrace no. 2 at both Fladbury, Worcestershire (Coope, 1962), and Brandon, Warwickshire (Shotton, 1968), and the Syston Terrace of the River Soar in Leicestershire (Bell *et al.*, 1972). These examples, which date from around 42–29 ka BP, equally suggest a climate of variable continentality and severity, with evidence for intensely cold as well as warmer episodes, although the landscape remained largely treeless tundra. At Upton Warren, the insects also corroborate the faunal evidence for large herbivores grazing the landscape, which notably include woolly rhinoceros as well as mammoth, reindeer and bison.

Recently, Howard *et al.* (2011) have suggested that the lowest and youngest Pleistocene terrace of the main Trent Valley floor and its tributary valleys (the Floodplain Sand and Gravel) may have been deposited as two separate pulses of braidplain aggradation either side of the Last Glacial Maximum. In the tributary valley of the River Soar in the Middle Trent, an initial phase of aggradation recorded between approximately 37 and 28 ka BP would broadly corroborate the age estimates derived from both luminescence dating of sediments and radiocarbon dating of bone at Whitemoor Haye. More widely, this is a period when aggradation is recorded in other catchments in eastern England (Rogerson *et al.*, 1992; Gao *et al.*, 2000; Lewin and Gibbard, 2010) and north-west Europe (van Huissteden *et al.*, 2001). At Baston Fen, Lincolnshire, observation of the presence/absence of ice wedge casts combined with OSL dating led Briant *et al.* (2004) to suggest that periods of decreased fluvial activity during the Late Devensian could be correlated with periods of aridity. Although this is an interesting hypothesis, the general absence of significant aeolian deposits in the West Midlands, coupled with the lack of long-term observation of working faces and any associated periglacial record at Whitemoor Haye, prevent any further exploration of the role of aridity at this site. Nevertheless, this observation echoes the inference of dry conditions made on the basis of several *C. antiquitatis* individuals at the site, given their intolerance of elevated precipitation and snow cover.

In Britain, the major corpus of evidence concerning Middle Devensian vertebrates comes from a handful of key cave sites such as Pin Hole in Creswell Crags, Derbyshire (Jacobi *et al.*, 1998), Coygan Cave, Carmarthenshire (Aldhouse-Green *et al.*, 1995), the Hyaena Den at Wookey Hole, Somerset (Jacobi and Hawkes, 1993), Picken's Hole at Crook Peak, Compton Bishop, Somerset (Tratman, 1964; ApSimon, 1986), and Kents Cavern, Devon (Pengelly, 1884). Well-dated open sites with multiproxy palaeoenvironmental evidence of Middle Devensian age are extremely rare, with only Upton Warren, Worcestershire (Coope *et al.*, 1961), Latton, Wiltshire (Lewis *et al.*, 2006), and Lynford, Norfolk (Schreve, 2006; Boismier *et al.*, 2012), provide detailed information for this time period. On the near continent, problems of dating and a lack of well-provenanced or stratified material from old excavations serve to hamper meaningful correlation with other NW European assemblages. The best potential correlatives come from a number of cave sites in the Belgian Ardennes, although stratigraphic interpretation is difficult. Layer 1A of Scladina Cave, Sclayn near Namur (Simonet, 1992; Stringer and Gamble, 1993), and the Mousterian levels at Trou Al'Wesse near Liège (Otte, 1979) have both been attributed to an interstadial around at 44 k ^{14}C a BP. It is therefore clear that the Whitemoor Haye site, from a secure stratigraphical context underpinned by radiocarbon and OSL dating, and with its superbly preserved partial rhinoceros skeleton and associated palaeobiological assemblages, is of exceptional importance for reconstructing the palaeoenvironmental history of the last glaciation.

Supporting information

Additional supporting information can be found in the online version of this article:

Table S1 The vertebrate remains from Whitemoor Haye.

Table S2. Coleoptera from Whitemoor Haye.

Table S3 Chironomidae assemblage from Whitemoor Haye.

Table S4. Trichoptera from Whitemoor Haye.

Table S5 Plant taxa represented in sediments from Whitemoor Haye Quarry.

Table S6. Pollen spectra from at Whitemoor Haye

Table S7 Habitat preferences, based upon the invertebrate assemblages.

Table S8. Number of taxa for Sections 4–6 in each Flow Group.

Table S9 Radiocarbon dates on three elements from the Whitemoor Haye partial rhinoceros skeleton.

Table S10 Summary of OSL dating from Sections 10 and 6 at Whitemoor Haye.

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Abbreviations. GI, Greenland Interstadial; MCR, Mutual Climatic Range; MIS, Marine Isotope Stage; OSL, optically stimulated luminescence.

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