An Early Pleistocene hippopotamus from Westbury Cave, Somerset, England: support for a previously unrecognized temperate interval in the British Quaternary record

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ABSTRACT: Although fossil assemblages from the late Early Pleistocene are very rare in Britain, the site of Westbury Cave in Somerset, England, has the potential to address this gap. The mammal fossils recovered previously from the Siliceous Member in Westbury Cave, though few in number, have hinted at an age for the deposits that is as yet unparalleled in Britain. Here, we describe the first bona fide occurrence of Hippopotamus in the British Early Pleistocene, discovered during recent reinvestigation of the Siliceous Member. The hippo fossil indicates a refined biochronological age of ca. 1.5–1.07 Ma for the Siliceous Member and a palaeoclimate that was warm and humid, which accords well with previous palaeoenvironmental inferences. A synthesis of late Early Pleistocene hippo occurrences suggests that the Siliceous Member hippo may have been part of an early colonization of north-west Europe by these megaherbivores, possibly during MIS (Marine Oxygen Isotope Stage) 31. Alternatively, it evidences a currently cryptic northward migration during an even earlier temperate phase. In either case, the Siliceous Member is likely to represent a warm period that has not been recognized previously in the British Quaternary record.

KEYWORDS: interglacial; Mammalia; palaeoclimate; Siliceous Member; Westbury Cave

Introduction

The late Early Pleistocene is a significant interval in the Quaternary period. It marks a major climatic shift in the periodicity of glacial/interglacial cycles (the Mid-Pleistocene Transition, MPT; Head and Gibbard, 2015; Berends et al., 2021) and the fossil record from this time bears witness to major faunal turnovers in terrestrial ecosystems, especially among mammals (e.g. the Villafranchian–Galerian transition in European land mammal ages; Rook and Martínez-Navarro, 2010; Madurell-Malapeira et al., 2014; Bellucci et al., 2015). Moreover, the earliest known hominin occurrences in the Mediterranean basin and north of the Alps are of late Early Pleistocene age (Parfitt et al., 2010; Arzarello et al., 2012; Toromoyano et al., 2013; Ashton et al., 2014).

Britain formed the north-western-most fringes of continental Europe during the late Early Pleistocene (Funnell, 1995) and, as such, it is a geographically important region for examining responses of the terrestrial biota to climate changes on the edge of Europe. Consequently, the almost complete lack of fossil-bearing sites of this age from Britain presents a notable problem. A well-known gap occurs in the British fossil record from ca. 1.8 Ma to ca. 0.8 Ma (Gibbard et al., 1991; Preece and Parfitt, 2012), with only one fossil assemblage from Happisburgh 3 argued to date to the younger part of this interval (Parfitt et al., 2010; but see Westaway, 2011). Very few sites known in Britain have potential to address this hiatus, but Westbury Cave in the Mendip Hills of Somerset, south-west England, has recently been identified as a candidate (Adams et al., 2019).

Westbury Cave is an exceptional site in the British Quaternary record. It is best known for its early Middle Pleistocene cave breccias (the Calcareous Member), which have yielded a spectacularly rich vertebrate assemblage (Bishop, 1982; Andrews et al., 1999). However, the stratigraphical and palaeontological importance of the underlying water-lain sediments (the Siliceous Member) has only recently been acknowledged (Adams, 2017; Adams et al., 2019). Reinvestigation of these sediments has provided strong support for their Early Pleistocene age, revealed the complexities of their internal stratigraphy and resulted in the development of a new depositional model (Adams et al., 2019). Here, we present the first description of Hippopotamus from recent excavations through the Siliceous Member. The fossil constitutes the earliest bona fide record of Hippopotamus in the UK and provides critical new biochronological and palaeoenvironmental information for the Early Pleistocene mammal assemblage in Westbury Cave. In combination with the few fossils reported previously from the Siliceous Member (Bishop, 1982; Gentry, 1999), the new record of Hippopotamus provides strong support for a late Early Pleistocene age for the deposits. In interpreting the significance of the find, we review the Pleistocene record of hippopotamus in Britain and produce a new synthesis of dated hippo occurrences in the late Early Pleistocene of western Europe.

Materials and methods

The Hippopotamus fossil was discovered in situ (by I.C.) in April 2016 during excavations (led by N.F.A.) of Siliceous Member cave sediments in Westbury Quarry (also known as...
Broadmead Quarry, National Grid ref. ST 5081 5036; Fig. 1A). The stratigraphical context of the fossil is well constrained to the depositional unit F1U1 of Section 1c (S1c; Fig. 1B–D) described by Adams et al. (2019). This unit is laterally continuous with units F2U2 in S1c and F5U3 in S1a, which have also yielded an important assemblage of other large and small fossil mammals currently under study (see Adams, 2017). Together, these units were interpreted as distal talus cone deposits (part of Facies Association B in Adams et al., 2019).

The fossiliferous horizons are bracketed by fine-grained sediments of reversed magnetization (Adams et al., 2019), indicating deposition during the Matuyama Reversal (2.60–0.77 Ma; magnetochron ages from Channell et al., 2020). Biochronology, using fossils described by Bishop (1982) and Gentry (1999) from original investigations of the Siliceous Member, indicates either a post-Olduvai, pre-Jaramillo age (1.77–1.07 Ma) or a post-Jaramillo, pre-Brunhes (0.99–0.77 Ma) age (but see Discussion). The former was tentatively suggested as more likely by Adams et al. (2019).

The dental nomenclature and terminology used herein follows Mazza (1995) and Boisserie et al. (2010). Comparative molar measurements were sourced from Faure (1985) and Mazza (1995). Taxonomy follows the two-species concept for Pleistocene hippos in Europe (Petronio, 1995; summarized below).

There has been variable usage of species concepts for Pleistocene Hippopotamus in Europe. Both H. antiquus and H. major have been used since the 19th century to describe large Early and early Middle Pleistocene hippos, with the later erection of H. incognitus for smaller Middle and Late Pleistocene hippos supposedly distinct from the extant hippopotamus, H. amphibius (Faure, 1984; Mazza, 1995). Although H. antiquus has since been identified as having priority over the species name H. major (Hooijer, 1942; Mazza, 1995), common usage of the latter made this synonymy contentious (Faure, 1985). Another species, H. tiberinus, was also proposed for some European specimens (Mazza, 1991), which has similarities to the African Early Pleistocene H. gorgops (van der Made et al., 2017a,b). In addition, there has been debate about whether Early and early Middle Pleistocene hippos exhibit wide variation within just one valid species, the extant H. amphibius, or whether they represent a process of phyletic gradualism that resulted in multiple species (Kahlke, 1997, 2001). Accordingly, some European Pleistocene specimens have been assigned to subspecies of the extant hippopotamus, e.g. H. amphibius antiquus and H. amphibius incognitus (Kahlke, 1997). Synonymy is suspected among these species/subspecies (Mazza, 1995; Petronio, 1995), but few formal acts of systematic synonymization have occurred and those that have (e.g. Faure, 1985) are often disregarded in favour of other schemes. A broadly accepted model has now emerged with two species of Hippopotamus in the Pleistocene of Europe (e.g. Petronio, 1995; Kahlke et al., 2011; Martínez-Navarro et al., 2015; Pandolfi and Petronio, 2015; Konidaris et al., 2018; Kierdorf and Kahlke, 2020): H. antiquus (= H. major = H. amphibius antiquus = H. tiberinus) and H. amphibius (= H. incognitus = H. amphibius incognitus). H. antiquus occurs in the European Early and early Middle Pleistocene until at least ca. MIS (Marine Oxygen Isotope Stage) 15 but possibly until ca. MIS 11 (Martino and Pandolfi, in press), while H. amphibius is known...
from ca. MIS 13 into the Late Pleistocene (Pandolfi and Petronio, 2015; Petronio et al., 2019; Martino and Pandolfi, in press). We follow this model, contrasting views notwithstanding (e.g. van der Made et al., 2017a,b), pending further systematic and phylogenetic studies.

**Institutional abbreviations**

NHMUK, Natural History Museum, London, UK; NWHCM, Norwich Castle Museum and Art Gallery, Norwich, UK; TTNCM, Somerset Museums Service, Somerset Heritage Centre, Taunton, UK.

**Results**

**Systematic palaeontology**

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Hippopotamidae Gray, 1821
Genus *Hippopotamus* Linnaeus, 1758

*Hippopotamus* cf. *antiquus* Desmarest, 1822

**Figure 2A–D**

**Material**: TTNCM 31/2021/1, left M1.

**Measurements**: Maximum length = 47.87 mm, anterior width = 42.78 mm, posterior width = 41.27 mm; Fig. 3A–F.

**Description**

The tooth is slightly oblong in occlusal view (length-to-width ratio of 1.12) and is characterized by four cusps, each with a distinctive trefoil-shaped wear pattern. This pattern is caused by the development of strong styles to the anterior (mesial) and posterior (distal) of each cusp. The four cusps are the paracone (anterior labial), protocone (anterior lingual), metacone (posterior labial) and metaconule (posterior lingual; also called the hypocone by some authors, but Boisserie et al. (2010) argue a true hypocone is not present in hippopotamids). The cusps are moderately worn, with the anterior pair slightly more so than the posterior. The protocone and, particularly, the paracone are inclined anteriorly. The transverse valleys between the anterior and posterior cusp pairs have outlets with widely tapering sides. This valley is broader between the paracone and metacone than it is between the protocone and metaconule. A strong cingulum is evident, particularly along the anterior margins of the paracone and protocone and the posterior margins of the metacone and metaconule. An entostylar pillar is only very weakly developed at the outlet of the lingual transverse valley. Although the tooth crown is near complete, a posterior part of the paracone and the ectostylar region are missing. Thus, it is not possible to assess the presence or strength of an ectostylar pillar at the labial transverse valley outlet. There are four roots, which are variably preserved but most complete beneath the metacone.
Figure 3. Measurements of the *Hippopotamus* cf. *antiquus* molar from the Siliceous Member, Westbury Cave, compared with first and second molars of *H. antiquus* (= *H. major*) from across western Europe (Faure, 1985; Mazza, 1995). (A–C) Upper molar dimensions. (D–F) Lower molar dimensions. Triangles and dashed lines show values for the Siliceous Member molar. Diamonds show published mean values, with bars indicating total range. Italicized numbers above the bars show sample sizes.}

**Remarks**

The relative dimensions of occlusal length and width indicate an upper molar; lower molars tend to be narrower in occlusal view. The absolute dimensions suggest a position as a first rather than second upper molar. Comparisons with molar measurements of *Hippopotamus antiquus* from across western Europe by Faure (1985) and Mazza (1995) support these deductions (Fig. 3A–F). The Siliceous Member specimen is shorter than most recorded *M*₂s (Fig. 3A) and *M*₃s (Fig. 3D) and is wider than most *M*₂s (Fig. 3E–F), but falls very close to average values for all three *M*_3 dimensions (Fig. 3A–C).

In addition, Mazza (1995) suggests that *M*₂_s are often more trapezoidal in occlusal view, with anterior widths greater than posterior widths (5.2 mm greater on average; Fig. 3B,C); this is also true of *M*₃’s (6.1 mm greater on average; Mazza, 1995). By contrast, *M*₁’s tend to have anterior and posterior widths that are more equal. The difference in anterior and posterior width of the Siliceous Member specimen is only 1.51 mm, providing further evidence for a position as a first, rather than second, upper molar.

A position as a third molar can be ruled out on anatomical grounds. In *H. antiquus*, the style posterior to the metaconule (posterior hypostyle in Mazza, 1995) is often weakly developed on the *M*_3, resulting in a comma- rather than trefoil-shaped wear pattern on this cusp. The *M*_3 of *H. antiquus* also typically has a well-developed tubercle along the posterior cingulum (Mazza, 1995; distoconule in Boisserie *et al.*, 2010), which acts as a supplementary cusp and augments the occlusal surface. A similar feature is found on the *M*_3, with the talonid bearing a prominent posterior tubercle (Mazza, 1995; hypoconulid in Boisserie *et al.*, 2010). These characters are not found on the *M*_1/*M*_2, nor on the Siliceous Member specimen.

The description above accords well with features typical of *H. antiquus* in western Europe, as set out in comprehensive detail by Mazza (1995). However, it is difficult to distinguish between *H. antiquus* and *H. amphibius* based on isolated molars alone. More dependable differences are found in the cranial and postcranial skeletons (Caloi *et al.*, 1980; Mazza, 1995; Pandolli and Petronio, 2015). Mazza (1995) tentatively pointed out a number of differences in *M*_3 morphology between species, including subtly contrasting occlusal proportions, differences in the shapes of the transverse valley outlets, and the variable presence and strength of ecto- and entostylar pillars. Unfortunately, all of these are variable within each species and do not constitute demonstrable taxon-specific rules. Based on similarity in morphology and dimensions to specimens of *H. antiquus*, we assign the Siliceous Member specimen to *H. cf. antiquus*. It is relevant to note that, at present, *H. antiquus* is the only widely accepted species of hippopotamus in western Europe during the Early Pleistocene (see above). Therefore, given the age of the Siliceous Member, assignment to this species also provides the best fit to current taxonomic and biogeographical models.

**Discussion**

**Taphonomy and deposition of the Siliceous Member**

Previous workers noted that the Siliceous Member faunal assemblage was dominated by rolled and heavily abraded teeth, which indicated considerable water transport (Bishop, 1982; Andrews and Ghalab, 1999). This ‘derived’ assemblage was argued to be of little use for palaeoecological reconstructions, since the distance and time required to abrade the fossils so heavily would result in a probable conflation of taxa spanning a long time interval (Andrews and Ghalab, 1999; Andrews and Stringer, 1999). While this is true, the provenance of finds from earlier investigations is unknown in relation to stratigraphy within the Siliceous Member, which was grouped as a single basal unit by Bishop (1982) and Andrews *et al.* (1999). As a result, the depositional context of those fossils is poorly constrained. The hippo molar described here differs quite markedly in its preservation to the very rounded large mammal (mostly bovid) molars observed by Andrews and Ghalab (1999). Despite some limited breakage and minor rounding of broken roots (Fig. 2C,D), the hippo
molar is well preserved and clearly travelled a much shorter distance before entering Wesbury Cave.

A solution to this taphonomic contrariety was advanced by the sedimentological study of Adams et al. (2019). Several distinct gravel facies of variable preservation potential were identified within the Siliceous Member. The coarse-grained Facies Associations C and D were interpreted as stream or flood deposits, and the lack of non-durable limestone clasts within the gravels suggested considerable bedload abrasion and attrition (Adams et al., 2019). By contrast, the preservation of limestone clasts within Facies Association B gravels attested to the shorter transport distance of this material. Together with bed geometry and particle size data, this evidence was used to interpret Facies Association B as a set of distal talus cone deposits (Adams et al., 2019). While rounded fossils could be conceivably found in all of these facies associations, well-preserved remains are only likely in the latter. The completeness of the hippo molar and its provenance in Facies Association B support this depositional model. Importantly, the recovery of well-preserved fossils from talus cone sediments highlights the fact that the Siliceous Member mammal assemblage is not highly derived in its entirety. The hippo molar is likely to be contemporaneous with talus cone deposition and similar finds will be of great value in refining Siliceous Member biochronology and palaeoecology.

Biochronology and palaeoenvironment of the Siliceous Member

Despite the suggestion that the Siliceous Member contains a derived faunal assemblage (Bishop, 1982; Andrews and Stringer, 1999), possibly spanning multiple time intervals and climatic episodes during the Early Pleistocene, there are no biochronological or palaeoenvironmental inconsistencies among the previously reported taxa to support this.

Several of these taxa are too poorly resolved taxonomically (Lynx sp. and Dama sp./Cervidae sp. indet.) to provide useful biochronological information (Bishop, 1982; Gentry, 1999). Other Siliceous Member mammals were identified to species (Castor fiber – Eurasian beaver, Stephanorhinus etruscus (= Dicerorhinus etruscus) – Etruscan rhinoceros, and Pachycrocuta brevirostris (= Hyena brevirostris) – giant short-faced hyena; Bishop, 1982) but have long ranges that span the entire Early Pleistocene (Barisone et al., 2006; Pandolfi et al., 2017; Marciszak et al., 2021). The most biochronologically useful taxa from past work (Fig. 4C,D; Bishop, 1982; Gentry, 1999) are the bovid Bovinae cf. Bison schoetensacki, an archaic water vole, Microtus arvalis, and Allophaiomys – the ancestor of modern grassland voles (Microtus spp.). Of these taxa, the identification of Leptobos is most tentative.

Bishop (1982) assigned the Siliceous Member bovids to Bovinae cf. Bison schoetensacki, whereas Gentry (1999) favoured assignment to Leptobos. The fragmentary and rolled nature of the teeth, as well as the difficulty in distinguishing between dental remains of Leptobos and primitive Bison (e.g. B. degliali, B. menneri, B. schoetensacki), has left the status of the bovids open to question (Mead et al., 2014; Cherin et al., 2019; Sorbelli et al., 2021). This taxonomic uncertainty has important implications, because Leptobos is limited to the Villafranchian land mammal age in Europe (ca. 3.5–1.0 Ma; Mead et al., 2014), which would preclude a post-Jaramillo age (Fig. 4D). In contrast, although rare early occurrences of Bison are known in the Late Villafranchian (Masini et al., 2013), this genus occurs mostly at younger sites, from the transitional Epivillafranchian age (ca. 1.2–0.9 Ma; Bellucci et al., 2015) and extending into the Middle Pleistocene (Breda et al., 2010; Petronio et al., 2019). Despite these uncertainties, it is clear from the small mammals that the Siliceous Member represents a period of the Early Pleistocene very rarely expressed in the British record.

Allophaiomys is a critical taxon in European small mammal biochronology during the mid- to late Early Pleistocene (e.g. Maul and Markova, 2007; Cuenca-Bescós et al., 2010), but its only reported British occurrence is in the Siliceous Member (Bishop, 1982). As identified by Gibbard et al. (1991), through comparisons with the more complete Dutch stratigraphy, a large gap exists in the British fossil record between the ‘Pastonian’ and ‘Cromerian’ stages (ca. 1.8–0.8 Ma). An important exception occurs at Happsibrough 3, where an assemblage correlographic to MIS 25 or 21 was discovered (0.99–0.77 Ma; Parfitt et al., 2010; but see Westaway, 2011). However, this site lacks Allophaiomys and instead has more advanced Microtus species (M. arvalis and M. oeconomus). Allophaiomys, like Leptobos, is rare after the Jaramillo subchron in central Europe (Maul and Markova, 2007), hinting that the most likely age for the Siliceous Member is within the interval 1.77–1.07 Ma. As a result, the Siliceous Member is likely to represent an unknown period of British faunal history.

The new record of Hippopotamus cf. antiquus supports this hypothesis, because the species has not been reported in situ from any other British Early Pleistocene site. Furthermore, hippo remains are only widespread in Europe from ca. 1.5 Ma (Rook and Martínez-Navarro, 2010; Martínez-Navarro et al., 2015). As summarized by Martino and Pandolfi (in press), the oldest record of hippo in Europe is controversial and for a long time was thought to be from the Upper Valdarno Basin in Tuscany, Italy (ca. 1.8 Ma). This was until Napoleon et al. (2003) argued that the hippo specimens were likely to be younger than the main Upper Valdarno faunal assemblage, partly due to their poorly resolved provenance and their similarities to hippo fossils from younger Italian sites (e.g. Colle Curti). Conversely, Martino and Pandolfi (in press) argue that it is difficult to deny the provenance of hippo fossils from the Upper Valdarno and point to several hippo-bearing localities within the Montevarchi Synthem of the Upper Valdarno Basin (dated to ca. 1.9–1.7 Ma; Fidolini et al., 2013). Even older Italian occurrences (ca. 2.2 Ma) have been proposed from Coste San Giacomo and from the Chiusi Basin (Bellucci et al., 2012, 2014; Pandolfi and Petronio, 2015), but doubt about these has been expressed because they were ex situ finds without stratigraphical context (Martínez-Navarro et al., 2015; Pandolfi and Petronio, 2015; Marra et al., 2018; Martino and Pandolfi, in press). Marra et al. (2018) suggest that the hippo fossils from Coste San Giacomo could have their provenance in younger deposits overlying the main fossiliferous strata, and it is possible that the surface-collected assemblage from the Chiusi Basin contains fossils of multiple ages (Pandolfi and Petronio, 2015). However, proponents of an older age estimate point to similarly old (Middle Villafranchian) records of Hippopotamus from Greece (Reimann and Strauch, 2008). Such old records have also been postulated to represent early colonizations of the Italian peninsula, without further northward dispersal, followed by local extinction before a later, more successful wave of colonization from Africa (van der Made et al., 2017a). Although not impossible, it is unlikely that hippo migrated to Britain before 1.5 Ma based on available European occurrences (see below). In combination with the evidence above, the new hippo find supports a refined age of ca. 1.5–1.07 Ma for this part of the Wesbury Cave sequence.

The mammal taxa currently known from the Siliceous Member also provide a coherent reccommendation to the palaeoenvironment in south-west England during the late Early Pleistocene. Bishop (1982) summarized the palaeoecology of the ‘Bed 1’ (Siliceous Member) assemblage as an open woodland
fauna of temperate climate, where bovids were the dominant faunal element. The presence of beaver and arctic water vole also attested to the presence of permanent surface water sources in the area (Bishop, 1982). These conclusions are clearly supported by the new record of hippopotamus. Hippos are generally regarded as thermophilous, water-dependent taxa and indicative of humid conditions, mild winters and average annual temperatures several degrees higher than present (Candy et al., 2006, 2010; but see below).

While the ecology of *H. antiquus* is considered largely similar to that of its extant relative, the anatomy and diet of the extinct form suggest even greater dependence on aquatic environments.

Figure 4. (A) The stacked marine oxygen isotope record, LR04 (Lisiecki and Raymo, 2005), showing glacial/interglacial cycles through the last 1.9 Ma, with magnetostratigraphy from Channell et al. (2020); abbreviations of geomagnetic reversals mentioned in the text: J., Jaramillo; O., Olduvai. The ages of British sites with *Hippopotamus* mentioned in the text, and the Late Early Pleistocene site of Happisburgh 3, are shown to the right. (B) Left mandible of *Hippopotamus antiquus* from Cromer, UK (NHMUK PV M 34018); Rv1, of Allophaiomys sp. (NHMUK PV M 33563b) and LP1 of *Pachycrocuta beavristris* (NHMUK PV M 33985). Images not to scale; adapted from figs. 40a and 42a and pl. 4 fig. 7 in Bishop (1982). (C) Examples of previously recorded mammal fossils from the Siliceous Member in Westbury Cave, including (from left to right): LM1 of *Mimomys savini* (NHMUK PV M 34018), RM1 of *Allophaiomys* sp. (NHMUK PV M 33563b) and LP3 of *Pachycrocuta brevirostris* (NHMUK PV M 33985). Images not to scale; adapted from figs. 40a and 42a and pl. 4 fig. 7 in Bishop (1982). (D) Ranges of biochronologically informative mammals from the Siliceous Member (Maul and Markova, 2007; Rook and Martínez-Navarro, 2010; Mead et al., 2014; Martínez-Navarro et al., 2015; Martino and Pandolfi, in press). (E) Occurrences of *Hippopotamus* in late Early Pleistocene sites across western Europe, with bars indicating approximate age uncertainties: (1) Venta Micena, Spain (Ros-Montoya et al., 2012); (2) Sainzelles, France (Thouveny and Bonifay, 1984; van der Made et al., 2017a); (3 & 4) Barranco León and Fuente Nueva-3, Spain (Blain et al., 2016); (5) Incarcal-I, Spain (Ros-Montoya et al., 2012; Alba et al., 2016); (6) Saticula, Italy (Busso Ermolli et al., 2010); (7) Madonna della Strada, Italy (Maggi et al., 2010); (8) Courtonelles, France (Brochet et al., 1983); (9) Cal Guardiola D2, Spain (Madurell-Malapeira et al., 2010); (10) Trinchera Elefante 14, Spain (TE14, Rodríguez et al., 2011; Cuencabascos et al., 2015); (11) Saint-Prest, France (Guérin et al., 2003); (12) Vallonnet Cave, France (Mouillé et al., 2006); (13) Kührlich A, Germany (van Kolfschoten and Turner, 1996); (14) Musbach 1, Germany (von Koenigswald and Heinrich, 1999); van der Made et al., 2017a); (15) Colle Curti, Italy (Coltorti et al., 1998; Mazza and Venta, 2011); (16) Castagnone, Italy (Siori and Sala, 2007); (17) Ellera di Corciano, Italy (Cerin et al., 2012); (18) Frantoio locality, Arda River, Italy (Bona and Sala, 2016); (19) Promano, Italy (Argenti, 2004); (20) Lefie sub-unit 9, Italy (Breda and Marchetti, 2007); (21) Fuensanta del Júcar, Spain (Mazo et al., 1999); (22) Vallparadís Estació 12, Spain (ETV72; Madurell-Malapeira et al., 2010); (23) Hét Gat, North Sea (Mol et al., 2003); (24 & 25) Maasvlakte 1, Netherlands and Noordzee I, North Sea (van Kolfschoten, 2001); (26) Untermassfeld, Germany (Kahlke, 2006; Kahlke et al., 2017a); (27) Durtfort, France (Brugal, 1995; Aguilar et al., 2009); (28) Huéscar-1, Spain (Mazo et al., 1985); Gibert et al., 2007; Ros-Montoya et al., 2018); (29) Vallparadís Estació 7, Spain (ETV77; Locarno-Fernández et al., 2015); (30) Cal Guardiola D7, Spain (Madurell-Malapeira et al., 2017); (31) Silvia, Italy (Palombo et al., 2003; Palombo, 2014). Hippo silhouette is from PhyloPic, by Zimices (phylopic.org/image/c2d68ebb-50ec-45f4-8cd1-6cf52ad02286), and is available under a CC BY 3.0 licence (https://creativecommons.org/licenses/by/3.0). [Color figure can be viewed at wileyonlinelibrary.com]
Isotopic dietary reconstructions show that H. antiquus fed largely on aquatic plants rather than the terrestrial grasses favoured by extant hippos (Palmqvist et al., 2003, 2008). Palmqvist et al. (2008) also propose that the anatomy of H. antiquus was more poorly adapted than that of H. amphibius to terrestrial locomotion, with a much larger body mass and shortened metapodials, while several other features were better adapted to an aquatic lifestyle (e.g. more elevated orbits). Therefore, H. antiquus is probably an even more reliable indicator of humid conditions than the extant species.

The probable habitat preferences of the rest of the Siliceous Member mammals are compatible with temperate conditions. They indicate a mixed environment of savanna-like grassland for grazers (bovids, ancestral grassland voles) and scavenging carnivores (hyaena), with nearby areas of open woodland or forest for browsers/mixed feeders (bovids, deer, rhinoceros), forest hunters (lynx) and species that favour wooded habitats (beaver). Hippos add the presence of a sizeable river or lake to this landscape.

**The Pleistocene record of hippo in Britain**

Hippopotamus is well known from several temperate periods in the British Pleistocene: the early Middle Pleistocene interglacial of the ‘Cromerian Complex’ (MIS 17–13) and the last interglacial (MIS 5e or the Ipswichian) in the Late Pleistocene.

Previously, the oldest records of Hippopotamus in Britain came from the East Anglian Crag Basin, where hippo remains have been recorded from numerous sites. These include East Runton, Cromer, Overstrand, Sidestrand, Trimingham, Mundesley, Bacton, Happisburgh, Norton Subcourse, Pakefield, Kessingland and Walton-on-the-Naze (Owen, 1846; Newton, 1882; Reynolds, 1922; Suckling, 1959; Stuart, 1974, 1982, 1986; Stuart and Lister, 2001; Lewis et al., 2004). One interesting exception is West Runton (Stuart, 1974), which lacks hippo despite a history of extensive fossil collecting. Although many hippo fossils are known from this region, very few have secure stratigraphical context. Most occurrences represent isolated bones or teeth, or fragments thereof, found loose on the beach, having eroded out of the cliffs or foreshore (Stuart, 1996).

Much of the coastal land in this area is made up of Early and early Middle Pleistocene sediments belonging to the Crag Group (Norwich Crag and Wroxham Crag Formations) and the Cromer Forest-bed Formation (Lee et al., 2004) and the Pakefield, Kessingland and Walton-on-the-Naze (Owen, 1846; Newton, 1882; Reynolds, 1922; Suckling, 1959; Stuart, 1974, 1982, 1986; Stuart and Lister, 2001; Lewis et al., 2004). One interesting exception is West Runton (Stuart, 1974), which lacks hippo despite a history of extensive fossil collecting. Although many hippo fossils are known from this region, very few have secure stratigraphical context. Most occurrences represent isolated bones or teeth, or fragments thereof, found loose on the beach, having eroded out of the cliffs or foreshore (Stuart, 1996).

The probable habitat preferences of the rest of the Siliceous Member mammals are compatible with temperate conditions. They indicate a mixed environment of savanna-like grassland for grazers (bovids, ancestral grassland voles) and scavenging carnivores (hyaena), with nearby areas of open woodland or forest for browsers/mixed feeders (bovids, deer, rhinoceros), forest hunters (lynx) and species that favour wooded habitats (beaver). Hippos add the presence of a sizeable river or lake to this landscape.

Hippopotamus is well known from several temperate periods in the British Pleistocene: the early Middle Pleistocene interglacial of the ‘Cromerian Complex’ (MIS 17–13) and the last interglacial (MIS 5e or the Ipswichian) in the Late Pleistocene.

Previously, the oldest records of Hippopotamus in Britain came from the East Anglian Crag Basin, where hippo remains have been recorded from numerous sites. These include East Runton, Cromer, Overstrand, Sidestrand, Trimingham, Mundesley, Bacton, Happisburgh, Norton Subcourse, Pakefield, Kessingland and Walton-on-the-Naze (Owen, 1846; Newton, 1882; Reynolds, 1922; Suckling, 1959; Stuart, 1974, 1982, 1986; Stuart and Lister, 2001; Lewis et al., 2004). One interesting exception is West Runton (Stuart, 1974), which lacks hippo despite a history of extensive fossil collecting. Although many hippo fossils are known from this region, very few have secure stratigraphical context. Most occurrences represent isolated bones or teeth, or fragments thereof, found loose on the beach, having eroded out of the cliffs or foreshore (Stuart, 1996).

Much of the coastal land in this area is made up of Early and early Middle Pleistocene sediments belonging to the Crag Group (Norwich Crag and Wroxham Crag Formations) and the Cromer Forest-bed Formation (Lee et al., 2006; Rose, 2009). These deposits often occur in direct superposition and fossils are known from horizons of both ages, resulting in site collections of mixed ages (Lister, 1996, 1998). Only hippo fossils from Pakefield/Kessingland (Stuart and Lister, 2001) and Norton Subcourse (Lewis et al., 2004) can be unambiguously linked to specific horizons within a site stratigraphy. Both sites date to the early Middle Pleistocene ‘Cromerian Complex’ (fig. 4A; Preece and Parfitt, 2012), and the normally magnetized sediments from both sites suggest an age in the Brunhes magnetochron (<0.773 Ma; Channell et al., 2020). However, the precise age of the hippo-bearing strata within the Cromer Forest-bed Formation at Pakefield and Norton Subcourse is contentious and open to different interpretations, which have included MIS 15, MIS 17 and late MIS 19 (e.g. Parfitt et al., 2005; Lee et al., 2006; Westaway, 2011; Preece and Parfitt, 2012). MIS 17/15 may be more likely since much of the MIS 19 interglacial, including its peak (MIS 19c), occurred during a period of reversed magnetization in the very latest part of the Matuyama magnetochron (Channell et al., 2020) that is likely to be unrepresented in the ‘Cromerian’ deposits of East Anglia (Candy et al., 2015). Whatever their precise age within the early Middle Pleistocene, the Pakefield and Norton Subcourse hippo fossils were hitherto the oldest well-provenanced records of hippo in the British Pleistocene.

Despite the occurrence of mammal-bearing Early Pleistocene sediments in the Crag Basin, no hippo remains have been demonstrated to have their provenance in these deposits. In addition, no other British Early Pleistocene site beyond the Crag Basin has records of hippo, e.g. Dove Holes Cave in Derbyshire (Spencer and Melville, 1974) and the Dewlish bone fissure in Dorset (Fishet, 1905; Carreck, 1955). Therefore, the Siliceous Member hippo represents the first bona fide occurrence of the genus and family in the British Early Pleistocene.

Nevertheless, some Crag Basin hippo specimens are more likely to represent Early Pleistocene occurrences than others. A careful analysis of the elephant and deer remains by Lister (1996) showed that some sites have mostly or entirely early Middle Pleistocene species (West Runton, Trimingham, Pakefield, Kessingland), while others are dominated by Early Pleistocene species (East Runton) or have mixed assemblages (Overstrand, Sidestrand, Mundesley, Bacton, Happisburgh). Therefore, the occurrence of hippo at East Runton is particularly noteworthy. While Lister (1996) argued that the small number of early Middle Pleistocene species at East Runton may derive from easterly exposures of the West Runton Freshwater Bed, or may have been transported to the locality by tidal processes, the fact that no hippo fossil has ever been recorded from West Runton renders this quite unlikely for the East Runton hippo specimens. The dominance of Early Pleistocene large mammals at East Runton suggests that hippo specimens from this locality are the most likely to be Early Pleistocene in age out of all Crag Basin occurrences.

Stuart (1986) suggested that most, if not all, Crag Basin hippo fossils were likely to be of early Middle Pleistocene ‘Cromerian’ age, because 40 of 87 Crag Basin hippo specimens from the NHMUK Savin Collection were recorded from cliff bases. He argued that, in general, ‘Cromerian’ deposits were found at the cliff bases in the area, while older deposits occurred on the foreshore. Nevertheless, 13 of 87 specimens were found on the foreshore, where Early Pleistocene sediments are exposed, and Early Pleistocene deposits are also found in the cliffs. The foreshore hippo specimens, particularly if from East Runton, could thus represent genuine Early Pleistocene occurrences, but this is currently not possible to demonstrate.

Although pollen analysis of sediment adherent to museum hippo specimens from Trimingham, Mundesley and Bacton was argued to support a ‘Cromerian’ age (Stuart, 1986), Stuart (1996) admitted that the later recognition of multiple interglacial-wards within the ‘Cromerian Complex’ prevented direct correlation to a single temperate episode. In addition, the high frequency of Abies pollen was used to rule out a ‘Pastonian’ age, since Abies was unknown from the British Early Pleistocene at the time (Stuart, 1986). The Abies fossil record has been extended into the late Early Pleistocene in Britain recently (Farjon et al., 2020) and, as a result, an abundance of Abies pollen no longer precludes an Early Pleistocene age.

A remarkable exception to the isolated and fragmentary hippo fossils from the Crag Basin is a well-preserved mandible of H. antiquus (NWHCM 1045.30.1) that was recovered from ‘freshwater clay-beds’ near Cromer (Owen, 1846, p. 399; Fig. 4B). Unfortunately, its precise provenance and age are poorly known (Stuart, 1986). The most likely case is that the mandible is of ‘Cromerian’ early Middle Pleistocene age. However, if these beds equate to the clay-rich strata that overlie the Weybourne Crag near Cromer and yield Early Pleistocene large mammals, this specimen may be of mid-Early Pleistocene/Pastonian age (ca. 1.8–1.7 Ma; see Lister, 1998). Although late Early Pleistocene deposits with fossils are very
Although this occurrence is dubious because it was not Early or early Middle Pleistocene deposits (Preece from Sidestrand (Preece et al., 2010) unlikely, the recent suggestions that hippos were on the Italian Peninsula (Schreve, 2009). Despite the supposed absence of hippo during MIS 9 age for this occurrence is considered more likely in Gloucester from what was thought to be an MIS 7/6 context, and Pakefield (Parfitt et al., 2005; Candy et al., 2010). Furthermore, it appears probable, but not undeniable, that the *Hippopotamus* remains from Sidestrand are associated with the early Middle Pleistocene ‘Cromerian’ deposits at this site. Consequently, it is possible to discuss the climate and environments of *Hippopotamus* migration into southern Britain during MIS 5e (Trafalgar Square), MIS 13 (Sidestrand) and an earlier ‘Cromerian’ interglacial (Pakefield, MIS 17/15). Significantly, these sites yield the warmest interglacial temperature reconstuctions of any British interglacial deposits. Coleopteran assemblages at all three of these sites contain southern and eastern European species indicating summer temperatures several degrees higher than the present day. This suggestion is supported by the presence, again at all three sites, of *Trapa natans* (the water chestnut), which is often reported as requiring mean July temperatures of >20 °C to successfully germinate (Candy et al., 2010, 2015). All three sites contain a rich assemblage of thermophilous flora and fauna (see discussion in Candy et al., 2010, 2015, 2016) and, therefore, produce the most robust record of enhanced – in this case taken to mean greater than Holocene (see Candy et al., 2010, 2016) – interglacial warmth of any interglacial deposits of the British Middle and Late Pleistocene. It is during these periods of enhanced warmth that *Hippopotamus* remains are found Britain.

Given the current biogeographical distribution of *Hippopotamus*, its presence in Britain during these particular interglacials would appear logical. However, it has to be stressed that human agency is the most likely primary control on the modern distribution of this taxon (Stoffel et al., 2015; Lewison and Pluháček, 2017), meaning that there is no way of reliably quantifying its fundamental environmental range or climatic tolerances. Certainly, for much of Quaternary history *Hippopotamus* appears to have been a pan-Mediterranean, as well as African, genus, extending into central and northern Europe as well as the Arabian peninsula during particularly wet or warm intervals (e.g. van der Made et al., 2017b; Stewart et al., 2019). In their review of thermophilous flora and fauna within the British Isles, Candy et al. (2010) suggested that the availability of permanent, open waterbodies was likely to be the main control on *Hippopotamus* distribution. As a result, the presence of hippo fossils required the occurrence of humid conditions with mild winters (to prevent seasonal freezing over of rivers and lakes). None of these environmental tolerances requires the occurrence of exceptionally warm interglacials; nonetheless, this taxon is currently only known from such intervals in Britain. Consequently, it is reasonable to assume that the warm interval indicated by the *Hippopotamus* remains in the Siliceous Member at Westbury Cave represents the occurrence of a humid interglacial characterized by mild winters and enhanced (greater than Holocene) warmth.

It is here worth emphasizing the observations of Candy et al. (2010) and Candy and McClymont (2013) that the evidence for enhanced warmth in multiple British early Middle Pleistocene sites, and in some North Atlantic marine cores, is in strong contrast to many long palaeoclimatic records that are routinely used to discuss Quaternary climate history. In records such as LR04 (Fig. 4A; Lisiecki and Raymo, 2005) and EPICA Dome C (Jouzel et al., 2007), interglacials MIS 19–13 (the interval within which both Sidestrand and Pakefield are positioned) appear significantly cooler than the Holocene and most late conditions under which *Hippopotamus* existed when they comprised part of the British fauna. Sites where *Hippopotamus* remains occur in situ with robust palaeoclimatic reconstructions are restricted to a number of MIS 5e sites, including Trafalgar Square, which is discussed here as it contains the richest and most detailed palaeoclimatic record (see Candy et al., 2016 for a review), and Pakefield (Parfitt et al., 2005; Candy et al., 2010). During the late Middle Pleistocene (MIS 11–7), *Hippopotamus* is thought to have been absent from Britain (Schreve, 2001). Only during the last interglacial (Ipswichian; MIS 5e) in the Late Pleistocene are hippo remains widespread and known from over 35 sites across the country (Sutcliffe, 1959; Stuart, 1986; Currant and Jacob, 2001). Although hippo has been described in Gloucester from what was thought to be an MIS 7/6 context, an MIS 5 age for this occurrence is considered more likely (Schreve, 2009). Despite the supposed absence of hippo during the late Middle Pleistocene, Schreve (1997) also drew attention to a hippo incisor fragment in the NHMUK collection (NHMUK PV OR 21653) from the MIS 9 interglacial site at Grays Thurrock, Essex (Schreve, 2001). This specimen was acquired at the same time as the rest of the Grays assemblage and is of a similar preservation type (Schreve, 1997), which led to the suggestion that the hippo occurrence could be genuine and that hippo presence during MIS 9 should not be dismissed out of hand (Schreve, 1997).

### Palaeoclimates during hippo occupation of the British Isles

Given the stratigraphical distribution outlined above, it is possible to make some observations about the climatic conditions under which *Hippopotamus* existed when they comprised part of the British fauna. Sites where *Hippopotamus* remains occur in situ with robust palaeoclimatic reconstructions are restricted to a number of MIS 5e sites, including Trafalgar Square, which is discussed here as it contains the richest and most detailed palaeoclimatic record (see Candy et al., 2016 for a review), and Pakefield (Parfitt et al., 2005; Candy et al., 2010). Furthermore, it appears probable, but not undeniable, that the *Hippopotamus* remains from Sidestrand are associated with the early Middle Pleistocene ‘Cromerian’ deposits at this site. Consequently, it is possible to discuss the climate and environments of *Hippopotamus* migration into southern Britain during MIS 5e (Trafalgar Square), MIS 13 (Sidestrand) and an earlier ‘Cromerian’ interglacial (Pakefield, MIS 17/15). Significantly, these sites yield the warmest interglacial temperature reconstructions of any British interglacial deposits. Coleopteran assemblages at all three of these sites contain southern and eastern European species indicating summer temperatures several degrees higher than the present day. This suggestion is supported by the presence, again at all three sites, of *Trapa natans* (the water chestnut), which is often reported as requiring mean July temperatures of >20 °C to successfully germinate (Candy et al., 2010, 2015). All three sites contain a rich assemblage of thermophilous flora and fauna (see discussion in Candy et al., 2010, 2015, 2016) and, therefore, produce the most robust record of enhanced – in this case taken to mean greater than Holocene (see Candy et al., 2010, 2016) – interglacial warmth of any interglacial deposits of the British Middle and Late Pleistocene. It is during these periods of enhanced warmth that *Hippopotamus* remains are found Britain.

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Middle and Late Pleistocene interglacials. It is therefore crucial to use climate records from the region within which fossils occur to inform palaeoenvironmental interpretations, rather than climate data that are distant from the study site. This is particularly important when discussing the Early Pleistocene of Britain, as very few detailed palaeoclimatic reconstructions are available for this region at this time. It is consequently tempting to rely on long records, such as LR04, to identify periods of enhanced warmth that may permit the migration of *Hippopotamus* into Britain. However, such an approach is highly problematic because two of the key sites that yield both *Hippopotamus* fossils and evidence for enhanced warmth appear relatively ‘cool’ in several long climate records.

**The late Early Pleistocene hippos of western Europe**

The temporal (Fig. 4E) and spatial (Fig. 5) patterns of *Hippopotamus* occurrences in western Europe during the late Early Pleistocene have useful implications for the probable age of Siliceous Member deposition. While not completely exhaustive, the comprehensive synthesis of sites herein captures numerous occurrences in the most well-known assemblages dated by biochronology, palaeomagnetism and other techniques (see refs in Fig. 4). The broad patterns identified are likely to be representative, but could be tested in future work.

As already mentioned, some early occurrences of hippo at ca. 2.2 Ma may represent the first colonization of Europe (Bellucci et al., 2012, 2014), but this is not universally accepted (Martínez-Navarro et al., 2015; Marra et al., 2018; Martino and Pandolfi, in press). Between ca. 1.9 and 1.5 Ma, hippo presence has been suggested from Italian sites in the Upper Valdarno, Mugello and Ellera basins (Martino and Pandolfi, in press), but these include controversial, unstratified and poorly dated records, and hippo has not been recorded in western Europe beyond the Italian peninsula at this time. More widespread occurrences are known after ca. 1.5 Ma (Fig. 4E; Rook and Martínez-Navarro, 2010; Martínez-Navarro et al., 2015). Between ca. 1.5 and 1.3 Ma, hippo is known from the Iberian peninsula (four sites: Venta Micena, Incarca-I, Barranco León and Fuente Nueva-3), with a more northerly occurrence at Sainzellez in the Massif Central of France and a possible occurrence at Saticula, Italy (Fig. 5), but age uncertainties are wide at this site. Hippo does not then occur at numerous sites until ca. 1.1–1.0 Ma, around the time of the Jaramillo subchron (a period of ‘normal’ polarity of the Earth’s magnetic field; Fig. 4E). It is during this period that hippo spreads north of the Alps/Massif Central and into north-west Europe (Germany and more northern parts of France). Hippo fossils from Courterolles in France could mark an earlier presence north of the Massif Central, but wide age estimates for the site (ca. 1.3–0.9 Ma; Brochet et al., 1983) also include the Jaramillo interval. The Early Pleistocene hippo from Westbury Cave is one of the most northern/north-western occurrences known so far in Europe, only rivalled by specimens from the Netherlands, where hippo remains are associated with Early Pleistocene assemblages dredged from the bottom of the North Sea (van Kolschoten, 2001; Mol et al., 2003). These Dutch records have poor age constraints, but ranges also overlap with the ca. 1-Ma/Jaramillo occurrences in north-west Europe (Fig. 4E). Several occurrences are known after the Jaramillo subchron, but these appear largely restricted to southern ranges near the Mediterranean coast in Spain, France and Italy, with the exception of the Dutch records if younger ages within their uncertainties are upheld.

Although the fossil record is notoriously incomplete and provides only a partial picture of animal palaeobiogeography, it can be used to construct testable hypotheses, upon which future data can be brought to bear. Available occurrences suggest that late Early Pleistocene hippos were widespread north of the Alps/Massif Central around the time of the Jaramillo subchron. The best available palaeomagnetic and biochronological information, summarized above, suggests an age of ca. 1.5–1.07 Ma for the Siliceous Member. Given these data, it is plausible that the Siliceous Member hippo was broadly coincident with other northern occurrences and represents part of a colonization of north-west Europe that took place towards the younger end of the Siliceous Member biochronological age estimate.

A younger age within the biochronological inference is also supported by the form of the *Allophaiomys* molar from the Siliceous Member (Bishop, 1982; Fig. 4C). The confluence between the anterior dentine fields (the fourth and fifth triangles of the occlusal surface and the anterior cap) is consistent with the ‘allophaiomyid’ molar morphotype and, although the posterior lobe is incomplete, it is possible to provide an estimate of ca. 48 for the A/L ratio (length of the anteroconid complex relative to maximum molar length; see van der Meulen and Zagwijn, 1974). An ‘allophaiomyid’ morphology and a high A/L ratio (>44.5) are features shared with ‘advanced’ *Allophaiomys* (sensu Maul and Markova, 2007), which occurs in central Europe ca. 1.2–1.0 Ma.

At present, most Jaramillo hippo occurrences in Europe cannot be constrained to a particular interglacial within the subchron due to the broad age uncertainties at most sites. However, the renowned site of Untermassfeld in Germany has been linked to the MIS 31 interglacial (ca. 1.06–1.08 Ma; Channell et al., 2020) through a combination of biochronology, magnetostratigraphy, lithostratigraphy and radiometric dating (see review by Kahlke, 2006; Maul et al., 2007; Gerdes et al., 2020) and is rich in *Hippopotamus* fossils, with over 800 individual hippo specimens (Kierdorf and Kahlke, 2020). Proxy records around the world indicate that MIS 31 was warmer than the current interglacial (Oliveira et al., 2017). This is confirmed at Untermassfeld by the discovery of several thermophilous vertebrates (including climate-sensitive reptiles, e.g. sand boa,
snake-eyed lizard and a disputed occurrence of pond turtle; Böhme, 2020) as well as local isotopic palaeotemperature reconstructions higher than present (Stephan et al., 2001; Kahlke, 2006). MIS 31 was clearly warm and humid enough to support hippo populations in north-west Europe and it is likely, but admittedly not yet demonstrable, that conditions were similarly favourable in Britain. In addition, similarities between the German and British records of Hippopotamus in the Middle and Late Pleistocene have been highlighted previously, with preferential migration into Britain potentially occurring via the Rhine River valley (Schreve et al., 2007; Schreve, 2012; Fig. 5). Given that hippos were present in Germany, France and possibly also the Netherlands during the Jaramillo subchron, it is not at all inconceivable that hippos migrated to the British Isles at a similar time.

MIS 31 is not the only interglacial during the Jaramillo subchron (e.g. MIS 29, ca. 1.03–1.01 Ma), but it is the only one that includes periods of both reversed and normal magnetization. MIS 31 straddles the lower Jaramillo boundary, beginning during a period of reversed magnetization around 1.09–1.08 Ma and terminating at ca. 1.06 Ma within the normal subchron (Oliveira et al., 2017; Channell et al., 2020). It is also the only Jaramillo interglacial with well-constrained, site-specific evidence in nearby Europe for enhanced (greater than Holocene) warmth; only under these palaeoclimatic conditions are hippos currently known in Britain during the Pleistocene (see above). A post-Jaramillo age for the Siliceous Member is unlikely due to the occurrence of Allophaiomys (and possibly also Leptobos), and an age within the Jaramillo subchron itself is precluded by the reversed polarity of the sediments, so an assignment of the Siliceous Member to early MIS 31 (of reversed magnetization) appears to be consistent with Jaramillo hippo presence in north-west Europe and is a leading hypothesis that warrants further investigation.

While the early part of MIS 31 provides a good fit to available biogeographical models, biochronological and palaeomagnetic constraints, and palaeoclimatic data, it is certainly not the only possibility. The Siliceous Member occurrence could also mark a currently cryptic migration of Hippopotamus into north-west Europe during an earlier temperate and humid phase in the late Early Pleistocene.

Conclusions

The hippopotamus molar described from the Siliceous Member represents the earliest occurrence of the genus and family in the British Pleistocene. Similarities in morphology and size to specimens from across western Europe suggest that the molar belongs to Hippopotamus cf. antiquus. The preservation of the fossil is consistent with its provenance in distal talus cone deposits and demonstrates that the Early Pleistocene faunal assemblage in Westbury Cave is not entirely highly derived, as previously believed. In combination with other palaeomagnetic and biochronological dating constraints, the Siliceous Member hippo supports a depositional age between ca. 1.5 and 1.07 Ma, a period unknown in the British fossil record before now. As a key thermophilous taxon, the presence of hippo bolsters the palaeoenvironmental inferences made from previously reported mammal taxa. It is likely that the Siliceous Member records an interglacial period, when temperatures were a few degrees higher than present, winters were mild and palaeoclimates were humid. A synthesis of dated hippo occurrences across western Europe suggests that the Siliceous Member hippo may have been part of a widespread colonization of north-west Europe that occurred from ca. 1.1 Ma, possibly during MIS 31. The Early Pleistocene sediments in Westbury Cave could record the early part of this interglacial, or could record an earlier temperate phase that would imply currently cryptic migrations of hippo into north-west Europe during the Early Pleistocene. In either case, the Siliceous Member is likely to represent a warm period in the Early Pleistocene that has not been recognized previously in the British Quaternary record.

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Conflict of interest statement—The authors declare no conflicts of interest.

Data Availability Statement

All data that support the findings are available in the main text or in referenced literature. The fossil specimen has been accessioned into a recognized public collection, where it is available for study.

References

Adams NF. 2017. Early Pleistocene palaeontology of Westbury Cave, Somerset. Palaeontology Newsletter 94: 79–84.
Adams NF, Candy J, Schreve DC et al. 2019. Deposition and provenance of the Early Pleistocene Siliceous Member in Westbury Cave, Somerset, England. Proceedings of the Geologists’ Association 130: 210–226. https://doi.org/10.1016/j.jgeola.2019.02.005
Aguilier J-P, Antoine P-O, Bonnet A et al. 2009. Compléments à la faune pléistocène de Dufort (Gard, Sud de la France). Bulletin de la Société d’Histoire Naturelle de Toulouse 145: 55–58.
Alba DM, Madurell-Malapeira J, Delson E et al. 2016. First record of macaques from the Early Pleistocene of Incarcal (NE Iberian Peninsula). Journal of Human Evolution 96: 139–144. https://doi.org/10.1016/j.jhevol.2016.05.005 [PubMed: 27302242]
Andrews P, Cook J, Currant A et al. (eds). 1999. Westbury Cave: The Natural History Museum Excavations 1976–1984. Western Academic & Specialist Press Ltd: Bristol.
Andrews P & Ghaleb B. 1999. Taphonomy of the Westbury Cave bone site. Pierre Schreve is thanked for assistance in the field and with fossil conservation. Thanks also to David Waterhouse for providing specimen information on the Cromer hippo mandible, currently on permanent display at Cromer Museum, and to Amal Kheisheb for curatorial assistance at TTNCM. N.F.A. was supported by an NERC doctoral studentship awarded through the Central England NERC Training Alliance (CENTA; grant ref. NE/L002493/1) and by the University of Leicester during this project. This paper is dedicated to Nigel Taylor and the late Sidney Alford for their enthusiastic support of our recent work on the cave deposits in Westbury Quarry.

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References

Adams NF. 2017. Early Pleistocene palaeontology of Westbury Cave, Somerset. Palaeontology Newsletter 94: 79–84.
Adams NF, Candy J, Schreve DC et al. 2019. Deposition and provenance of the Early Pleistocene Siliceous Member in Westbury Cave, Somerset, England. Proceedings of the Geologists’ Association 130: 210–226. https://doi.org/10.1016/j.jgeola.2019.02.005
Aguilier J-P, Antoine P-O, Bonnet A et al. 2009. Compléments à la faune pléistocène de Dufort (Gard, Sud de la France). Bulletin de la Société d’Histoire Naturelle de Toulouse 145: 55–58.
Alba DM, Madurell-Malapeira J, Delson E et al. 2016. First record of macaques from the Early Pleistocene of Incarcal (NE Iberian Peninsula). Journal of Human Evolution 96: 139–144. https://doi.org/10.1016/j.jhevol.2016.05.005 [PubMed: 27302242]
Andrews P, Cook J, Currant A et al. (eds). 1999. Westbury Cave: The Natural History Museum Excavations 1976–1984. Western Academic & Specialist Press Ltd: Bristol.
Andrews P & Ghaleb B. 1999. Taphonomy of the Westbury Cave bone site. In Westbury Cave: The Natural History Museum Excavations 1976–1984, Western Academic & Specialist Press Ltd: Bristol.
Andrews P & Ghaleb B. 1999. Taphonomy of the Westbury Cave bone assemblages. In Westbury Cave: The Natural History Museum Excavations 1976–1984, Andrews P, Cook J, Currant A, Stringer C (eds). Western Academic & Specialist Press Ltd: Bristol; 87–126.
Andrews P, Stringer C. 1999. The palaeoecology of the faunas from Westbury Cave. In Westbury Cave: The Natural History Museum Excavations 1976–1984, Andrews P, Cook J, Currant A, Stringer C (eds). Western Academic & Specialist Press Ltd: Bristol; 195–210.
Argenti P. 2004. Plio-Quaternary mammal fossiliferous sites of Umbria (central Italy). Geologica Romana 37: 67–78.
Arzarello M, Pavia G, Peretto C et al. 2012. Evidence of an Early Pleistocene hominin presence at Pirro Nord (Apricena, Foggia, southern Italy): P13 site. Quaternary International 267: 56–61. https://doi.org/10.1016/j.quaint.2011.01.042
Ashton N, Lewis SG, De Groote I et al. 2014. Hominin footprints from Early Pleistocene deposits at Happisburgh, UK. PLoS ONE 9: e88329. https://doi.org/10.1371/journal.pone.0088329 [PubMed: 24516637]
Barisone G, Argenti P, Kotsakis T. 2006. Plio-Pleistocene evolution of the genus Castor (Rodentia, Mammalia) in Europe: C. fiber plicidens
of Pietralla (Perugia, Central Italy). Geobios 39: 757–770. https://doi.org/10.1016/j.geobios.2005.10.003
Bellucci L, Bonafò F, Corrado P et al. 2014. Evidence of Late Gelasian dispersal of African fauna at Coste San Giacomo (Anagni Basin, central Italy): Early Pleistocene environments and the background of early human occupation in Europe. Quaternary Science Reviews 96: 72–85. https://doi.org/10.1016/j.quascirev.2013.10.011
Bellucci L, Mazzini I, Scardia G et al. 2012. The site of Coste San Giacomo (Early Pleistocene, central Italy): palaeoenvironmental analysis and biochronological overview. Quaternary International 267: 30–39. https://doi.org/10.1016/j.quaint.2011.04.006
Bellucci L, Sardella R, Rook L. 2015. Large mammal biochronology framework in Europe at Jaramillo: the Epivillafranchian as a formal biochron. Quaternary International 389: 84–89. https://doi.org/10.1016/j.quaint.2014.11.012
Berends CJ, Köhler P, Lourens LJ et al. 2014. Seasonality in the early Middle Pleistocene of Britain, in relation to the Mid-Pleistocene Transition. Reviews of Geophysics 59: e2020RG000727. https://doi.org/10.1029/2020RG000727
Bishop MJ. 1982. The mammal fauna of the early Middle Pleistocene of Britain – a preliminary report on amphibia and reptiles from the Early Pleistocene site of Untermassfeld – Biostratigraphic analysis of the herpetofauna. In The Pleistocene of Untermassfeld near Meiningen (Thuringen, Germany): Part 4, Kahle R-D (ed). Verlag des Römisch-Germanischen Zentralmuseums: Mainz; 1141–1158.
Boisserie J, Lihoreau F, Orlic M et al. 2010. Morphology and phylogenetic relationships of the earliest known hippopotamids (Cetartiodactyla, Hippopotamidae, Kenyapotaminae). Zoological Journal of the Linnean Society 158: 325–366. https://doi.org/10.1111/j.1096-3642.2009.00548.x
Bona F, Sala B. 2016. Villafranchian-Galerian mammal faunas transition in South-Western Europe. The case of the late Early Pleistocene mammal fauna of the Frantoio locality, Arda River (Castell’Arquato, Piacenza, Northern Italy). Geobios 49: 329–347. https://doi.org/10.1016/j.geobios.2016.06.002
Breda M, Collinge SE, Parfitt SA et al. 2010. Metric analysis of ungulate mammals in the early Middle Pleistocene of Britain, in relation to taxonomy and biostatigraphy: I: Rhinocerotidae and Bovidae. Quaternary International 228: 136–156. https://doi.org/10.1016/j.quaint.2010.05.010
Breda M, Marchetti M. 2007. Pleistocene mammal faunas from the Lefle Basin (Bergamo, northern Italy): revision and new data. Courier Forschungsinstitut Senckenberg 259: 61–77
Brochet G, Chaline J, Poplin F. 1983. Courterolles (Yonne), une faune à rhinocéros et à ovins de la fin du Moustérien du Bassin parisien: le rhinocéros: ex gr. elasmotherium. C. R. Acad. Sci. (Paris) 297: 641–645
Brochet G, Chaline J, Poplin F. 1983. Courterolles (Yonne), une faune à rhinocéros et à ovins de la fin du Moustérien du Bassin parisien: la diversité de la faune. C. R. Acad. Sci. (Paris) 297: 637–640
Brochet G, Chaline J, Poplin F. 1983. Courterolles (Yonne), une faune à rhinocéros et à ovins de la fin du Moustérien du Bassin parisien: la diversité de la faune. C. R. Acad. Sci. (Paris) 297: 637–640.
Channell JET, Singer BS, Jicha BR. 2020. Timing of Quaternary geomagnetic reversals and excursions in volcanic and sedimentary archives. Quaternary Science Reviews 228. 106114. https://doi.org/10.1016/j.quascirev.2019.106114
Chen M, Bizzarri R, Buratti N et al. 2012. Multidisciplinary study of a new Quaternary mammal-bearing site from Ellera di Corciano (central Umbria, Italy): preliminary data. Rendiconti online della Società Geologica Italiana 21: 1075–1077.
Chen M, D’Alloceo V, Masani F. 2019. New bovid remains from the Early Pleistocene of Umbria (Italy) and a reappraisal of Leptobos merlai. Journal of Mammalian Evolution 26: 201–224. https://doi.org/10.1007/s10914-017-9421-x
Coltorti M, Albanielli A, Bertini A et al. 1998. The Colle Curti mammal sites in the Colfiorito area (Umbria-Marche Apennine, Italy): geomorphology, stratigraphy, paleomagnetism and palynology. Quaternary International 47-48: 107–116. https://doi.org/10.1016/S1040-6182(97)00076-1
Cuenca-Bescós G, Blain HA, Rofes J et al. 2015. Comparing two different Early Pleistocene microfaunal sequences from the caves of Atapuerca, Sima del Elefante and Gran Dolina (Spain): biochronological implications and significance of the Jaramillo subchron. Quaternary International 389: 148–158. https://doi.org/10.1016/j.quaint.2014.12.059
Cuenca-Bescós G, Rofes J, López-García JM et al. 2010. Biochronology of Spanish Quaternary small vertebrate faunas. Quaternary International 212: 109–119. https://doi.org/10.1016/j.quaint.2009.06.007
Currant A, Jacobi R. 2001. A formal mammalian biostratigraphy for the Late Pleistocene of Britain. Quaternary Science Reviews 20: 1707–1716. https://doi.org/10.1016/S0277-3791(01)00035-X
Dickinson MR, Lister AM, Penkman KEH. 2019. A new method for enamel amino acid racemization dating: a closed system approach. Quaternary Geochronology 50: 29–46. https://doi.org/10.1016/j.quageo.2018.11.005
Duval M, Falguères C, Bahain J et al. 2012. On the limits of using combined U-series/ESR method to date fossil teeth from two Early Pleistocene archaeological sites of the Orce area (Guadix-Baza basin, Spain). Quaternary Research 77: 482–491. https://doi.org/10.1016/j.quarsci.2012.01.002
Eawy A, Horne DJ, Parfitt SA et al. 2020. Early Pleistocene conifer macrofossils from Happisburgh, Norfolk, UK, and their environmental implications for early hominin occupation. Quaternary Science Reviews 232. 106115. https://doi.org/10.1016/j.quascirev.2019.106115
Faure M. 1984. Hippopotamus incognitus nov. sp., un hippopotame (Mammalia, Artiodactyla) du Pleistocene d’Europe occidentale. Geobios 17: 427–437. https://doi.org/10.1016/S0016-6955(84)80017-0
Faure M. 1985. Les hippopotames quaternaires non insulaires d’Europe occidentale. Nouvelles Archives du Musée d’Histoire Naturelle de Lyon 23: 13–79.
Fidolini F, Ghinassi M, Magi M et al. 2013. The Plio-Pleistocene fluvio-lacustrine Upper Valdarno Basin (central Italy): stratigraphy and Basin fill evolution. Italian Journal of Geosciences 132: 13–32. https://doi.org/10.3301/IJG.2012.06
Fisher O. 1905. On the occurrence of Elephas meridionalis at Devils (Dorset). Second communication: human agency suggested. Quarterly Journal of the Geological Society 61: 35–38. https://doi.org/10.1144/GSL.JGS.1905.061.01-046
Funnell BM. 1995. Global sea-level and the (p)eninsula of late Cenozoic Britain. Geological Society, London, Special Publications 96: 3–13. https://doi.org/10.1144/GSL.SP.1995.096.01.02

Candy I, Schreve D, White TS. 2015. MIS 13–12 in Britain and the North Atlantic: understanding the palaeoclimatic context of the earliest Acheulean. Quaternary Science Reviews 30: 593–609. https://doi.org/10.1016/j.quascirev.2015.09.005
Candy I, White TS, Elias S. 2016. How warm was Britain during the Last Interglacial? A critical review of Ipswichian (MIS 5e) palaeo-temperature reconstructions. Journal of Quaternary Science 31: 857–868. https://doi.org/10.1016/j.quascirev.2015.09.005
Carreck NJ. 1955. The Quaternary vertebrates of Dorset, fossil and sub-fossil. Proceedings of the Dorset Natural History and Archaeological Society 75: 164–188.
Gentry AW. 1999. Fossil ruminants (Mammalia, Artiodactyla) from Westbury Cave. In Westbury Cave: The Natural History Museum Elevation 1976–1984, Andrews P, Cook J, Curran A, Stringer C (eds). Western Academic & Specialist Press Ltd; Bristol; 139–174.

Geddes A, Gätter A, Linnemann U et al. 2020. In situ U-Pb geochronology of re-deposited travertine from the Early Pleistocene site of Untermassfeld. In The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany): Part 4, Kahlike R-D (ed). Verlag des Römisch-Germanischen Zentralmuseums: Mainz; 1105–1116.

Gibbard PL, West RG, Zagwijn WH et al. 1991. Early and early Middle Pleistocene faunas in the southern North Sea basin. Quaternary Science Reviews 10: 23–52. https://doi.org/10.1016/0277-3791(91)90029-T

Gibert L, Scott G, Martin R et al. 2007. The Early to Middle Pleistocene boundary in the Baza Basin (Spain). Quaternary Science Reviews 26: 2067–2089. https://doi.org/10.1016/j.quascirev.2007.06.012

Guérin C, Dewolf Y, Lautridou J-P. 2003. Révision d’un site paléontologique célèbre: Saint-Prest (Chartres, France). Geobios 36: 55–82. https://doi.org/10.24090/geo.36.1.05

Head MJ, Gibbard PL. 2015. Early–Middle Pleistocene transitions: linking terrestrial and marine realms. Quaternary International 389: 7–46. https://doi.org/10.1016/j.quaint.2015.09.042

Hooijer DA. 1942. On the nomenclature of some fossil hippopotami. Archives Néerlandaises de Zoologie 6: 279–282. https://doi.org/10.1163/235651642X00077

Jouzel J, Masson-Delmotte V, Cattani O et al. 2007. Orbital and millennial Antarctic climate variability over the past 800,000 years. Science 317: 793–796. https://doi.org/10.1126/science.1141038 [PubMed: 17615306]

Kahlke R-D. 1997. Die Hippopotamus Reste aus dem Unterpleistozän von Untermassfeld. In Das Pleistozän von Untermassfeld bei Meiningen (Thüringen, Germany): Teil 1, Kahlike R-D (ed). Dr Rudolf Habelt GmbH; Bonn; 277–374.

Kahlke R-D. 2001. Schädelreste von Hippopotamus aus dem Unterpleistozän von Untermassfeld. In Das Pleistozän von Untermassfeld bei Meiningen (Thüringen, Germany): Teil 2, Kahlike R-D (ed). Dr Rudolf Habelt GmbH; Bonn; 483–500.

Kahlke R-D. 2006. Untermassfeld: A late Early Pleistocene (Epipillafranchian) fossil site near Meiningen (Thuringia, Germany) and its position in the development of the European mammal fauna. BAR International Series 1578: 1–141.

Kahlke R-D, García N, Kostopoulos DS et al. 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. Quaternary Science Reviews 30: 1368–1395. https://doi.org/10.1016/j.quascirev.2010.07.020

Kierdorf U, Kahlike R-D. 2020. Pathological findings on remains of hippopotamids from the Early Pleistocene site of Untermassfeld. In The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany): Part 4, Kahlike R-D (ed). Verlag des Römisch-Germanischen Zentralmuseums: Mainz; 1251–1272.

Konidaris GE, Athanassiou A, Tourloukis V et al. 2018. The skeleton of a straight-tusked elephant (Palaeoloxodon antiquus) and other large mammals from the Middle Pleistocene butchering locality Marathousa 1 (Megalopolis Basin, Greece): preliminary results. Quaternary International 497: 65–84. https://doi.org/10.1016/j.quaint.2017.12.001

Lee JR, Candy I, Haslam R. 2018. The Neogene and Quaternary of England: landscape evolution, tectonics, climate change and their expression in the geological record. Proceedings of the Geologists’ Association 129: 452–481. https://doi.org/10.1016/j.pgeola.2017.10.003

Lee JR, Rose J, Candy I et al. 2006. Sea-level changes, river activity, soil development and glaciaion around the western margins of the southern North Sea Basin during the Early and early Middle Pleistocene: 1997–1999. From Paketić, Ž., Ćurčić, A. Stringa's Quaternary Science 21: 155–179. https://doi.org/10.1007/s00248-005-0957

Lewis SG, Parfitt SA, Preece RC et al. 2004. Age and palaeoenvironmental setting of the Pleistocene vertebrate fauna at Norton Subcourse, Norfolk. In The Quaternary Mammals of Southern and Eastern England: Field Guide, Schreve DC (ed). Quaternary Research Association: London; 5–17.
Geobios 40: 207–217. https://doi.org/10.1016/j.geobios.2006.05.005

Sorbelli L, Alba DM, Cherin M et al. 2021. A review on Bison schoetensacki and its closest relatives through the early-Middle Pleistocene transition: insights from the Valfparadis Section (NE Iberian Peninsula) and other European localities. Quaternary Science Reviews 261. 106933. https://doi.org/10.1016/j.quascirev.2021.106933

Spencer HEP, Melville RV. 1974. The Pleistocene mammalian fauna of Dove Holes, Derbyshire. Bulletin of the Geological Survey of Great Britain 48: 43–53.

Stephan E, Uerpmann H-P, Cramer B 2001. Paläotemperaturbestimmungen nach 818O-Werten von Equiden-Resten aus dem Unterpleistozän von Untermassfeld. In Das Pleistozän von Untermassfeld bei Meiningen (Thüringen): Teil 3, Kahle R-D (ed.). Dr Rudolf Habelt GmbH: Bonn; 917–930.

Stewart M, Loys J, Price GJ et al. 2019. Middle and Late Pleistocene mammal fossils of Arabia and surrounding regions: implications for biogeography and hominin dispersals. Quaternary International 515: 12–29. https://doi.org/10.1016/j.quaint.2017.11.052

Stoffel C, Dufresnes C, Okello JBA et al. 2015. Genetic consequences of population expansions and contractions in the common hippopotamus (Hippopotamus amphibius) since the Late Pleistocene. Molecular Ecology 24: 2507–2520. https://doi.org/10.1111/mec.13179 [PubMed: 25827243]

Stuart AJ. 1982. Pleistocene vertebrates in the British Isles. Longman: London.

Stuart AJ. 1986. Pleistocene occurrences of Hippopotamus in Britain. Quärtärpaläontologie 6: 209–218.

Stuart AJ. 1996. Vertebrate faunas from the early Middle Pleistocene of East Anglia. In The early Middle Pleistocene in Europe, Turner C (ed). Balkema: Rotterdam; 9–24.

Stuart AJ, Lister AM. 2001. The mammalian faunas of Pakefield/Kessingland and Corton, Suffolk, UK: evidence for a new temperate episode in the British early Middle Pleistocene. Quaternary Science Reviews 20: 1677–1692. https://doi.org/10.1016/S0277-3791(01)00034-8

Sutcliffe AJ. 1959. The hippopotamus in Britain. Bulletin of the Mammal Society of the British Isles 11: 36–40.

Thouveny N, Bonifay E. 1984. New chronological data on European Plio-Pleistocene faunas and hominid occupation sites. Nature 308: 355–358. https://doi.org/10.1038/308355a0

Toro-Moyano I, Martínez-Navarro R, Agustí J et al. 2013. The oldest human fossil in Europe, from Orce (Spain). Journal of Human Evolution 65: 1–9. https://doi.org/10.1016/j.jhevol.2013.01.012 [PubMed: 23481345]

d van der Made J, Rosell J, Blasco R. 2017a. Faunas from Atapuerca at the Early–Middle Pleistocene limit: the unglaciated from level TD8 in the context of climatic change. Quaternary International 433: 296–346. https://doi.org/10.1016/j.quaint.2015.09.009

d van der Made J, Sahnouni M & Boulaghbraief K. 2017b. Hippopotamus gorgops from El Kherba (Algeria) and the context of its biogeography. In Proceedings of the II Meeting of African Prehistory: Burgos 15-16 April, 2015, Sahnouni M, Semaw S, Rios Garaizar J (eds). CENIEH: Burgos; 135–169.

d van der Meulen AJ, Zagwijn WH. 1974. Microtus (Allophaiomys) pliocaenicus from the Lower Pleistocene near Brielle, The Netherlands. Scripta Geologica 21: 1–12.

d van Kolfschoten T, Turner E. 1996. Early Middle Pleistocene mammalian faunas from Kärlich and Miesenheim I and their biostatigraphical implications. In The early Middle Pleistocene in Europe, Turner C (ed). Balkema: Rotterdam; 227–253.

von Koenigswald W, Heinrich W-D. 1999. Mittelpleistozäne Säugerfaunen aus Mitteleuropa – der Versuch einer biostatigraphischen Zuordnung. Käupia 9: 53–112.

Westaway R. 2011. A re-evaluation of the timing of the earliest reported human occupation of Britain: the age of the sediments at Happisburgh, eastern England. Proceedings of the Geologists’ Association 122: 383–396. https://doi.org/10.1016/j.jgeola.2011.03.002

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