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Abstract: Fluvial sedimentary archives have the potential to preserve a wide variety of palaeontological evidence, ranging from robust bones and teeth found in coarse gravel aggradations to delicate insect remains and plant macrofossils from fine-grained deposits. Over the last decade, advances in Quaternary biostratigraphy based on vertebrate and invertebrate fossils (primarily mammals and molluscs) have been made in many parts of the world, resulting in improved relative chronologies for fluviatile sequences. Complementary fossil groups, such as insects, ostracods and plant macrofossils, are also increasingly used in multi-proxy palaeoclimatic and palaeoenvironmental reconstructions, allowing direct comparison of the climates and environments that prevailed at different times across widely separated regions. This paper reviews these topics on a regional basis, with an emphasis on the latest published information, and represents an update to the 2007 review compiled by the FLAG-inspired IGCP 449 biostratigraphy subgroup. Disparities in the level of detail available for different regions can largely be attributed to varying potential for preservation of fossil material, which is especially poor in areas of non-calcareous bedrock, but to some extent also reflect research priorities in different parts of the world. Recognition of the value of biostratigraphical and palaeoclimatic frameworks, which have been refined over many decades in the 'core regions' for such research (particularly for the late Middle and Late Pleistocene of NW Europe), has focussed attention on the need to accumulate similar palaeontological datasets in areas lacking such long research histories. Although the emerging datasets from these understudied regions currently allow only tentative conclusions to be drawn, they represent an important stage in the development of independent biostratigraphical and palaeoenvironmental schemes, which can then be compared and contrasted.

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Fossils from Quaternary fluvial archives: sources of biostratigraphical, biogeographical and palaeoclimatic evidence

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Abstract

Fluvial sedimentary archives have the potential to preserve a wide variety of palaeontological evidence, ranging from robust bones and teeth found in coarse gravel aggradations to delicate insect remains and plant macrofossils from fine-grained deposits. Over the last decade, advances in Quaternary biostratigraphy based on vertebrate and invertebrate fossils (primarily mammals and molluscs) have been made in many parts of the world, resulting in improved relative chronologies for fluviatile sequences. Complementary fossil groups, such as insects, ostracods and plant macrofossils, are also increasingly used in multi-proxy palaeoclimatic and palaeoenvironmental reconstructions, allowing direct comparison of the climates and environments that prevailed at different times across widely separated regions. This paper reviews these topics on a regional basis, with an emphasis on the latest published information, and represents an update to the 2007 review compiled by the FLAG-inspired IGCP 449 biostratigraphy subgroup. Disparities in the level of detail available for different regions can largely be attributed to varying potential for preservation of fossil material, which is especially poor in areas of non-calcareous bedrock, but to some extent also reflect research priorities in different parts of the world. Recognition of the value of biostratigraphical and palaeoclimatic frameworks, which have been refined over many decades in the 'core regions' for such research (particularly for the late Middle and Late Pleistocene of NW Europe), has focussed attention on the need to accumulate similar palaeontological datasets in areas lacking such long research histories. Although the emerging datasets from these understudied regions currently allow only tentative conclusions to be drawn, they represent an important stage in the development of independent biostratigraphical and palaeoenvironmental schemes, which can then be compared and contrasted.

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Fig. 2 Idealized tranverse section through the Lower Thames terrace sequence, east of London, including details of Mammal Assemblage Zones (after Bridgland and Schreve, 2001), updated to include biostratigraphically significant invertebrate species and archaeological data.

Fig. 3 Correlation of Hoxnian fluvial sequences in the Lower Thames with the stratotype at Hoxne (after White et al., 2013). The occurrence of the 'Rhenish' suite of freshwater molluscs is critical to linking the Swanscombe and Clacton sequences and thence to the pollen stratigraphy of the type-Hoxnian (sub-stages labelled). Units for which there is clear palaeontological or sedimentological evidence for the prevailing climate are colour-coded, and tentative correlations with the marine oxygen isotope stages (MIS) of the deep-sea record are also shown.

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1. Introduction

The study of fossil assemblages recovered from fluvial deposits is well-established as an important element of multi-disciplinary Quaternary research, providing a basis for regional relative dating frameworks (e.g. Gliozzi et al., 1997; Schreve, 2001a; Schreve and Bridgland, 2002; Bridgland et al., 2004; Markova, 2007; Megirian et al., 2010) and for detailed palaeoclimatic and palaeoenvironmental analyses (e.g. Coope, 2010; Schreve and Candy, 2010; Candy et al., 2010, 2015, 2016; Kahlke et al., 2011; Limondin-Lozouet et al., 2010; Rule et al., 2012; White et al., 2013). The contribution of the Fluvial Archives Group (FLAG) to these research areas over the last 20 years has been considerable: two UNESCO-sponsored International Geological Correlation Programme (IGCP) projects, entitled 'Global correlation of Late Cenozoic fluvial deposits' (IGCP 449) and 'Fluvial sequences as evidence for landscape and climatic evolution in the Late Cenozoic' (IGCP 518), ran under the auspices of FLAG between 2000 and 2007 (Bridgland et al., 2007; Westaway et al., 2009). The former included a thematic biostratigraphy subgroup, which compiled data on faunal assemblages from fluvial sequences in different parts of the world, resulting in the publication of a review of progress in faunal correlation of Late Cenozoic fluvial sequences (Schreve et al., 2007); following the conclusion of these IGCP projects, data has continued to accumulate as part of the ongoing efforts of members of FLAG (Cordier et al., 2017).

This paper provides updated reviews, organized on a regional basis, of advances in Pleistocene vertebrate and invertebrate biostratigraphy made during the 20-year life of FLAG; as such, it is intended to be a companion to the report of the IGCP 449 biostratigraphy subgroup (Schreve et al., 2007), which remains a benchmark review of biostratigraphical frameworks derived from fluvial archives around the world. As was the case with that paper, much of the most detailed work has been undertaken in regions such as NW and Central Europe, which have enjoyed long traditions of Pleistocene palaeontological research, particularly for the late Middle and Late Pleistocene (Fig. 1). This review also extends its scope beyond that of its predecessors to include considerations of the palaeoenvironmental, palaeoecological and biogeographical information that can be derived from fossil assemblages, and the potential for Pleistocene fluvial archives to enhance knowledge of long-term Quaternary climate change.

Insert Figure 1 hereabouts

Fluvial archives have several advantages over other types of terrestrial sedimentary sequences that commonly preserve fossils (such as those from lake basins or caves), the most significant of these being the potential chrono-stratigraphical control provided by river terraces, which have great value as regional templates for the terrestrial Quaternary record (Bridgland, 2000, 2006; Antoine et al., 2007; Bridgland and Westaway, 2008a, 2014; Bridgland et al., 2004, 2006, 2017; Mishra et al., 2007; Vandenberghe, 2015). The nature of rivers also means that Pleistocene fluvial sequences have the potential to preserve a variety of plant and animal fossils derived from terrestrial, freshwater and estuarine environments, recording concurrent changes in a diverse range of palaeoenvironmental settings. Lacustrine sequences, although undoubtedly sources of more continuous and higher-resolution longer-timescale records than rivers, usually represent only the deepest part of a lake basin from which the longest sediment sequences can be obtained; such records are therefore often lacking in fossils indicative of local terrestrial environments (with the notable exception of wind-borne pollen) and are (usually) isolated from marine influences. Conversely, cave sequences, which are often significant repositories of vertebrate fossils (particularly mammals), usually lack pollen and invertebrate assemblages. Fluvial archives therefore have an unrivalled capacity to provide insights into changing Quaternary climates and environments through time, due to the wide range of fossil types available (which include pollen, plant macrofossils, mammals, molluscs, ostracods and insects), coupled with the chronological control provided by river terraces. Together, these proxies can be used to generate local biostratigraphical frameworks, which can then be extended into other regions and into different depositional contexts outside river valleys. Moreover, where fluvial sequences interdigitate with other sediment types, such as glacigenic or estuarine-marine deposits, biostratigraphical evidence can be used to constrain the age of regional glacial and sea-level histories (e.g. Bridgland et al., 1999; Matoshko et al., 2004; White et al., 2010, 2013, 2017; Vis et al., 2010), which can then provide further stratigraphical ('event stratigraphy') markers. It should be noted, of course, that this potential can only be realized in areas conducive to the preservation of fossils, and that fluvial sequences are subjected to the same taphonomic complications known to affect other Quaternary sedimentary archives.

Much of the recent palaeontological research summarized here has been undertaken as part of multidisciplinary projects, often driven by archaeologically-motivated research questions (see Chauhan et al., 2017). In Europe and Asia, these have often focussed on the timing of hominin occupations relative to changing Pleistocene climate and environments (e.g. Parfitt et al., 2005, 2010; Antoine et al., 2015, 2016; Maddy et al., 2015; Peretto et al., 2015), whereas further afield, in regions such as North America and Australia, attention has been more focussed on potential human impacts, particularly on megafaunal populations (e.g. Prideaux et al., 2010; Prescott et al., 2012; Sandom et al., 2014; Cooper et al., 2015; Stuart, 2015). The potential for fossils to provide important chronological and palaeoenvironmental frameworks within which to interpret the archaeological record has also inspired research in (initially) less promising regions of the world that have previously received little attention, such as the deserts of the Arabian Peninsula (e.g. Groucutt et al., 2015; Stimpson et al., 2015, 2016). The resulting palaeontological data have the potential to be interpreted on a variety of scales, ranging from considerations of changing climatic conditions during a single interglacial in a given region (e.g. Candy et al., 2016) to comparisons between different interglacials (e.g. Limondin-Lozouet and Preece, 2014) and even identification of patterns at the marine oxygen isotope substage level (Schreve, 2001b; Candy and Schreve, 2007; Ashton et al., 2008; White et al., 2013). Key to such studies have been important advances in the application of independent geochronological methodologies to Quaternary fluvial archives (reviewed in detail by Rixhon et al., 2017). Advances in radiometric dating techniques, such as optically stimulated luminescence (OSL), electron spin resonance (ESR) and uranium-series have provided crucial chronological control (e.g., Rittenour, 2008; Kock et al., 2009; Voinchet et al., 2015;). In tectonically-active areas, the presence of interbedded volcanic deposits can provide further opportunities for constraining the age of the fluvial sediments through the application of argon–argon dating (e.g. Maddy et al., 2012; Marra et al., 2016). In addition, amino-acid racemization dating (AAR) based on the calcitic opercula of the freshwater gastropod genus *Bithynia* has been shown to be more reliable than previous AAR methodologies, allowing the development of a robust aminostratigraphy for the British Quaternary with potential for application in other regions (Penkman et al., 2007, 2011, 2013; cf. Westaway, 2009).

2. NW and Central Europe

A substantial body of research has been undertaken over the last decade in this important region, particularly in southern Britain and northern France. This is partly a feature of preservation potential; the unequal global distribution of fossiliferous fluvial sediments corresponds closely with that of calcareous bedrock outcrops, which promote fossil preservation, limiting detailed biostratigraphical research to regions dominated by limestone and chalk. Calcareous tufas have provided an important additional source of data (Dabkowski, 2014), albeit from sediment sequences usually outside major fluvial systems. Tufa sequences have been recorded across Europe (Pentecost, 1995; Sancho et al., 2015), but are particularly well represented in northern France and Britain, where they have mainly been attributed to MIS 11, MIS 5e and the Holocene (Dabowski, 2014; Limondin-Lozouet and Preece, 2014). The Triassic Muschelkalk outcrop in Germany also gives rise to notable occurrences of calcareous spring deposits formed on former subaerial floodplains, although these are generally more lithified than their Ango-French counterparts and have thus generally been termed travertines. Important multiple travertines are interbedded with the terrace deposits of the Ilm at Weimar (Schreve and Bridgland, 2002) and the Wipper at Bilzingsleben (Mania, 1995). Although tufa and travertine deposits tend to be highly localized, they can preserve fossils that rarely survive in other fluvial sedimentary settings; this wide variety of palaeontological data is therefore particularly suitable for both biostratigraphy and palaeoclimatic reconstructions. As well as molluscs and vertebrates, plant remains (sometimes in the form of imprints of rapidly-encrusted leaves or fruits) are also common, although pollen is rarely well preserved (Dabkowski, 2014). The calcareous nature of tufas and travertines also means that they are suitable for a range of geochemical analyses (e.g. Dabkowski et al. 2012, 2015), and appropriate for radiometric dating using U-series techniques (e.g. Candy and Schreve, 2007; Sierralta et al., 2010).

2.1 Britain

Quaternary palaeontology in Britain has benefitted from government funding of multidisciplinary research projects through bodies such as English Heritage (now Historic England) and schemes such as the Aggregates Levy Sustainability Fund (ALSF). The English Rivers Palaeolithic Survey (TERPS), which commenced in 1991, resulted in an important baseline archive for Pleistocene archaeological research (Wymer, 1999), but provided only basic information pertaining to the palaeontological evidence that accompanied Palaeolithic assemblages. More detailed reviews of regional Pleistocene fossil records were subsequently provided by projects funded by the ALSF, such as the Trent Valley Palaeolithic Project (TVPP), which conducted an exhaustive review of both the palaeontological and archaeological records of the English Midlands (Schreve, 2007; Bridgland et al., 2014), and the Medway Valley Palaeolithic Project (MVPP), which conducted similar research in Kent (Briant et al., 2012; Chauhan et al, this volume). These projects were able to study fossiliferous localities that lacked archaeological material, adding valuable palaeontological and palaeoclimatic data to the underlying TERPS dataset. An overview of all the ALSF-funded projects was provided by White (2016). Additional data was accumulated during the lifetime of the Ancient Human Occupation of

Britain Project (AHOB), funded by the Leverhulme Trust, which underook research at numerous fluvial localities (Ashton et al., 2011; see http://ahobproject.org/database).

The data accumulated by these research projects have continued to test and reinforce the biostratigraphical model developed by Schreve (2001a; Fig. 2), which proposed a succession of Mammal Assemblage-Zones (MAZs) representing post-Anglian (MIS 12) interglacials. An important aspect of recent research has been the recognition of greater climatic complexity recorded in terrestrial interglacial sequences, leading to a renewed appreciation of the potential ability of multi-proxy palaeontological analyses to discern marine oxygen isotope substages (e.g. Schreve, 2001b; Ashton et al., 2008; Koutsodendris et al., 2010, 2011; White et al., 2013; Candy et al., 2014, 2016). In Britain and northern Europe, this has been especially relevant to sequences attributed to the MIS 11 Hoxnian/Holsteinian Interglacial (e.g. Preece et al., 2007; Ashton et al., 2008; Candy et al., 2014), which is particularly well represented in the terrestrial record.

2.1.1 The Lower Thames

The terrace deposits of the River Thames, particularly in its lower reach, represent one of the most important terrestrial archives of the Middle and Late Pleistocene in the world. In addition to key MIS 9 and MIS 7 sites published earlier in the lifetime of FLAG (Schreve et al., 2007 and references therein), new data have been obtained from several important Lower Thames localities over the last decade, including several MIS 11 sites: Dierden's Pit, Swanscombe (White et al., 2013), Southfleet Road, Swanscombe (Wenban-Smith, 2013), East Hyde, Tillingham (Roe, 2001; White, 2012) and Clacton-on-Sea (White, 2012). Further work has also been undertaken on the MIS 9 sequence at Purfleet (Bridgland et al., 2013) and other MIS 9 localities downstream in eastern Essex (Roe and Preece, 2011; Roe et al., 2009, 2011), providing further insight into the differentiation of MIS 11 and MIS 9 in the British terrestrial record (Bridgland et al., 2001; Thomas, 2001; Roe et al., 2009). Over the wider Thames valley, mammalian fossils have assisted with the correlation of the Upper and Middle Thames terraces (Bridgland and Schreve, 2009).

Insert Figure 2 hereabouts

At Swanscombe, the biostratigraphical and palaeogeographical significance of the 'Rhenish' suite of freshwater molluscs, an important feature of the MIS 11 faunal succession in the Lower Thames, has been firmly established by new evidence from Dierden's Pit (White et al., 2013). The Swanscombe sequence, together with its downstream correlatives at East Hyde and Clacton, indicates that the six ‘Rhenish’ species did not colonize the Thames simultaneously, but appeared in a distinctive sequence that can be tied to particular stages in the development of the vegetation. At both Swanscombe and Clacton, ‘Rhenish’ taxa are largely absent from the earliest fluvial deposits, with the pioneer species *Pisidium clessini* and *Theodoxus danubialis* first appearing during pollen zone Ho II. These, together with *Belgrandia marginata*, become established at the onset of Ho III, just before the first evidence for estuarine conditions (in the form of brackish indicator species) appears at both sites. They are followed by *Corbicula fluminalis*, which appears during Ho IIIb, and *Borysthenia naticina*, which is absent from Clacton but appears in significant numbers slightly later than *Corbicula* at both Swanscombe and East Hyde (White et al., 2013). The timing of the first appearance of the final 'Rhenish' species, *Viviparus diluvianus*, is less clear-cut, since it is a rare component of the Swanscombe fauna (Kerney, 1971) and is only represented by derived shells at Clacton. However, at East Hyde it appears to be present from early in the sequence, suggesting it was established in the lower Thames by at least pollen zone Ho IIIa (White et al., 2013). It has therefore been possible, on the basis of multiple strands of fossil evidence, to correlate MIS 11 fluvial sequences in the Lower Thames and to establish the timing of sea-level change and the migration of the estuarine environment during that interglacial (White et al., 2013; Fig. 3). This has shown that sea-levels rose relatively late in the interglacial, during Ho III, with a significant period during which the Thames was confluent with continental rivers such as the Scheldt; this was presumably also true of other fluvial systems flowing into the southern North Sea basin. This palaeogeographical situation allowed distinctive groups of invertebrate and vertebrate species (including humans) to colonize Britain (White et al., 2013).

Insert Figure 3 hereabouts

Other significant recent advances in knowledge of the Lower Thames sequence have arisen from work undertaken as part of developer-funded archaeological appraisal, particularly that related to construction of the high-speed railway connection to the Channel Tunnel (e.g. Bridgland et al., 2013; Wenban-Smith 2013) and within the remit of work funded by the ALSF. The construction of the Channel Tunnel Rail Link led to the unexpected discovery of an elephant-butchery site, preserved within deposits of a south-bank Thames tributary at Southfleet Road, Swanscombe (Wenban-Smith et al., 2006; Wenban-Smith, 2013). The carcass of an extinct straight-tusked elephant (*Palaeoloxodon antiquus*) was surrounded by an undisturbed scatter of flint tools (Wenban-Smith, 2015). Fossil assemblages recovered from the Southfleet Road sequence included vertebrates, molluscs, ostracods and pollen; the absence of 'Rhenish' molluscs indicates that the sequence pre-dates the Middle Gravels at Swanscombe and is therefore probably equivalent to the Lower Loam at Barnfield Pit, a conclusion consistent with the presence of Clactonian artefacts (Wenban-Smith, 2013). The vertebrate assemblage is strikingly similar to those from Swanscombe (Basal Gravel-Lower Loam) and Clacton, both of which have been assigned to the Swanscombe MAZ (Schreve, 2001a).

Work at the important MIS 9 sequence at Purfleet, undertaken as part of various developer-funded projects, allowed assessment of the palaeontological assemblages from the site, together with new analyses of stable isotopes and geochronology (Bridgland et al., 2013). This work confirmed the attribution of the interglacial to MIS 9 through the application of OSL and AAR and contributed new palaeoecological information. The MIS 9 interglacial has also been studied at various sites downstream in eastern Essex (Roe and Preece, 2011; Roe et al., 2011), allowing enhancement of knowledge of the evolution of the highstand MIS 9e estuary in the Lower Thames valley. Further south, the MVPP produced amino acid racemization data from several fossiliferous localities in eastern Essex, including the MIS 11 sequences at Clacton-on-Sea, East Hyde, Bradwell Hall, the MIS 9 sequences at Shoeburyness, Cudmore Grove, East Wick and the Last Interglacial (MIS 5e) site at East Mersea. The famous Levallois site at Baker's Hole, located in the Ebbsfleet Valley, NW Kent, has also been the subject of recent research following the construction of the Channel Tunnel Rail Link and Ebbsfleet International station (Scott et al., 2010; Wenban-Smith, 2014). This locality, dated to MIS 7, represents the last surviving remnant of what was (before quarrying) a wide area containing Levalloisian lithic remains in undisturbed primary context, associated with assemblages of large mammals, molluscs, small vertebrates and ostracods; publication of detailed biostratigraphical and palaeoenvironmental analyses is in progress.

2.1.2 The River Trent and its tributaries

The Trent, Britain's third longest river, had until recently received considerably less attention than other British fluvial systems. Significant new insights into the origin and evolution of the Trent system have resulted from the Trent Valley Palaeolithic Project (TVPP), which conducted an exhaustive review of the geological, palaeontological and archaeological records of the English Midlands (Howard et al., 2007; White et al., 2007, 2010; Bridgland et al., 2014, 2015). The dating of the Trent terraces has been underpinned by biostratigraphical data, together with aminostratigraphic and OSL dating programmes and uplift modelling (Penkman et al., 2011, 2013; Bridgland et al., 2014; Westaway et al., 2015; Westaway, 2017). Pleistocene fossil assemblages from the Trent catchment are both less common and less well known than equivalent records from the aforementioned Lower Thames sites and adjacent catchments, such as the Warwickshire-Worcestershire Avon. The upper and middle reaches of the Trent include few calcareous rocks, fossils being preserved there only under exceptional circumstances, such as within the Allenton Terrace deposits south-west of Derby (Bridgland et al., 2014) and the floodplain gravels at Whitemoor Haye (Schreve et al., 2013). Both of these sites are located at the confluences of tributary rivers with the main Trent. At Allenton, calcareous gravels enriched by Carboniferous limestone clasts from upstream in the tributary Derwent valley are responsible for the localized preservation of vertebrate assemblages that include hippopotamus, on the basis of which these deposits have been attributed to MIS 5e (Bridgland et al., 2014). The younger Whitemoor Haye locality, at the Tame-Trent confluence, is situated within low-lying 'floodplain terrace' deposits, dated by radiocarbon and OSL to around 41–43 k cal a BP, placing them within the Middle Devensian (MIS 3; Schreve et al., 2013). This site is prone to waterlogging, another effective means of preserving organic remains; palaeotemperature reconstructions, based on beetle and chironomid assemblages, have indicated mean July temperatures of +8 to +11 °C and mean January temperatures of between −22 and −16 °C (Schreve et al., 2013).

The most significant fossil assemblages from the Trent catchment have been recovered from its lower reach, where numerous sites have now been recorded in the Balderton–Southrey Terrace of the Trent and in the Fulbeck and Tattershall terraces of its tributaries, the Witham and Bain, respectively (Bridgland et al., 2014, 2015; Fig. 4). A significant aspect of the late Middle and Late Pleistocene record in the Trent is the absence of deposits belonging to the MIS 11 and MIS 9 interglacials, which are well represented in fluvial systems further south, most notably the Thames. This has been attributed to extensive glaciation of the English Midlands during MIS 8 (White et al., 2010, 2017; Bridgland et al., 2014). The oldest fossiliferous sediments known from the Trent system are therefore those preserved within the Balderton-Southrey terrace and its equivalents in the Witham and Bain valleys (Brandon and Sumbler, 1988, 1991; Schreve, 2007; Bridgland et al., 2014). The Balderton Terrace of the Lower Trent is predominantly a cold-climate aggradation, from which characteristic fossils such as *Mammuthus primigenius* (woolly mammoth), *Coelodonta antiquitatis* (woolly rhinoceros) and *Ovibos moschatus* (musk ox) have been recovered (Brandon and Sumbler, 1988, 1991; Bridgland et al., 2014). Earlier studies of these vertebrate assemblages also recognised the presence of interglacial species (Brandon and Sumbler, 1988, 1991; Lister and Brandon, 1991), which were subsequently established to have been derived from highly fossiliferous fine-grained deposits preserved low down in the sequence, typically filling channels cut into the Lias Clay bedrock or the lowermost part of the Balderton Formation (Bridgland et al., 2014). The fossil assemblages from these basal channels are representative of interglacial conditions and include molluscs, ostracods, small vertebrates, pollen, plant macrofossils and insects (White et al., 2007; Bridgland et al., 2014). The best record to date has come from Norton Bottoms, where significant exposures of fine-grained organic-rich sediments were recorded between 2006 and 2008 (White et al., 2007; White, 2012; Bridgland et al., 2014). Amongst the large mammal remains was a virtually complete cranium and horn cores of an adult aurochs (*Bos primigenius*), together with well-preserved molluscan assemblages (some specimens retaining their periostracum) that included the bivalves *Corbicula fluminalis* and *Pisidium clessini* and the land snail *Candidula crayfordensis*, none of which are known in Britain after MIS 7 (see Bridgland et al., 2014). Insect assemblages from Norton Bottoms are also a close match with those from British MIS 7 sites, lacking the exotic components that characterize MIS 9 and MIS 5e (Coope, 2001; Murton et al., 2001; Green et al., 2006; Bridgland et al., 2014); these have provided mutual climatic range (MCR) estimates for July temperatures (T^{max}) of +16 to +18°C and January temperatures (T^{min}) of -11 to +5°C (Bridgland et al., 2014). Complementary data derived from ostracod assemblages using the mutual ostracod temperature range (MOTR) method (Horne, 2007; Horne et al., 2012) have provided similar temperature estimates of T^{max} +15 to +21°C and T^{min} -4 and +3°C (Bridgland et al., 2014).

Insert Figure 4 hereabouts

Other sequences containing fine-grained sediments have been recorded in the Witham Valley, notably from boreholes at Coronation Farm and Stainfield (Bridgland et al., 2014). These yielded molluscs, pollen, plant macrofossil and insect remains; the molluscan assemblages contained no biostratigraphically-significant species, but the presence of *Bithynia* opercula allowed AAR dating to be applied, which suggested an age within MIS 7 (Penkman, 2007; Bridgland et al., 2014). In the valley of the River Bain, a left-bank tributary of the Trent-Witham system, quarrying at Tattershall Thorpe revealed interglacial sediments that contained fossils not found in deposits attributed to MIS 5e (Holyoak and Preece, 1985 and references therein), providing some of the earliest indications that both MIS 7 and MIS 5e were preserved in the terrace deposits in that area. The Last Interglacial (Ipswichian, MIS 5e) is represented in three parts of the Trent system, all of them areas where the main river is joined by a significant tributary. In the Middle Trent, sites at the confluence of the River Derwent with the Trent, at Boulton Moor and Allenton, have yielded hippopotamus fossils, together with beetles and plant remains (Arnold-Bemrose and Deeley, 1896; Jones and Stanley, 1974, 1975). In the Witham Valley, hippopotamus was also found at several sites in the vicinity of Fulbeck (Brandon and Sumbler, 1988, 1991; Howard et al., 1999; Bridgland et al., 2014), and further downstream MIS 5e sediments (without hippopotamus) were found at Tattershall Castle (Holyoak and Preece, 1985; Bridgland et al., 2014).

As well as providing age constraints for the terrace deposits, the new recognition of widespread MIS 7 interglacial deposits in the Lower Trent has been critical in the identification of a late Middle Pleistocene (post-Anglian–pre-Devensian) glaciation in Britain during MIS 8, a considerable rarity globally. Indeed, widespread biostratigraphical evidence for MIS 7 deposits in Britain as far north as Bielsbeck in East Yorkshire appear to exclude the possibility of an eastern British glaciation south of the River Humber during MIS 6 (White et al., 2010, 2017). No interglacial sequences attributable to MIS 11 or 9 have been identified in the Trent system, providing evidence (albeit negative) for widespread destruction of this part of the late Middle Pleistocene record (White et al., 2010, 2017). Dating evidence from the Trent fluvial archive, in the form of biostratigraphy and aminostratigraphy, has been critical in constraining the age of this glaciation, demonstrating the utility of fluvial records where they interdigitate with glacial deposits (see Cordier et al., this issue).

2.1.3 The Fenland rivers

The rivers flowing into the basin of the Wash in eastern England were recently studied as part of another ALSF project (the Fenland Rivers of Cambridgeshire Project), which concluded in 2008 (Boreham et al., 2010). These included the Witham (before the latest Pleistocene this was the lower Trent; see Bridgland et al., 2014, 2015), Welland, Nene, Great Ouse and Cam, all of which have yielded well-preserved fossil assemblages. Morphostratigraphical approaches to fluvial deposits within the Fen Basin are extremely difficult to apply, since this is an area that has undergone very little uplift, resulting in poor differentiation of the Pleistocene terraces. Biostratigraphical approaches have also been attempted (Bridgland and Schreve, 2001), although the precise correlations of several key interglacial deposits in the Fen Basin with the marine oxygen isotope stage record remain controversial due to mixed or inadequate biostratigraphical signals (Boreham et al., 2010). This is largely due to the preservation of sediments representing more than one interglacial in close proximity beneath a single terrace surface (Boreham et al., 2010). Research in the Peterborough area has revealed considerable complexity in the fluvial deposits preserved there (Langford and Briant, 2004; White et al., 2010, 2016; Bridgland et al., 2014; Langford et al., 2014a, b). Once again, occurences of *Corbicula fluminalis* and *Hippopotamus amphibius* have been key to distinguishing the Last Interglacial (Ipswichian, MIS 5e) from earlier interglacials in the Wash fluvial systems. The resulting synthesis of data enabled common patterns in these archives to be discerned, but also highlighted many significant differences between these rivers, all of which have shared a downstream valley during periods of low sea-level.

2.2 France

Multidisciplinary research projects investigating fluvial archives in NW France have largely focussed on the Somme and Seine river valleys. Over the last decade, several important palaeontological datasets from these areas have provided significant chronological and palaeoenvironmental information relevant to understanding Pleistocene climates and human occupation (see Chauhan et al., this issue). The French fluvial record is well-dated and includes several interglacial sequences particulary rich in diverse fossil groups that allow palaeoclimatic comparisons with nearby British records and other datasets at a European scale (e.g. Limondin-Lozouet and Preece, 2014). Alongside mammalian evidence (see Auguste, 2009), molluscan evidence remains a key element of French biostratigraphical schemes. The Lateglacial–Holocene molluscan successions recorded at numerous fluvial sites have been central to understanding the palaeoenvironmental significance of Pleistocene vegetational changes and climatic conditions (Limondin-Lozouet, 2011). During transitional climatic phases, the stages of recolonization by molluscan faunas show common features, such as the occurrence of specific taxa and well-defined biotope successions. These malacological characteristics have been correlated with climatic phases and botanical evolution. For example, in the early Holocene of NW Europe the replacement of the landsnail *Discus ruderatus* by its congener *Discus rotundatus* has been linked to the spread of *Corylus* (Preece and Day, 1994; Limondin-Lozouet et al., 2005). The same faunal succession has also been identified within Pleistocene interglacial sequences at La Celle in the Seine Valley, dated to MIS 11, and at Caours in the Somme basin, dated to MIS 5e. Although pollen was not preserved at either of these sites, the first appearance of *D. rotundatus* can be used to identify the development of deciduous forest, replacing the pioneer open forest biotope (Limondin-Lozouet, 2011; Fig. 5).

Insert Figure 5 hereabouts

2.2.1 The Somme and Nord Pas-de-Calais

Research undertaken over the last 20 years on the fluvial terraces and loess sequences of the Somme Basin, and on the interactions between human populations and changing environmental conditions, has adopted interdisciplinary approaches for the analysis of Quaternary sequences and associated Palaeolithic sites (Antoine et al., 2003, 2007, 2010; Bahain et al., 2007, 2010; Bridgland et al., 2006). These studies, mainly targeting fluvial sequences, have highlighted the impact of cyclic climatic changes on sedimentation and river morphology, and especially the role of the 100 ka climatic cycles for the last million years, giving rise to stepped terrace formation (Antoine et al., 2007). Interglacial climatic optima are recorded by calcareous tufa sequences, which are especially well preserved in the cases of MIS 11 and 5e.

At the Carrière Carpentier site at Abbeville, sediments (the 'White Marl') dated to MIS 15 using ESR (584 ± 48 ka) and their stratigraphical position within the Somme terrace system have yielded molluscs, large vertebrates and small mammals (Antoine et al., 2015, 2016; Voinchet et al., 2015). A noteworthy occurrence within the small vertebrate faunas are rodent molars tentatively attributed to *Arvicola cantiana/mosbachensis*. The presence of this taxon is indicative of a younger age in the early Middle Pleistocene, i.e. younger than MIS19-17 (Antoine et al., 2016). The large mammal fauna includes the Hundsheim rhinoceros (*Stephanorhinus hundsheimensis*), wild boar (*Sus scrofa priscus*) and red deer (*Cervus elaphus*), representing the Cromerian faunal association known from West Runton and Pakefield. When compared with British Cromer Forest-bed sites, the mammalian fauna from Carrière Carpentier appears to be contemporaneous with Pakefield, more recent than West Runton, but older than the Boxgrove fauna (Antoine et al., 2016). The Carrière Carpentier sequence is within Alluvial Formation VII of the Somme system (Antoine, 1994, 2000) and is associated with two other sites located in the same terrace, Carrière Léon and Moulin Quignon (Bahain et al., 2016). Characteristic freshwater mollusc species from this alluvial formation include *Tanousia* cf. *stenostoma*), *Borysthenia naticina* and *Bithynia troschelii*, which form an assemblage typical of Cromerian interglacial fluvial deposits in NW Europe (Meijer and Preece, 1996; Preece, 2001). Specimens of of *T.* cf. *stenostoma* from Moulin Quignon are similar to those of Little Oakley (Bahain et al., 2016). This occurrence represents the first record of this species in France; in Britain it is unknown after MIS 13.

Recent archaeological rescue excavations in the Somme valley have led to the discovery of several alluvial sequences containing molluscan faunas (Locht et al., 2013). At Rue Boileau in Amiens, a sequence exposed in a pit adjacent to the famous site of Saint Acheul includes a white silt horizon that has been correlated on morphostratigraphical grounds with the Saint Acheul tufa; the latter has been dated to MIS 11 on the basis of a characteristic '*Lyrodiscus* assemblage' of land snails, supported by U/Th dating (Limondin-Lozouet and Antoine, 2006). The molluscan fauna from Rue Boileau contains several critical species typical of this assemblage, together with several xerophilous taxa (*Cernuella virgata, Candidula unifasciata*) previously unknown from St Acheul (Locht et al., 2013). This assemblage has therefore been tentatively attributed to a later phase of the interglacial, post-dating the climatic optimum, when heavily-forested environments were being replaced by more open habitats characterised by xerophilous land snails (Limondin-Lozouet et al., 2015).

The important fluvial sequence preserved at Caours represents the only Eemian (MIS 5e) interglacial sequence in the Somme basin (Antoine et al., 2006). Overlying a periglacial gravel bed allocated to MIS 6 (Alluvial Formation I of the Somme system), the fluvial fine-grained sequence consists of calcareous silts and tufa deposits including thin organic layers, from which a wealth of palaeontological material has been recovered, most notably non-marine molluscs. These have provided a record of the glacial-interglacial transition between MIS 6 and MIS 5. Cold-tolerant faunas similar to those of the Younger Dryas, including some boreo-alpine taxa (*Columella columella*), were replaced by numerous thermophilous taxa, highlighting a hiatus corresponding to the very earliest part of the interglacial (Limondin-Lozouet, 2011). Following this, the malacological succession indicates the development of forest environments during an early part of MIS 5, followed by the climatic optimum of MIS 5e and a subsequent cooling (Limondin-Lozouet and Preece, 2014). Several species of Central European and Mediterranean origin (e.g. *Daudebardia rufa, Ruthenica filograna, Platyla polita*) occurred during the Eemian climatic optimum and constitute the first record of a regional biostratigraphical marker for the last interglacial (Limondin-Lozouet and Preece, 2014; Fig. 5). In addition, the Caours site has yielded archaeological material, providing an important record of human occupation in northern France during the Last Interglacial. It has now been identified as a butchery site, with lithic industries directly associated with mammalian remains (Auguste, 2009). A further important aspect of the Caours sequence is evidence for palaeomagnetic reversal thought to represent the Blake Event; identification of this geomagnetic excursion, which has been correlated with the start of the continental Eemian Stage, indicates that the palaeoclimatic and archaeological records from Caours post-date the MIS 5e interglacial peak (Sier et al., 2015).

To the north of the Somme basin, in the neighbouring region of Nord Pas-de-Calais, a fluvial sequence was discovered in 2012 at Waziers (Hérisson et al., 2015). This sequence comprises several peat layers overlying fluvial silts and sands, deposited in a large meandering system. Preliminary geomorphological and palaeontological observations, including the presence of loess covering the fluvial deposits and the peat and the occurrence of assemblages of interglacial mammals (aurochs and red deer) and aquatic molluscs (*Belgrandia marginata, Anisus septemgyratus*) suggested an Eemian age for this sequence. This was corroborated by a minimum age of 103 +3.5/-3.4 ka obtained by U/Th dating of calcareous charophyte oogonia, extracted from a fine-grained tufa layer directly underlying the peat (Hérisson et al., 2015). This site is only the second to provide evidence of Neanderthal occupation during the Eemian in Northern France.

Finally, the late MIS 5 fluvial sequence at Ailly-sur-Noye, located ~30 km south of Amiens, includes three Palaeolithic levels (Locht et al., 2013). The oldest lithic industries and associated mammals (*Bos primigenius*, *Equus* sp.) lie at the top of a basal fluvial gravel attributed to the late Saalian/Eemian on the basis of its geomorphological position within the terrace system. The upper part of the sequence, consists of coarse gravels (also containing Palaeolithic artefacts), covered by a thin calcareous tufa crust with facies typical of interglacial tufa deposits like those described at Caours and likely to represent MIS 5e. Above this, the sediments consist of fine grey silts capped by a calcareous mud containing two further archaeological levels characterized by Levallois material. Molluscan faunas from these deposits are '*Arianta*' assemblages typical of transitional climatic phases (Puisségur, 1976); further evidence for deteriorating climatic conditions is provided by a decline in the numbers of the aquatic snail *Belgrandia marginata*, a well-known thermophilous species typical of Pleistocene interglacial sequences that occurs in abundance at Caours (Antoine et al., 2006). The molluscan evidence indicates a transitional context from an interglacial phase to an early glacial episode, thought to represent the period spanning MIS 5d to MIS 5a (Locht et al., 2013); this is the first regional malacological record for this time period in France.

2.2.2 The Seine

New research undertaken at the site of Saint-Pierre-lès-Elbeuf has provided additional evidence for the age and palaeontological content of the important sequence there (Cliquet et al., 2009). Above the lowermost palaeosol (Elbeuf IV) lies a white sand and a calcareous tufa from which a characteristic '*Lyrodiscus* assemblage' was obtained: this fauna is a regional biostratigraphical marker correlated with the MIS 11 interglacial. Systematic malacological sampling within this unit has demonstrated a high level of homogeneity within the molluscan population, which is largely dominated by forest land snails (up to 80 % of the total shells). This implies that the tufa accumulated relatively rapidly during the optimum phase of MIS 11. New IRSL dates obtained from the Elbeuf IV soil (475 ± 38 ka) and on the white sand (396 ± 32 ka) confirm the MIS 11 correlation (Cliquet et al., 2009).

The Upper Seine valley preserves another significant tufa sequence at the site of La Celle, which has been known for more than a century as an important source of non-marine molluscs and plant macrofossil impressions. New research at this site has been undertaken in order to improve understanding of the palaeontological assemblages and to provide additional chronological control, which has been correlated with MIS 11 (Limondin-Lozouet et al., 2006, 2010). Dating evidence has been provided by the geomorphological position of the site, within an old terrace of the Seine deposited prior to the 'Nappe de Soucy' of the Yonne valley system dated at 350–300 ka (Limondin-Lozouet et al., 2006), together with the occurrence of land snails characteristic of the '*Lyrodiscus* fauna', known from several French and British tufa sequences of MIS 11 age (Rousseau et al., 1992; Limondin-Lozouet and Antoine, 2006; Preece et al., 2007). Additional age control has now been provided by radiometric dating (ESR/U-series on tooth enamel of horse and ESR quartz), which have produced a mean age of ~400 ka (Bahain et al., 2010; Voinchet et al., 2015). However, although this geochronological evidence indicates an age equivalent to MIS 11, the existing methods do not allow precise timing within the interglacial. The La Celle tufa provides the longest known MIS 11 malacological succession in NW Europe, which has been used to generate detailed reconstructions of the development of forest cover (Limondin-Lozouet et al., 2010, 2015) and as a biostratigraphical standard against which other MIS 11 malacological successions can be compared (Limondin-Lozouet et al., 2015). Successive appearances of forest species, first from an Atlantic corridor and later from central and southern Europe, allow characterization of vegetational development. The initial immigrants indicate the spread of closed habitats, while a peak in the diversity of thermophilous snails corresponds to the optimum phase of deciduous forest expansion. A subsequent decrease in forest species, together with an expansion of hygrophilous taxa, indicates the decline of closed canopy conditions. The occurrence of critical forest species, especially those now extinct or occurring far beyond their modern ranges, provides a framework within which molluscan successions from other tufa sites in northern France and southern Britain can be understood (Fig. 6).

Insert Fig. 6 hereabouts

Leaf impressions from La Celle have allowed the identification of 24 taxa, including some Mediterranean plants such as *Buxus*, *Ficus* and *Celtis* (Limondin-Lozouet et al., 2010). Mammalian remains from La Celle (Auguste, 2009; Limondin-Lozouet et al., 2010) include *Macaca sylvanus* (Barbary macaque) and *Hippopotamus amphibius*; the former last occurred in Britain during MIS 9, whereas the latter was absent from Britain during MIS 11 (Schreve, 2001a); the occurrence of hippopotamus in northern France during MIS 11 is therefore of particular interest, perhaps indicating a biogeographical barrier that prevented this species colonizing Britain at that time.

2.3 Germany and Belgium

One of the key sites in this region is the multiperiod locality at Schöningen, Germany, the evidence from which was summarized by Schreve et al. (2007). Debate on the age of this sequence has continued over the last decade and was recently summarized by Urban and Bigga (2015). As is the case in Britain, the occurrence of *Theodoxus danubialis* has been attributed biostratigraphical significance in Germany, where *T. serratiliniformis* (= *danubialis*) has been suggested to indicate an MIS 11 age (e.g. Meng and Wansa, 2005, 2008). This is by no means certain; in the middle Neckar valley (SW Germany), an exposure of fluvial gravels at the site of Bietigheim-Bissingen, ~20 m above the modern River Enz, yielded a molluscan fauna including *Theodoxus serratiliniformis* and *Cochlostoma scalarinum saueri* (Bibus and Rähle, 2003). On the basis of terrace stratigraphy and molluscan biostratigraphy, these deposits were dated to MIS 13, although this age is not accepted by Meng (2007).

In the southern North Sea Basin the western coastal plain of Belgium preserves a complex sequence of Pleistocene marine and fluvio-estuarine deposits. Recent analysis of brackish and freshwater fossil assemblages (including ostracods, pollen and Foraminifera) recovered from boreholes in this region have indicated deposition near the upper tidal limit of an estuary (Bogemans et al., 2016). Of biostratigraphical and biogeographical significance is the occurrence, in the Zoutenaaie core, of a single valve of the freshwater ostracod *Scottia browniana*, which is unknown in the nearby

British record after MIS 11 (Whittaker and Horne, 2009). Given that the oldest of the Belgian channel fills are suggested to date to MIS 9 (Bogemans et al., 2016; cf. Vanhoorne, 2003), it is possible that this fossil has been reworked; however, its presence might also indicate that *S. browniana* became extinct in continental Europe later than in Britain. This might well be expected, since the fluctuating island status of Britain from MIS 12 onwards enhances turnover in faunal composition and biogeographical differences.

3. Eastern Europe and Russia

Faunal evidence in this region has been recovered from the significant fluvial archives preserved in the valleys of the south-flowing rivers of the East European Platform, the Dniester, Dnieper, Don and Volga, and has been key to unravelling their age and evolution (Matoshko et al., 2002, 2004; Schreve et al., 2007; Bridgland and Westaway, 2008, 2014). To the south-west of the Russian Plain, several fossiliferous localities are known within the Prut and Danube basins, although these are predominantly represented by lacustrine sequences (see Markova and van Kolfschoten, 2012). Several important Middle Pleistocene faunal localities are known from the Dnieper, mostly recovered from fluvial deposits assigned to Terrace IV, correlated with the Likhvin Interglacial (=MIS 11) on the basis of pollen and mammalian biostratigraphy (Markova, 2006; Markova and van Kolfschoten, 2012; Fig. 7). Amongst the best studied of these are the mammal assemblages from Gunki, Pivikha and Chigirin (Fig. 7). The Gunki site has also yielded a molluscan fauna, considered to represent the Early Euksinian (Markova and van Kolfschoten, 2012). In the Don and Desna basins, the earliest small mammal faunas have been correlated with the early Middle Pleistocene (Markova, 2007). Here, faunal assemblages have been correlated with both interglacial and glacial stages (Fig. 7). The biostratigraphical significance of several mollusc species from the Don Basin was highlighted by Kondrashov (2007), who noted that the occurrence of species such as *Borysthenia intermedia*, *Lithoglyphus jahni* and *Viviparus fasciatus* allows correlation of the Don basin faunas with the early Middle Pleistocene Cromerian faunas of Western Europe. In the Volga basin, a small mammal fauna that includes *Arvicola cantiana*, *Lagurus transiens-lagurus* and *Clethrionomys rufocanus* has been described from a fluvial sequence at Rybnaya Sloboda, at the mouth of the right-bank tributary Kama River, and has been attributed to the Likhvin Interglacial on biostratigraphical grounds (Markova and van Kolfschoten, 2012; Fig. 7). Similar faunas have been reported from sites in the middle and lower Volga, at Chernyi Yar and Spasskoe (Markova and van Kolfschoten, 2012). To these can be added a considerable amount of vertebrate, molluscan and vegetational data that has been collected since the 1960s in the southern Urals region, summarized in a flurry of papers published since 2007 detailing the records of the Belaya and Lemeza rivers (e.g. Chlachula, 2010; Danukalova et al., 2007, 2008, 2009, 2011, 2016; Puchkov and Danukalova, 2009; Yanina, 2013; Yakovlev et al., 2013). Changes to the fauna and flora in this area appear to have been more muted than the adjacent northwestern territories due to the absence of local glaciers during some cold stages (Danukalova et al., 2009).

Insert Figure 7 hereabouts

Further afield, in Ukraine, mollusc and ostracod assemblages have been described from a sequence of Early–early Middle Pleistocene fluvial gravels and loams exposed in a quarry at Skala Podil'ska, in the valley of the River Dniester (Boguckyj et al., 2009). The freshwater mollusc assemblages from the basal fluvial gravels (Unit I) include *Theodoxus serratiliniformis* (=*danubialis*) and *Viviparus lungershauseni* (= *fasciatus*; Kondrashov, 2007). Also present was the ostracod *Limnocythere tuberculata*, which is also indicative of the Early Pleistocene (Dykan, 2003). The overlying loams of Unit III also contained *T. danubialis*, together with *Lithoglyphus neumayri*. The ostracod fauna from this upper unit contained species characteristic of colder water bodies (Boguckyj et al., 2009). Palaeoclimatic research in Russia has also been significantly advanced by the development of the QUINSIB database, which contains details of over 600 fossil insect localities (Kuzmina, 2014). The development of this resource has allowed large amounts of unpublished data and published sources in Russian to be made widely accessible.

4. Southern Europe and Iberia

4.1 Spain and Portugal

A surge of interest in Iberian fluvial systems followed the successful FLAG Biennial Meeting at Castelo Branco in 2010, particularly with the development of improved chronological frameworks for several fluvial systems in Spain and Portugal (such as the Tagus/Tejo, Minho, Douro/Duero, Mondego and Guadiana rivers), which have been considerably refined through the application of new luminescence techniques (Cunha et al., 2008; Vis et al., 2008; Martins et al., 2010; Antón et al., 2012; Ramos et al., 2012; Viveen et al., 2012, 2013; Carvalhido et al., 2014; Sancho et al., 2016). However, with the exception of a few notable regions previously summarized by Schreve et al. (2007), preservation of palaeontological material is generally poor across the Iberian Peninsula and the terraces of these rivers have yielded relatively little new fossil material (e.g. Cunha et al., 2012). Fluvial archives such as that preserved in the Ter River basin, northeastern Spain, have proved difficult to date due to the absence of fossiliferous deposits (Garcia, 2015). A notable recent discovery is the site of Barranc de la Boella (Catalonia, Spain), where vertebrate remains (including a butchered elephant) were recovered in association with stone tools from deposits of the Francolí river (Vallverdú et al., 2014). Dating of this site was based on palaeomagnetic and cosmogenic determinations, supported by biostratigraphical evidence derived from the vertebrate faunas, which included *Mimomys savini* and *Mammuthus meridionalis*, suggesting a late Early Pleistocene age (Mosquera et al., 2015).

In central Spain, faunal assemblages have been recovered from the sites of Pinedo and Cien Fanegas near Toledo, in the +25–30 m terrace of the River Tajo (Tagus), which have also yielded Acheulian archaeology. These gravels been dated to between 290 and 220 ka using AAR and luminescence (pIR–IRSL) techniques, spanning a period between MIS 9 and 7 (López-Recio et al., 2015). The gravel pit at Pinedo has yielded fossils of straight-tusked elephant, together with hippopotamus, rhinoceros, deer, horse and bovids (López-Recio et al., 2015). Elsewhere in the Middle Tajo, large mammal assemblages have been recovered in association with stone tools from the 40 m terrace at Toledo; these include *Mammuthus trogontherii*, *Equus caballus*, *Hippopotamus amphibius*, *Megaloceros savini*, *Eliomys quercinus*, *Allocricetus bursae*, *Microtus brecciensis* and *Apodemus sylvaticus*, all characteristic of the Middle Pleistocene (Sesé et al., 2000). Palaeoclimatic studies from this region include reconstructions based on herpetofaunal assemblages from three Spanish localities dated to MIS 11, including the fluvial deposits at Áridos-1, in the valley of the River Jarama SE of Madrid, and the fluvio-lacustrine sequence at Ambrona (Blain et al., 2015). These herpetofaunal assemblages include numerous taxa of high environmental and climatic sensitivity, which can be used as valuable indicators of palaeoclimate, through the application of MCR analyses (e.g. Martínez-Solano and Sanchiz, 2005; Blain et al., 2008).

4.2 Italy

The Pleistocene vertebrate succession in the Italian peninsula is relatively well known (e.g. Gliozzi et al., 1997), although much of this evidence has been recovered from cave and fissure-fill sequences in karstic regions (e.g. Sardella et al., 2003; Pandolfi and Petronio, 2011a, b; Pandolfi et al., 2013). The potential relationships between these isolated cave sequences and local fluvial systems have not yet been explored in detail, but research in other regions suggests that biostratigraphical schemes can be usefully developed in this way (e.g. Yang et al., 2011; Bridgland et al., 2014, Westaway, 2016). In the mountainous regions of northern and central Italy, fossil assemblages have also been obtained from lacustrine sequences, with fluvio-deltaic deposits sometimes represented (e.g. Girotti et al., 2003; Limondin-Lozouet et al., 2017). Arguably the best known Italian fluvial archives are those from the Tiber River basin, the record for which spans much of the Pleistocene. The palaeo-Tiber and its tributaries have been extensively studied in the area around Rome (Caloi et al., 1998; Di Stefano et al., 1998; Milli et al., 2004; Petronio et al., 2011). Recent work on this system has been undertaken by Marra et al. (2014), who identified six biochronological units (Slivia, Ponte Galeria, Isernia, Fontana Ranuccio, Torre in Pietra and Vitinia), spanning a period from ~600 ka to at least MIS 7, although this scheme has been criticised (Sardella et al., 2015; cf. Marra et al., 2015).

In central Italy, fossiliferous fluvial sequences representing a period spanning the Early Pleistocene to the early Middle Pleistocene have been recorded in trenches and boreholes at several localities in the Anagni Basin (Bellucci et al., 2012, 2014). The important Coste San Giacomo locality, known since the late 1970s, has yielded a Villafranchian large mammal fauna, including taxa such as *Mammuthus meridionalis*, *Hippopotamus* sp., *Equus stononis*, *Gazella borbonica, Sus strozzi* and *Homotherium* sp. More recently, microfaunal assemblages obtained from the Coste San Giacomo 1 core, drilled in 2009, have allowed more detailed palaeoecological reconstructions to be attempted (Bellucci et al., 2012, 2014). Analyses of small vertebrate, ostracod, pollen and charophyte assemblages, together with sedimentological data, indicate an initially forested landscape giving way to an open alluvial plain fed by sand-bed rivers (Bellucci et al., 2014). In addition, the ostracod assemblage contained sufficient extant taxa to attempt summer and winter air temperature reconstructions using the MOTR method, providing estimates of mean July temperatures of between 15°C and 22°C and mean January temperatures of between -5°C and 5.2°C. However, it should be noted that the assemblage used for these estimates was derived from 8 separate assemblages recovered from a large section of the borehole (Bellucci et al., 2014) and may therefore represent an averaging of a long period of time. Small vertebrate assemblages included the biostratigraphically significant Early Pleistocene vole *Mimomys pliocaenicus*; this species, together with evidence from pollen biostratigraphy and magnetostratigraphy, suggests a Gelasian age for the Coste San

Giacomo faunal unit, falling somewhere between 2.2 and 1.95 Ma (Bellucci et al., 2014).

5. The Levant and the Arabian Peninsula

Fossil preservation in the Levant is relatively poor, despite the widespread presence of calcareous bedrock. It has been suggested that the formation of calcreted gravels, a characteristic of such semi-arid regions (e.g. Candy et al., 2004, 2005), might be responsible for the loss of faunal remains - in the Upper Orontes, for example, cemented Pleistocene terrace deposits appear to have undergone repeated decalcification and re-cementation, resulting in the weathering-out of calcareous clasts and, presumably, calcareous fossils (Bridgland et al., 2012). The general absence of biostratigraphical data from fluvial sequences (although see Tchernov, 1981, 1994 for reviews of data from cave and lake sequences in Israel) is mitigated by the presence of Pleistocene lava flows interbedded within the terrace sequences of many of the Turkish and Syrian fluvial systems that can be dated using various radiometric techniques (Sharkov et al., 1998; Bridgland et al., 2007; Demir et al., 2007, 2012, Seyrek et al., 2008; Westaway et al., 2009; Maddy et al. 2012).

Beyond the Levant, in the interior of the now hyper-arid Arabian Peninsula, significant fluvial archives are largely absent; however, fossils have been recovered from lacustrine sequences in the Nefud and Rub' al Khali deserts (e.g. Thomas et al., 1998; Groucutt et al., 2014; Stimpson et al., 2014, 2016). Most of these assemblages have been dated to the Late Pleistocene (MIS 5e and younger) and Holocene, although in exceptional circumstances older assemblages have been preserved (see below, Stimpson et al., 2014, 2016). As new sites are discovered and recorded, there is increasing potential to develop biostratigraphical schemes linking Arabian lake sites to Levantine fluvial systems.

5.1 The Levant

Productive new research in Syria, investigating the terraces of the River Orontes (Bridgland et al., 2003, 2012) and on the catchments of Mesopotamian rivers such as the Euphrates and Tigris (Demir et al., 2007, 2008, 2012; Westaway et al., 2009) has been curtailed in recent years due to ongoing conflicts in this war-torn region. The summary of research provided by Schreve et al. (2007) therefore remains largely up to date, with the exception of a handful of recently-published papers detailing research undertaken before 2009 (e.g. Bridgland et al., 2012). Fossiliferous sequences are also relatively rare in accessible reaches of these rivers in Turkey (e.g. Demir et al., 2007, 2008, 2012; Westaway et al., 2009; Seyrek et al., 2014a, b). Vertebrate faunas have provided important biostratigraphical evidence constraining the ages of the Orontes terraces (Bridgland et al., 2003, 2012; Bridgland and Westaway, 2007; Mishra et al., 2007). Biostratigraphical evidence provided by the vertebrate assemblages from Latamneh has necessitated the reattribution of the Orontes QfIII terrace in the Middle Orontes to an age of 1.2–0.9 Ma, leading to a revision of the age model for the Orontes terrace sequence (Bridgland et al., 2012; cf. 2003). Given this revision, it is no longer tenable to attribute the Middle Orontes terraces to formation in response to 100 ka Milankovitch climatic forcing (cf. Bridgland and Westaway, 2008b). A revised model for the evolution of that reach of the Orontes, resulting from this modification of the supposed age of the key biostratigraphical marker, sees similarities between the incision history in the Hama –

Latamneh area and those determined from the Euphrates in its southern Turkish and Syrian reaches, related to the crustal characteristics of the Arabian Platform (Bridgland et al., 2017). Downstream from Latamneh, molluscan and ostracod faunas were obtained from river-cliff locations at Karkour, alongside the Orontes channel as it traverses the subsiding Ghab Basin, including the ostracod *Cyprideis torosa*. This taxon is generally associated with brackish environments, developing noded valves in salinities below ~5‰, but can also tolerate hypersaline conditions in lakes and water bodies prone to desiccation, which is presumably how it comes to be in the Ghab sediments. The faunas here also include freshwater elements, both ostracods and molluscs, the latter including the large viviparid gastropod *Apameaus apameae* (Bridgland et al., 2012), which is also recorded at the key comparator (biostratigraphically somewhat younger) Israeli locality at Gesher Benot Ya'aqov, in the Jordan Valley, where it is an index fossil for the definition of the 'upper freshwater series' or '*Viviparus* Beds' of the Benot Ya'aqov Formation (Picard, 1963; Tchernov, 1973; Goren-Inbar and Belitzky, 1989; Bar-Yosef and Belmaker, 2010). The last appearance of *Apameus apamae* in the Jordan Valley was at ~ 240 ka, on the basis of U-series dating (Kafri et al., 1983; Moshkovitz and Magaritz, 1987; Heller, 2007); its presence at two localities in the Ghab basin, Syria (Bridgland et al., 2012) and at the site of Alaattin Köyü in Turkey (Seyrek et al., 2014) therefore suggests a latest Early Pleistocene to late Middle Pleistocene age for these deposits.

5.2 The Arabian Peninsula

In recent years, the Arabian Peninsula (Saudi Arabia, Yemen, Oman and the United Arab Emirates) has emerged as an important region for research into low-latitude Quaternary environmental change (e.g. Petraglia, 2007; Parker, 2009; Armitage et al., 2011; Groucutt and Petraglia, 2012; Delagnes et al., 2012). Expansions of plant and animal communities, including humans, into and through the Arabian interior have occurred on several occasions, corresponding with humid climatic phases during the Pleistocene, when savanna-type landscapes prevailed in what are now hyper-arid regions (Vaks et al., 2007, 2013; Rosenberg et al., 2011, 2013; Breeze et al., 2015; Jennings et al., 2015a, 2017; Parton et al., 2015a). However, the highly fragmentary nature of Arabian terrestrial sequences, compounded by poor stratigraphical and chronological control on associated palaeontological assemblages, has hampered the construction of biostratigraphical and palaeoenvironmental frameworks.

A major hindrance to better regional understanding of the Arabian record is the lack of perennial fluvial systems and their resulting sedimentary archives; evidence for fluvial activity consists largely of poorly-dated gravels and alluvial deposits resulting from ephemeral and highly seasonal catchments (for recent reviews see Breeze et al., 2015, 2016). The principal drainage across central Arabia consists of several eastward-flowing wadis that presently carry water only seasonally. It is likely that these systems were repeatedly activated during humid periods in the Pleistocene and early Holocene (Powers et al., 1966; Chapman, 1971; Anton, 1984; Edgell, 2006), although some are now choked in places by dunes (Holm, 1960), suggesting that they have been inactive as continuous systems for a considerable period of time. At a smaller scale, more localized alluvial fans have formed around the bases of steep-sided jebels and dykes, from which intermittent streams flowed during wet phases (e.g. Parton et al., 2015b; Jennings et al., 2015b). It has been suggested that most of the trans-Arabian wadi systems were incised in their current configurations by the early Quaternary, based on relationships between basal gravel deposits and dated lava flows (Al-Sayari and Zötl, 1978; Anton, 1984). Younger terraces have also been dated using early radiocarbon techniques (e.g. Jado and Zötl, 1984) but, given the unreliability of these methods, these ages require verification. More recent dating programmes have applied OSL and U-series techniques to fluvial deposits in south-central Arabia (e.g. Maizels, 1987, 1990; Blechschmidt et al., 2009; Mclaren et al., 2009; Parton et al., 2010, 2013; Rose et al., 2011; Sitzia et al., 2012; Atkinson et al., 2013), contributing to an increasingly detailed chronology for the Late Pleistocene and Early Holocene. However, the general absence of substantial fluvial archives in Arabia is reinforced by the fact that the most significant stratified archaeological assemblages reported in recent years have been found in association with either lacustrine sequences, representing a source of fresh water, or raw materials suitable for stone tool production (e.g. Armitage et al., 2011; Delagnes et al., 2013; Hilbert et al., 2014; Groucutt et al., 2015; Jennings et al., 2015b; Scerri et al., 2015).

6. Data from other regions

Beyond the 'core regions' of NW and Central Europe, palaeontological datasets from fluvial sequences are increasingly used as a basis for regional biostratigraphies and palaeoenvironmental reconstructions. At the time of the last review (Schreve et al., 2007), these consisted entirely of mammalian data; since then, significant new information, including invertebrate and floral assemblages, have been published and are included in the summaries below.

6.1 China and the Far East

In China, the Nihewan Formation, comprising fluvio-lacustrine sediments containing abundant mammalian fossils, is widely distributed in the Nihewan Basin of northern Hebei Province. This region has yielded the densest concentration of Early Pleistocene Palaeolithic sites outside Africa (Dennell, 2013), together with fossil assemblages (vertebrates, molluscs, pollen) that have long been considered to be of Early Pleistocene age, although alternative ages ranging from late Pliocene to Middle or Late Pleistocene have also been proposed (Zhao et al., 2010). ESR dating of quartz obtained from the Majuangou and Banshan sites provided ages of between 1.70 and 1.35 Ma (Liu et al., 2014). Further south in the Three Gorges region, located in the transitional zone between the upper and middle reaches of the Yangtze (Changjiang) River, several fossiliferous fluvial sequences have now been reported (Pei et al., 2013). Seven fluvial terraces (T_7–T_1) have been identified and dated using ESR, TL, OSL and radiocarbon techniques (Pei et al., 2013). The site at Jingshuiwan, assigned to T_2 and dated to 75.9 ± 3.7 to 64.5 ± 4.1 ka using OSL, yielded an assemblage of 58 mammalian fossils including *Stegodon orientalis* (Pei et al., 2010).

In northwest Hunan Province, the terraces of the Suoxi River have been dated using ESR and TL techniques, allowing them to be correlated with neighbouring karstic cave systems (Yang et al., 2011). Although none of the dated localities in this study proved to be fossiliferous, presumably due to the local sandstone bedrock, such research highlights the potential for fluvial archives to provide chronological evidence that can be linked to calcareous sequences with potential to provide palaeontological data. Palaeoclimatic research in East Asia using methods such as beetle MCR estimates has been hampered by a lack of knowledge of modern distributions of beetle species and the sparse distribution of meteorological stations, especially in Siberia (Shiyake, 2014). Japan is exceptional in having conditions that have allowed application of the Mutual Climatic Range (MCR) method, having a dense meteorological observation network and higher quality distribution data for its extant beetle fauna (Shiyake, 2014). Experimental work at the site of Nojiriko, Nagano Prefecture has provided the first MCR reconstructions from East Asia (Shiyake, 2014).

6.2 South Asia

The Indian subcontinent has yielded a range of palaeoecological and biostratigraphical data, in the form of vertebrate and invertebrate fossil assemblages, pollen records and archaeological material, much of which has been recovered from fluvial sediments of the Narmada, Godavari, Manjra, Son, Ghod, Krishna and Mahanadi rivers (Chauhan, 2008). Most of these deposits have been assigned ages no older than the Middle Pleistocene, although some formations in the Narmada Valley might date to the Early Pleistocene (Tiwari and Bhai, 1997; Tiwari, 2001). The application of modern dating techniques has shown that many of these sedimentary units have the potential to be significantly older or younger than previously thought (Chauhan 2008 and references therein), a situation that is also prevalent in the Levant (Bridgland et al., 2012) and Arabia (e.g. Thomas et al., 1998, contra Stimpson et al., 2014, 2015). Until reliable chronological frameworks are available for these fluvial archives, their usefulness in terms of regional biostratigraphy remains somewhat limited.

The Siwalik deposits of northern India, Pakistan, Nepal and Myanmar represent one of the best-studied fluvial sequences in Asia. The Upper Siwaliks have been divided into three subdivisions, the youngest two of which (the Pinjor and Boulder Conglomerate Formations) represent most of the Quaternary, spanning the period from 2.58 to 0.2 Ma (Prasad, 2001; Mishra et al., 2010). Mammalian fossils are adundant within the Pinjor Formation (2.58 to 0.6 Ma), which has yielded at least 98 vertebrate species including *Elephas hysudricus*, *Stegodon insignis*, *Rhinoceros*, *Sivatherium*, *Equus sivalensis*, *Bos acutifrons* and *Cervus palaeindicus*, together with carnivores such as *Canis pinjorensis*, *Crocuta felina* and *Pachycrocuta brevirostris* (Nanda, 2002, 2008). However, the stratigraphic range of most of these species within the Pinjor Formation is unknown, limiting their biostratigraphical application (Dennell et al., 2008). Nevertheless, reconstructions of the palaeoecology of the fluvial landscapes within which the Pinjor Formation was deposited have been attempted (Dennell et al., 2008), including predator-prey interactions and the circumstances under which fossil assemblages were accumulated and buried.

Two younger faunal horizons, roughly equivalent to the late Middle and Upper Pleistocene respectively, are preserved on the Indo-Gangetic plain in India and in Sri Lanka (Nanda, 2008; Mishra et al., 2010), although these have yielded only 16 and 26 mammalian taxa, respectively. These 'post-Siwalik' faunas suggest that a large proportion of the Upper Siwalik Pinjor fauna became extinct during the Middle Pleistocene. Because the stratigraphical relationships between these numerous fluvial localities remain unclear, it has not yet been possible to propose a testable biostratigraphical framework for the region. However, a relative chronostratigraphic, biostratigraphic and archaeological correlation for the Narmada Basin formations has been proposed (Badam, 2007; Patnaik et al., 2009). At Hathnora, assemblages of vertebrates (including herpetiles and fish), molluscs, ostracods, charophytes and pollen, in association with archaeological material, have been reported (Patnaik, 2000; Patnaik et al., 2009). Freshwater molluscs have also been recovered from the sites at Bhedaghat and Devakachar (Hirdepur Formation), including 18 species of gastropods and bivalves (Kotlia and Joshi, 2011). Several lines of evidence suggest that Southeast Asia was dominated by a mosaic of savannah, open woodland and evergreen forest throughout much of the Pleistocene, leading to suggestions that this region served as a refugium for hominins and other mammal species during glacial periods (Louys and Turner, 2012)

Well-dated fossiliferous sequences in Southeast Asia are relatively rare and are predominantly preserved in caves, although the syntheses described here include some data from fluvial deposits. Broad characteristics of the extinctions of Pleistocene large vertebrates in this region were recently reported by Louys et al. (2007), together with consideration of the palaeoenvironmental requirements of many of these species (Louys and Meijaard, 2010). Many species which became extinct appear to have been endemic to specific areas, with others suffering severe range reduction before their eventual demise. Members of the latter group include proboscideans (*Stegodon* and *Palaeloxodon*), the pygmy hippopotamus (*Hexaprotodon*), the orangutan (*Pongo*), hyenas (*Crocuta* and *Hyaena*), the giant panda (*Ailuropoda*), tapirs (*Tapirus* and *Megatapirus*), rhinoceroses (*Rhinoceros*), and the giant Asian ape, *Gigantopithecus*. The loss of these species is likely to have been the result of a combination of climatic changes (Louys et al., 2007) and human impacts (Corlett, 2007). Unlike other regions which experienced megafauna extinctions, such as South America (see below), eustatic changes in sea level in Southeast Asia seems to have been an important factor (Louys et al., 2007).

On the island of Java, Indonesia, fluvial deposits of the Solo River have recently yielded both vertebrate fossils and archaeological material. An extensive survey of the region around Matar, close to the site at Ngandong (where fossils of *Homo erectus* were recovered in the early 1930s), revealed the presence of at least three river terraces; palaeontological and archaeological assemblages were recovered from the First and Second terraces (Fauzi et al., 2016). Tentative comparisons with other Pleistocene faunal localities on Java suggest that the Matar assemblage is younger than the Middle Pleistocene Kedungbrubus Fauna but older than the Punung Fauna, since it contains several species (such as *Stegodon trigonocephalus*, *Bubalus paleokarabau*, *Bibos paleosondaicus* and *Hexaprotodon sivalensis*) that occur in the former but not in the latter (Fauzi et al., 2016). The Punung Fauna, the type locality for which is Punung Cave, Indonesia, has been dated to 128±15 and 118±3 ka using luminescence and U-series techniques (Westaway et al., 2007). Further work is required in order to understand fully the regional biostratigraphy.

Insert Fig. 8 hereabouts

6.3 North and South America

A significant proportion of Pleistocene palaeontological research on these continents has been driven by a desire to understand the reasons for megafaunal extinctions (e.g. Faith et al., 2009; Haynes, 2009; Scott, 2010; Doughty et al., 2013) and the timing of the first human colonization of the Americas (e.g. Goebel et al., 2008; Rothammer and Dillehay, 2009; Pitblado, 2011), as well as dynamics between the two (e.g. Gill et al., 2009). Fluvial archives are also potential sources of palaeontological evidence relevant to debates surrounding the Great American Biotic Interchange (GABI), a period of faunal exchanges between North and South America. The isolation and faunal endemism of South America ended with the formation of the Panamanian land bridge and the onset of the GABI, with the first of four major faunal exchanges now thought to coincide with the base of the Pleistocene at ~2.6 Ma (Reguero et al., 2007; Woodburne, 2010). Further major pulses, at 1.8, 0.7 and 0.125 Ma (Fig. 8) appear to have coincided with periods of lower sea-level, leading to the suggestion that expanded coastal regions, cooler climates and associated changes to local flora promoted animal dispersals at these times (Woodburne, 2010).

Insert Fig. 9 hereabouts

There are few Pleistocene sites in South America from which well-dated fossil material has been recovered from secure stratigraphical contexts; correlations between localities have therefore frequently been based on the biostratigraphical scheme proposed for the fossiliferous beds of the Pampean region of Argentina, which has been periodically updated over the last two decades (e.g. Cione and Tonni, 1999, 2001, 2005). The Quaternary mammal faunas of South America have also been reviewed from time to time by several authors (see Prado and Alberdi, 2009 and references therein). Major phases of mammalian dispersal occurred during the Pleistocene Ensenadan and Lujanian biochrons (Fig. 9), which have also been dated on the basis of the Pampean sequence (Cione and Tonni, 1999, 2001, 2005). Biostratigraphical significance has been ascribed to four species of *Neosclerocalyptus* (Glyptodontidae) which occurred during the Pleistocene in the Pampean region of Argentina (Zurita et al., 2009a). Two of these, *Neoclerocalyptus pseudornatus* and *N. ornatus* are indicative of the Ensendan Stage, the former occurring between 1.07 and 0.98 Ma and the latter between 0.98 and 0.40 Ma (Fig. 9). Two other species, *N. gouldi* and *N. paskoensis*, are thought to reperesent the Bonaerian and Lujanian stages, respectively (Zurita et al., 2009a; Fig. 9). This biostratigraphical scheme has therefore become a standard with which other South America sequences are now routinely compared (e.g. Lopes et al., 2010; Tonni et al., 2009; Beilinson et al., 2015).

In Bolivia, the Tarija Valley preserves some of the richest Pleistocene mammal localities in South America, although the dating of these assemblages remains unclear (Coltorti et al., 2007; Tonni et al., 2009; Zurita et al., 2009b). A Middle Pleistocene age has been suggested on the basis of mammalian biostratigraphy (e.g. Tonni et al, 2009 and references therein), although they have also been attributed to a much younger period on the basis of radiocarbon dating (~44 – 21 ka BP). A similar lack of reliable dating for fossiliferous sites has hampered the bio- and chronostratigraphical correlation of South American Pleistocene faunas elsewhere; in Brazil, Lopes *et al.* (2010) published ESR dates of between 226 and 34 ka for a vertebrate assemblage from Chuí Creek; this broad age range, spanning a time period encompassing the final part of MIS 7 until MIS 4, is probably due to the reworked nature of the Chuí Creek vertebrate assemblages (Pereira et al., 2012). In Venezuela, strata such as the Taima Taima fossil bed and fluvial sites at Muaco, Cucuruchú, and Quebrada Ocando have been dated on the basis of biostratigraphy (Carlini et al., 2008).

In Uruguay, the fossiliferous beds of the Sopas Formation have yielded vertebrate faunas, together with freshwater molluscs, plant remains and other trace fossils (Ubilla et al., 2004, 2009, 2016; Ubilla and Martínez, 2016). The mammalian assemblage includes extinct taxa, such as the capybara *Neochoerus aesopi*, the glyptodont *Neuryurus rudis*, and two extinct species of deer (*Antifer ultra* and *Morenelaphus brachyceros*). This assemblage has been correlated on the basis of biostratigraphy with the Lujanian Stage (Late Pleistocene–Early Holocene) of the Pampean region of Argentina; this is supported by radiocarbon AMS dates from the vertebrate material range from 39,900 ± 1,100 to 33,560 ± 700 BP (cal 45,389 to 42,025 ya) and TL/OSL ages derived from the sediments range from 71,400 ± 11,000 to 27,400 ± 3,300, indicating a MIS 3 age for the fauna (Ubilla et al., 2016). Palaeoenvironmental evidence suggests that the Sopas formation represents open habitats, savannahs and woodlands (Ubilla et al., 2016).

Insert Fig. 10 hereabouts

6.4 Australia

In Australia, Quaternary palaeoenvironmental research based on fluvial archives has a long pedigree in two important regions of the continent: the arid interior of the Lake Eyre Basin, where fluvial, lacustrine and aeolian sequences representing the last ~300 ka are preserved (recently reviewed in detail by Habeck-Fardy and Nanson, 2014), and the extensive meandering river systems of southeastern Australia, particularly the well-dated terraces of the Lachlan and Macquarie rivers in the Murray-Darling Basin (Kemp and Spooner, 2007; Yonge and Hesse, 2009; Kemp and Rhodes, 2010). Faunal and floral responses to Pleistocene climate change in these regions remain less well understood, primarily due to the rarity of stratified fossil assemblages and significant issues with directly dating fossil material (Price et al., 2013; Westaway et al., 2017). As is the case in North America, much research in Australia has been focussed on the extinction of megafaunal species during the Late Pleistocene; approximately 96 % of the large mammal fauna was extinct by ~45 ka, a period broadly concurrent with human colonisation, although the extent to which these extinctions can be directly related to human activity remains a source of considerable debate (e.g. Koch and Barnosky, 2006; Prideaux et al., 2007, 2010; Price et al., 2015; Dortch et al., 2016; Johnson, 2016; Johnson et al., 2016; Westaway et al., 2017; Fig. 11). Overhunting and the burning of the landscape by people, with a corresponding abrupt reduction in plant diversity, have been suggested as causal factors (Porch and Kershaw, 2010; Rule et al., 2012), but significant climate change in the period between 50 and 46 ka, resulting in a major shift to more arid conditions and a corresponding drop in water levels in Lake Eyre and Lake Frome, is also considered to have played an important role (Murphy et al., 2011; Cohen et al., 2012, 2015; Sakaguchi et al., 2013).

In the Lake Eyre Basin, fossils of 21 megafaunal mammal species have now been recorded (Webb, 2008, 2009), including a giant wombat-like marsupial (*Diprotodon*), giant short-faced kangaroo (*Procoptodon goliah*), a large flightless bird (*Genyornis newtoni*), giant goanna (*Varanus priscus*) and the 'marsupial lion' (*Thylacoleo carnifex*). In addition, smaller mammal species have been recovered from the upper Katipiri Formation (MIS 6–4), including the Southern brown bandicoot (*Isoodon obesulus*), the extinct Eastern hare wallaby (*Lagorchestes leporides*), the Pale field rat (*Rattus tunneyi*) and the Western grey kangaroo (*Macropus fuliginosus*); the fossil occurrences of the three extant species are well beyond their modern distributions (Webb, 2009). However, the lack of chronological control for much of this fossil material means that the first and last appearances of many mammal species in the wider Lake Eyre Basin remain poorly understood. Better biostratigraphical evidence has been forthcoming in eastern Australia, where vertebrate and molluscan assemblages (44 taxa in total) have been recovered from the Darling Downs, within fluvial deposits of the Kings Creek (Price and Sobbe, 2005; Price et al., 2011). Palaeoenvironmental analyses have indicated that a mosaic of local habitats, including vine thickets, scrublands and open grasslands, prevailed during the late Pleistocene; increasing aridity led to a contraction of the more wooded environments in favour of grassland. Dating of the Kings Creek sequences using a variety of techniques (OSL, U-series and radiocarbon) has shown that individual megafaunal species responded independently to climatic and environmental change, revealing a more complex staggered extinction pattern in southeastern Austrial prior to the arrival of humans (Price et al., 2011; Fig. 11).

Insert Fig. 11 Australian biostrat chart

7. Synthesis

Regional biostratigraphies based on mammalian and molluscan assemblages continue to contribute significantly to the dating and correlation of Pleistocene fluvial deposits on a global scale. However, the quality of these datasets varies widely, depending on the potential for preservation of fossils in a given region and the priority given to palaeontological and biostratigraphical research. The period since the 2007 review of regional biostratigraphies has seen a steady accumulation of data in many parts of the world. Those based on mammalian and molluscan assemblages, in particular, have continued to be tested and developed, especially in NW Europe, and clearly have a significant role to play in the dating and correlation of Quaternary deposits. Biostratigraphical frameworks are still predominantly based on mammals and other vertebrates, which is not surprising considering the robust nature of their fossils. Molluscs are also commonly used. Other groups, such as reptiles, amphibians, ostracods and insects are still only infrequently used as a dating tools (e.g. Gleed-Owen, 1988, 1999, Coope, 2001; Griffiths, 2001; Whittaker and Horne, 2009; Borodin et al., 2013), but can provide invaluable complementary information as palaeoclimatic indicators. The relative rarity of non-mammalian vertebrate remains, which has been noted in fluvial sequences in regions such as Europe (Holman, 1998; Roe et al., 2009), Australia (Price and Sobbe, 2005) and Africa (Stoetzel et al., 2012) is usually attributed to taphonomic biases caused by the relative fragility of these fossils, although only a few studies specifically addressing this issue have been published (e.g. Pinto Llona and Andrews, 1996, 1998).

The predominance of work in the cooler temperate regions is in large part a result of the common preservation there of vertebrate and molluscan faunas in fluvial contexts that coincide with calcareous settings. In the warmer temperate Mediterranean region limestone abounds but dryland soil processes have led to reprecipitation of calcareous cements that seems to have coincided with the destruction of fossils. It is probably no accident that the key late Early Pleistocene fauna site of Latamneh in the Orontes in Syria is in one of the few reaches of that river with terrace gravels that are not calcareously cemented (Bridgland et al., 2012). The only other Orontes sites with significant faunas are preserved in the Ghab, where the presence of fossils might owe much to waterlogging in this fluvio-lacustrine subsiding basin (see Section 5).

There is an increasing need for research to address the validity of inferred patterns of faunal (including hominin) exchange between neighbouring regions. These have the potential to address important questions about the timing and nature of palaeoenvironmental change in response to climate change, by identifying key drivers of dispersal and the waxing and waning of biogeographical barriers. Of critical importance when comparing adjacent regions is the accuracy of chronological frameworks, which are required to establish whether significant palaeoenvironmental changes and faunal turnovers occured synchronously in different regions, or whether leads and lags can be identified. It is often not possible to detect diachroneity in faunal change due to the lack of precision in radiometric methods, especially in the Early and Middle Pleistocene. Improved dating is thus required to determin patterns of north–south exchange between refugia (in the Northern Hemisphere), an issue of further relevance in respect of Latamneh, which has been suggested as a possible cold-stage assemblage that includes taxa represented in interglacials further north (Bridgland et al., 2012).

Detailed analyses are also important when it comes to reconstructing palaeoenvironmental change through longer fluvial sequences, with the potential to detect smaller-scale climatic oscillations, potentially correlateable with oxygen isotopic substages (e.g. Schreve, 2001b; White et al., 2013). These problems are well known to Quaternary biostratigraphers and palaeoecologists. The value of biostratigraphical and palaeoecological data has led to such studies becoming an increasingly common element of multi-disciplinary research; such projects are often driven primarily by archaeological research questions. Evidence corroborating and strengthening established biostratigraphical frameworks (Schreve, 2001a, b) has been obtained, together with substantial new understanding of the palaeoclimatic and palaeoecological significance of numerous plant and animal species that occur commonly within fossil assemblages (e.g. Candy et al., 2012, 2015, 2016).

Certain taxa appear to have been extremely widespread at particular times during the Pleistocene, only for their ranges to fragment in response to subsequent environmental pressures. The distribution of the hippopotamus (*Hippopotamus amphibius*) has long had significance in Britain, where it is a distinctive marker-fossil for the Last Interglacial (MIS 5e) (Sutcliffe, 1964; Currant and Jacobi, 2001; Schreve, 2001a, 2009). Similarly, distinctive freshwater mollusc species such as those of the 'Rhenish suite' characteristic of the MIS 11 Thames were clearly able to disperse rapidly across large parts of Europe. These two examples illustrate the potential for fluvial systems to connect otherwise separate biogeographic provinces, linking regional biostratigraphic schemes at certain times. Terrestrial species, for which large rivers are potential barriers to dispersal, are less likely to be able to profit from fluvial connectivity. However, in the case of the '*Lyrodiscus*' fauna that characterises molluscan faunas in Britain and northern France during MIS 11, some continuity in woodland habitat was clearly required to allow this biome to develop.

Some of the most significant patterns in the palaeontological record are evident at the extremities of regions and in differences between continental and island records. For example, in NW Europe the well established British biostratigraphical record differs from that of its nearest continental neighbours; both regions benefit from excellent preservation of fossils and well-dated fluvial stratigraphies, allowing direct comparison of the faunas and floras of Pleistocene interglacials. The occurrence of hippopotamus in Britain and on the near-continent continues to be a point of difference, for example. This taxon occurs in abundance in Britain during the Late Pleistocene only during the Last Interglacial (MIS 5e, Ipswichian), whereas in northern France it has been found in assemblages dated to MIS 11 and MIS 7.

Palaeoclimatic reconstructions based on multiple fossil proxies have proved particularly useful for understanding interglacials, especially on the northern fringes of Europe. This sort of research has only been possible in regions where long, detailed sedimentary sequences are preserved. In Britain, much of this evidence has been derived from fossils of a diverse range of thermophilous flora and fauna that now occur in more southerly parts of continental Europe, or even further afield. At a basic level, qualitative measures of enhanced warmth (or cold) can be shown by the relative abundances of thermophilous or cryophilous species within fluvial deposits. More precise palaeotemperature estimates can be obtained from quantitative methods based on palaeoecological proxies, which now have a long pedigree within Quaternary research in northwest Europe (e.g. Atkinson et al., 1987; Zagwijn, 1996; Horne et al., 2012). Such approaches employ the known climatic tolerances, or the mapped climatic range, of extant plant or animal species in order to infer the warmest (Tmax) and coldest (Tmin) temperatures under which a given assemblage of species could survive (Candy et al., 2010). Fossils of these indicator species (or assemblages of groups of species) within Pleistocene fluvial deposits can thus be used as proxies for the palaeotemperature regime that prevailed at the time the deposit accumulated; within longer sequences, it is also possible to infer significant climatic changes from the fossil record.

Consideration of the ecological preferences of mollusc and ostracod species is important and can bolster arguments from faunal comparison data that can otherwise seem circular or overly reliant of negative (absence) evidence. An interesting observation from recent years has been the occurrence of halophytic taxa in warm-climate fluvio-lacustrine settings, where evaporation enhances salinity. This was noted in the reach of the Orontes in northern Syria, where the aforementioned subsiding Ghab basin is crossed (Bridgland et al., 2012). At that land-locked locality there is a low potential for confusion with an estuarine environment, but in more coastal settings the co-occurrence of certain species could raise problems for environmental interpretation.

8. Conclusions

Since the last major review of biostratigraphical data derived from Quaternary fluvial archives in 2007, significant new research on Pleistocene fossil assemblages has been undertaken on almost every continent. Established regional biostratigraphical frameworks have been challenged, modified and, in many cases, strengthened by the new data generated by this work. Over the 20-year lifespan of FLAG, much of the evidence summarized here has been obtained from fluvial sequences in the NW European 'hotspot' that includes Britain and France, together with important archives from Germany, Iberia and Italy and Eastern Europe. Research in Europe has included the reporting of new sites, dating or re-dating of known localities to improve chronological control, and the development of high-resolution palaeoenvironmental reconstructions based on fossil assemblages and geochemical analyses. There have also been important advances in understanding of the palaeoclimatic and palaeoecological significance of numerous plant and animal species that occur commonly within Pleistocene fossil assemblages; in combination with improved chronological frameworks, these provide important evidence for changing climate and environments through time.

In the Levant and South Asia, where the archaeological record has driven the research agenda, the recognition of the utility of fossil assemblages as chronological and palaeoevironmental tools has led to them being increasingly studied, despite considerable taphonomic difficulties. The Arabian Peninsula, in particular, has been the subject of an increased focus of studies relating to hominin dispersals out of Africa, but because well preserved fluvial deposits are largely absent in this arid region, fossils have mainly been derived from lacustrine and cave sequences. The potential for developing biostratigraphical correlation schemes, linking the Arabian record to better-preserved fluvial archives in neighbouring regions such as the Levant, is therefore an exciting possibility for future research.

Europe and the Middle East have in common long-timescale records of human occupation; beyond these areas, in the Americas and Australia, human impacts came much later and have been studied mainly in the context of human contributions to the extinctions of Pleistocene megafaunas. The chronology of the Great American Biotic Interchange, together with refinements in South American biostratigraphical schemes in countries such as Brazil, Argentina and Bolivia continue to be major areas of research. Similarly, in Australia, frameworks of faunal extinctions have been developed. Australia has an apparently impoverished Middle and Late Pleistocene biostratigraphical record compared with other parts of the world, and many of the species that went extinct during this period are poorly dated. Archaeological sites attesting to potential human impact are rare and detailed ecological information for most extinct megafauna is lacking. As a result, the processes leading to megafaunal extinction remain unclear, although the weight of evidence points to a direct human impact as a major cause of extinction.

Although it is now possible to generate reliable radiometric dates for river terrace sequences in many parts of the world, enabling their correlation with the globally applicable marine oxygen isotope record, in some regions this remains extremely difficult. Where such robust chronological frameworks exist, providing fossils are also well preserved, it is possible to explore more detailed patterns in the occurrences of plant and animal species during the Pleistocene.

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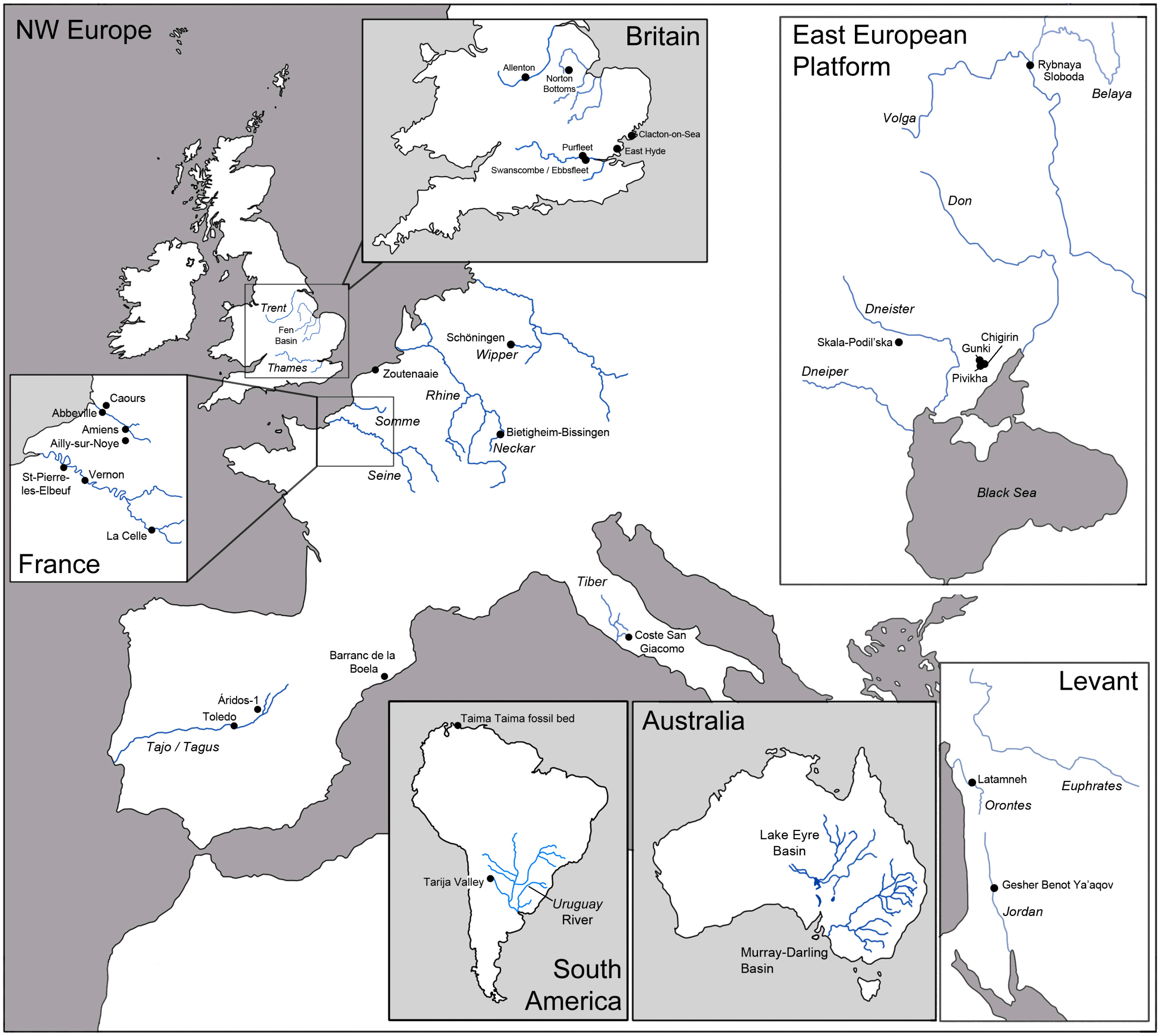
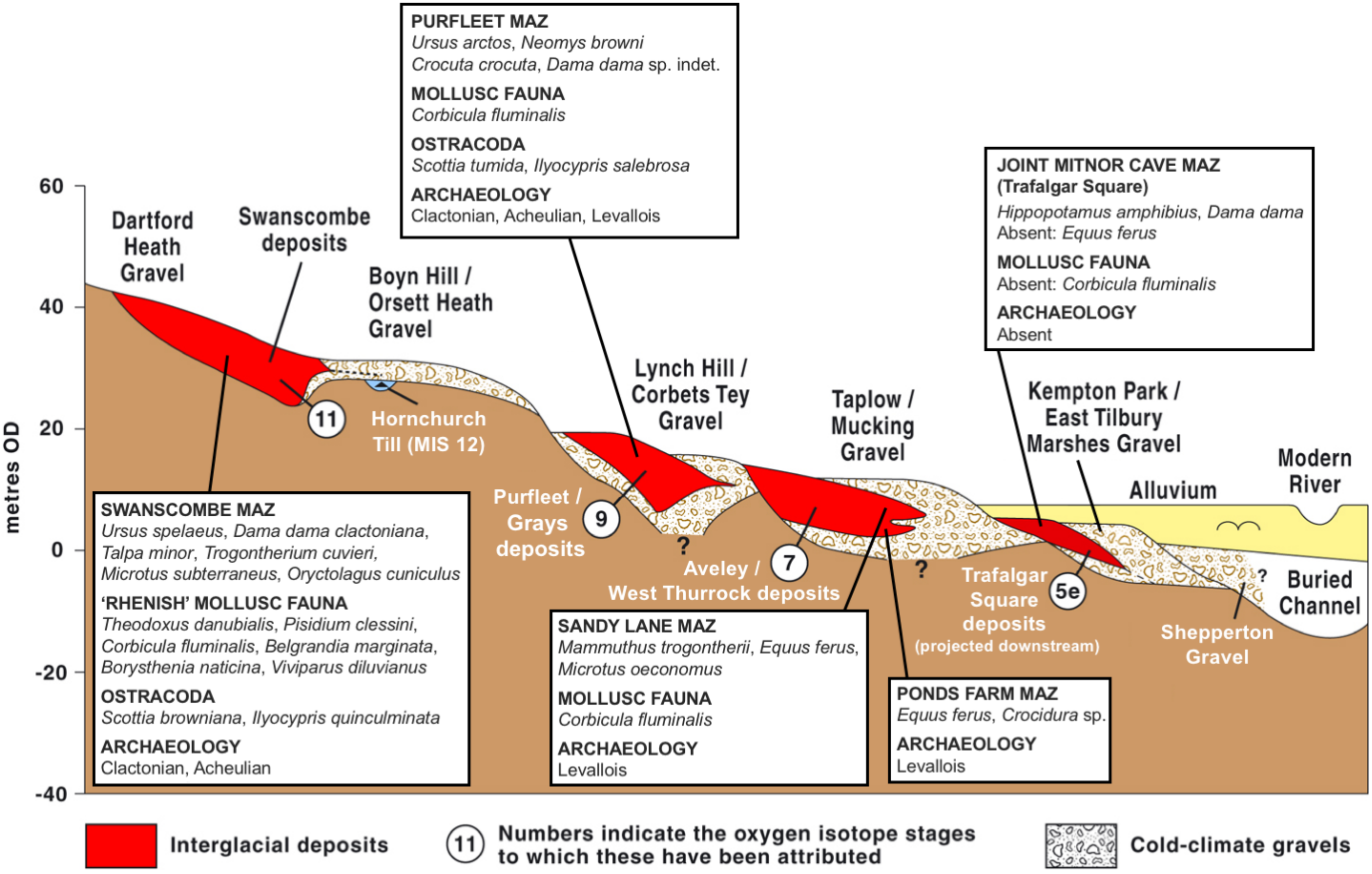
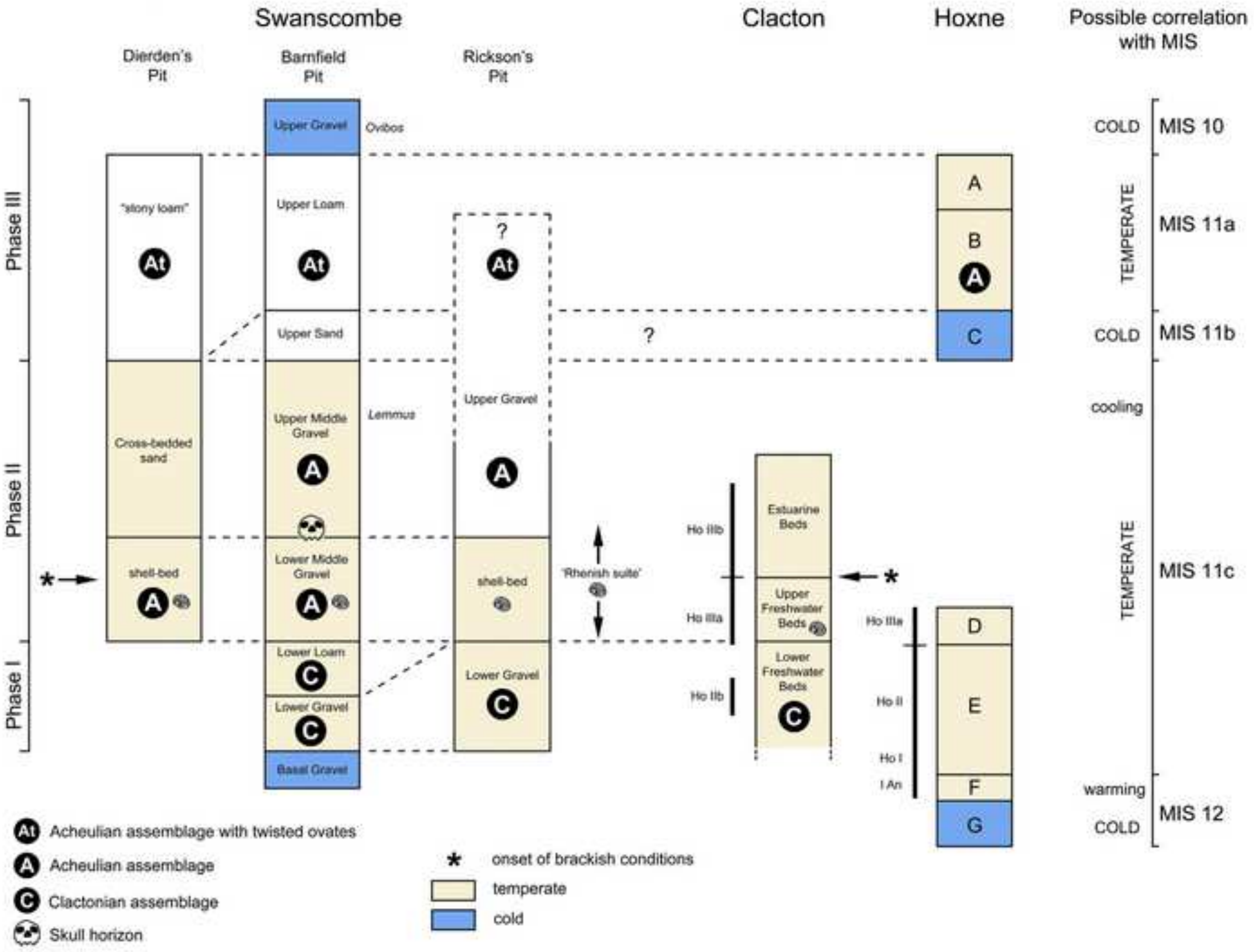
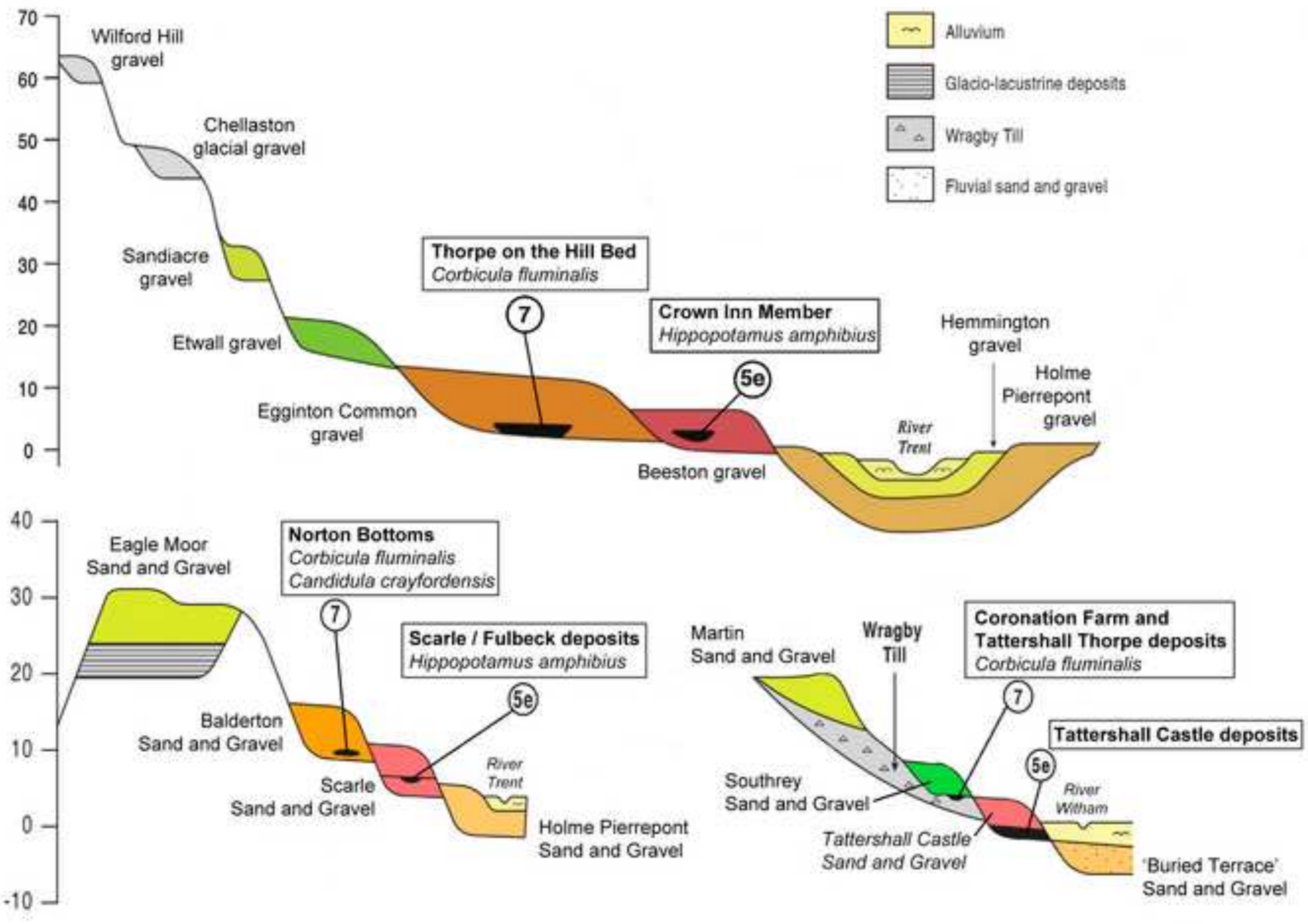
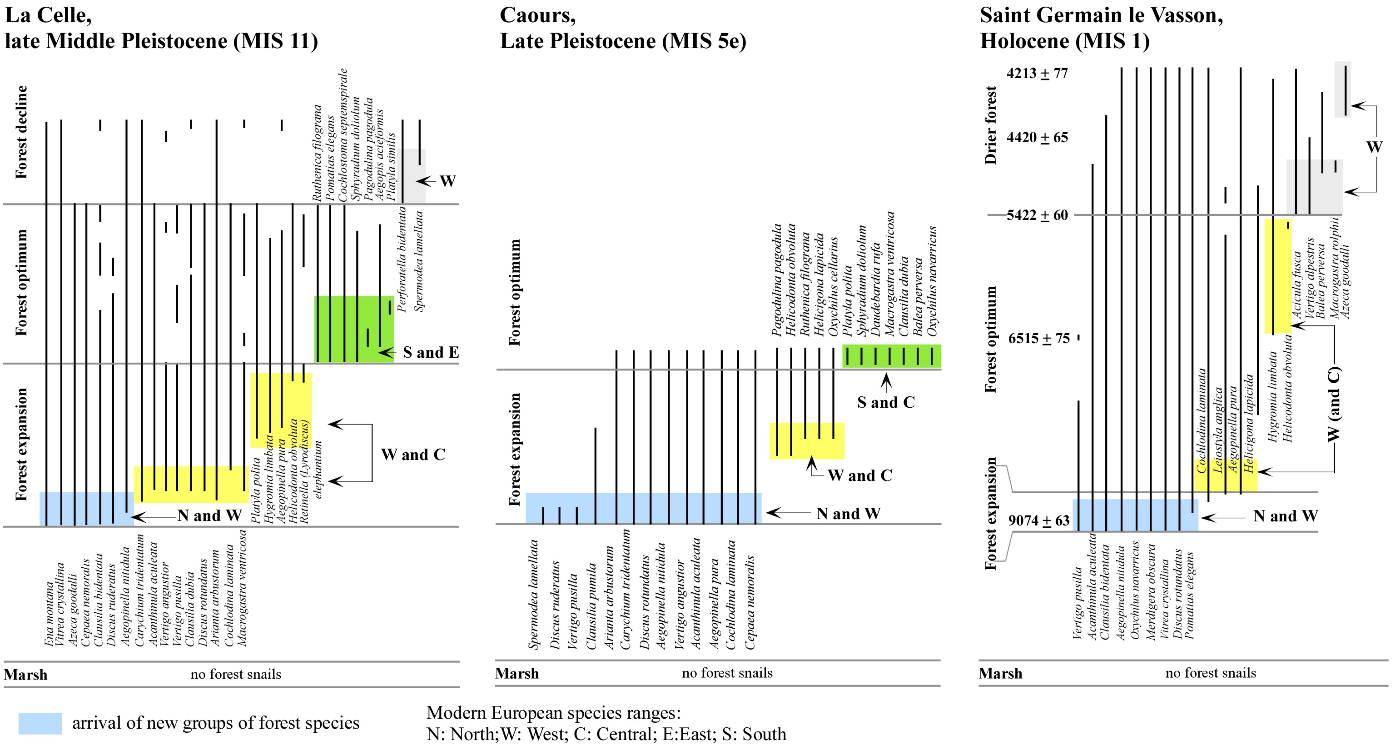
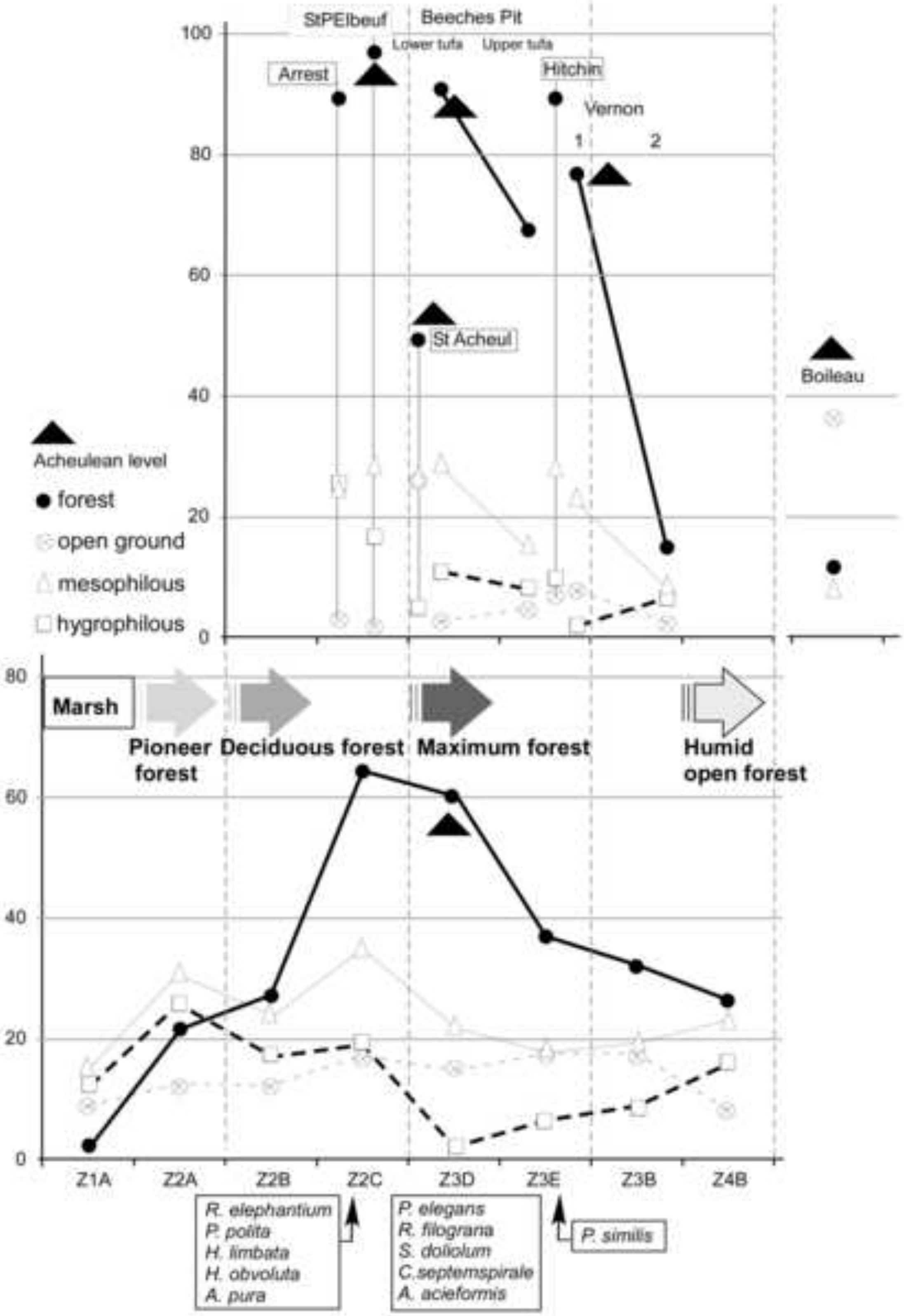

NW Europe
Britain
Allenton
Norton Bottoms
Clacton-on-Sea
Purfleet
East Hyde
Swanscombe / Ebbsfleet
Trent
Fen Basin
Thames
France
Caours
Abbeville
Amiens
Ailly-sur-Noye
St-Pierre-les-Elbeuf
Vernon
La Celle
Zoutenaaie
Schöningen
Wipper
Rhine
Somme
Seine
Bietigheim-Bissingen
Neckar
East European Platform
Rybnaya Sloboda
Belaya
Volga
Don
Dneister
Skala-Podil'ska
Chigirin
Gunki
Pivikha
Dneiper
Black Sea
Tiber
Coste San Giacomo
Barranc de la Boela
Áridos-1
Toledo
Tajo / Tagus
Levant
Latamneh
Orontes
Euphrates
Gesher Benot Ya'aqov
Jordan
Taima Taima fossil bed
Tarija Valley
Uruguay River
South America
Australia
Lake Eyre Basin
Murray-Darling Basin

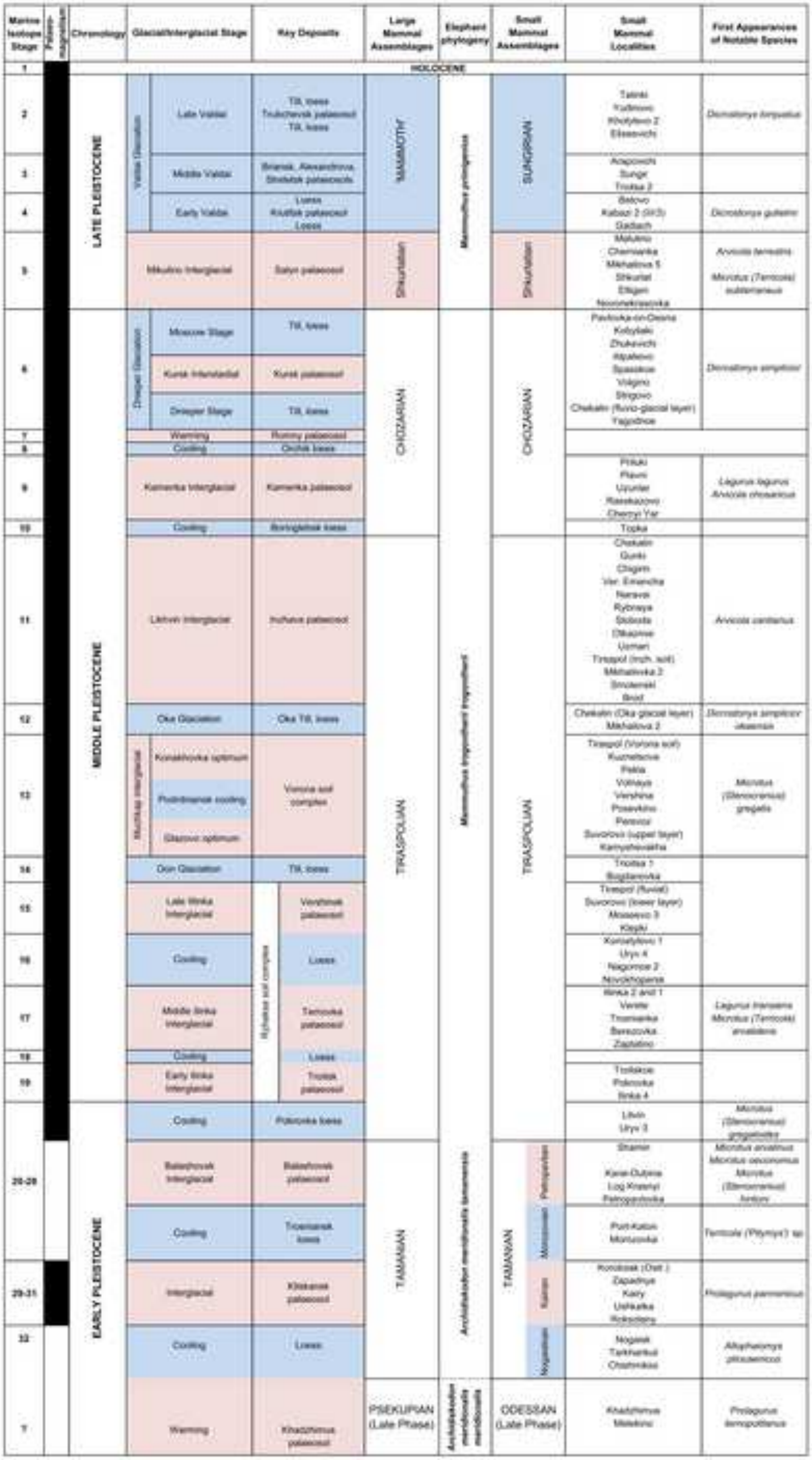

PURFLEET MAZ
Ursus arctos, Neomys browni
Crocuta crocuta, Dama dama sp. indet.
MOLLUSC FAUNA
Corbicula fluminalis
OSTRACODA
Scottia tumida, Ilyocypris salebrosa
ARCHAEOLOGY
Clactonian, Acheulian, Levallois
JOINT MITNOR CAVE MAZ (Trafalgar Square)
Hippopotamus amphibius, Dama dama
Absent: Equus ferus
MOLLUSC FAUNA
Absent: Corbicula fluminalis
ARCHAEOLOGY
Absent
60
40
20
0
-20
-40
metres OD
Dartford Heath Gravel
Swanscombe deposits
Boyn Hill / Orsett Heath Gravel
Lynch Hill / Corbets Tey Gravel
Taplow / Mucking Gravel
Kempton Park / East Tilbury Marshes Gravel
Modern River
Alluvium
11
Hornchurch Till (MIS 12)
Purfleet / Grays deposits
9
?
Aveley / West Thurrock deposits
7
?
Trafalgar Square deposits (projected downstream)
5e
?
Buried Channel
Shepperton Gravel
SWANSCOMBE MAZ
Ursus spelaeus, Dama dama clactoniana,
Talpa minor, Trogontherium cuvieri,
Microtus subterraneus, Oryctolagus cuniculus
'RHENISH' MOLLUSC FAUNA
Theodoxus danubialis, Pisidium clessini,
Corbicula fluminalis, Belgrandia marginata,
Borysthenia naticina, Viviparus diluvianus
OSTRACODA
Scottia browniana, Ilyocypris quinculminata
ARCHAEOLOGY
Clactonian, Acheulian
SANDY LANE MAZ
Mammuthus trogontherii, Equus ferus,
Microtus oeconomus
MOLLUSC FAUNA
Corbicula fluminalis
ARCHAEOLOGY
Levallois
PONDS FARM MAZ
Equus ferus, Crocidura sp.
ARCHAEOLOGY
Levallois
Interglacial deposits
11
Numbers indicate the oxygen isotope stages to which these have been attributed
Cold-climate gravels


Swanscombe
Clacton
Hoxne
Possible correlation with MIS
Dierden's Pit
Barnfield Pit
Rickson's Pit
Phase III
Phase II
Phase I
Upper Gravel
Ovibos
"stony loam"
At
Upper Loam
At
?
At
A
B
A
C
Upper Sand
?
Cross-bedded sand
Upper Middle Gravel
A
Lemmus
Upper Gravel
A
shell-bed
A
Lower Middle Gravel
A
shell-bed
'Rhenish suite'
Estuarine Beds
Upper Freshwater Beds
Lower Freshwater Beds
C
Ho IIIb
Ho IIIa
Ho IIb
Ho IIIa
Ho II
Ho I
I An
D
E
F
G
Lower Loam
C
Lower Gravel
C
Lower Gravel
C
Basal Gravel
COLD
MIS 10
TEMPERATE
MIS 11a
COLD
MIS 11b
cooling
TEMPERATE
MIS 11c
warming
MIS 12
COLD
At Acheulian assemblage with twisted ovates
A Acheulian assemblage
C Clactonian assemblage
Skull horizon
* onset of brackish conditions
temperate
cold


70
60
50
40
30
20
10
0
Wilford Hill gravel
Chellaston glacial gravel
Sandiacre gravel
Etwall gravel
Egginton Common gravel
Thorpe on the Hill Bed
Corbicula fluminalis
7
Crown Inn Member
Hippopotamus amphibius
5e
Beeston gravel
Hemmington gravel
Holme Pierrepont gravel
River Trent
Alluvium
Glacio-lacustrine deposits
Wragby Till
Fluvial sand and gravel
40
30
20
10
0
-10
Eagle Moor Sand and Gravel
Norton Bottoms
Corbicula fluminalis
Candidula crayfordensis
7
Scarle / Fulbeck deposits
Hippopotamus amphibius
5e
Balderton Sand and Gravel
Scarle Sand and Gravel
River Trent
Holme Pierrepont Sand and Gravel
Martin Sand and Gravel
Wragby Till
Coronation Farm and Tattershall Thorpe deposits
Corbicula fluminalis
7
Tattershall Castle deposits
5e
River Witham
Southrey Sand and Gravel
Tattershall Castle Sand and Gravel
'Buried Terrace' Sand and Gravel

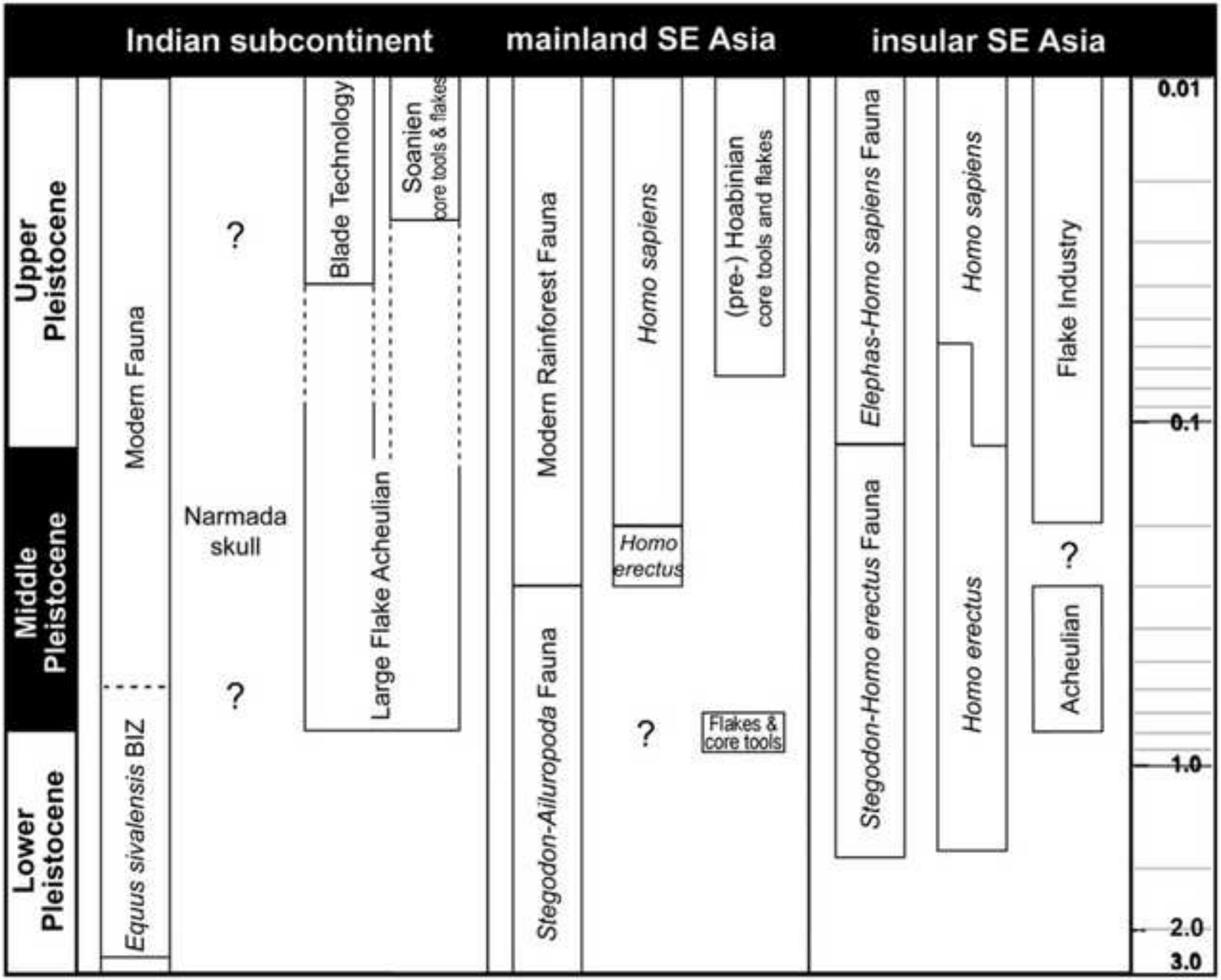

La Celle,
late Middle Pleistocene (MIS 11)
Forest decline
Forest optimum
Forest expansion
Marsh
no forest snails
Ena montana
Vitrea crystallina
Azeca goodalli
Cepaea nemoralis
Clausilia bidentata
Discus ruderatus
Aegopinella nitidula
Carychium tridentatum
Acanthinula aculeata
Vertigo angustior
Vertigo pusilla
Clausilia dubia
Discus rotundatus
Arianta arbustorum
Cochlodina laminata
Macrogastra ventricosa
N and W
Platyla polita
Hygromia limbata
Aegopinella pura
Helicodonta obvoluta
Retinella (Lyrodiscus) elephantium
W and C
Ruthenica filograna
Pomatias elegans
Cochlostoma septemspirale
Sphyradium doliolum
Pagodulina pagodula
Aegopis acieformis
Platyla similis
S and E
Perforatella bidentata
Spermodea lamellata
W
Caours,
Late Pleistocene (MIS 5e)
Forest optimum
Forest expansion
Marsh
no forest snails
Spermodea lamellata
Discus ruderatus
Vertigo pusilla
Clausilia pumila
Arianta arbustorum
Carychium tridentatum
Discus rotundatus
Aegopinella nitidula
Vertigo angustior
Acanthinula aculeata
Aegopinella pura
Cochlodina laminata
Cepaea nemoralis
N and W
Pagodulina pagodula
Helicodonta obvoluta
Ruthenica filograna
Helicigona lapicida
Oxychilus cellarius
W and C
Platyla polita
Sphyradium doliolum
Daudebardia rufa
Macrogastra ventricosa
Clausilia dubia
Balea perversa
Oxychilus navarricus
S and C
Saint Germain le Vasson,
Holocene (MIS 1)
Drier forest
Forest optimum
Forest expansion
Marsh
no forest snails
4213 ± 77
4420 ± 65
5422 ± 60
6515 ± 75
9074 ± 63
Vertigo pusilla
Acanthinula aculeata
Clausilia bidentata
Aegopinella nitidula
Oxychilus navarricus
Merdigera obscura
Vitrea crystallina
Discus rotundatus
Pomatias elegans
N and W
Cochlodina laminata
Leiostyla anglica
Aegopinella pura
Helicigona lapicida
Hygromia limbata
Helicodonta obvoluta
W (and C)
Acicula fusca
Vertigo alpestris
Balea perversa
Macrogastra rolphii
Azeca goodalli
W
arrival of new groups of forest species
Modern European species ranges:
N: North;W: West; C: Central; E:East; S: South

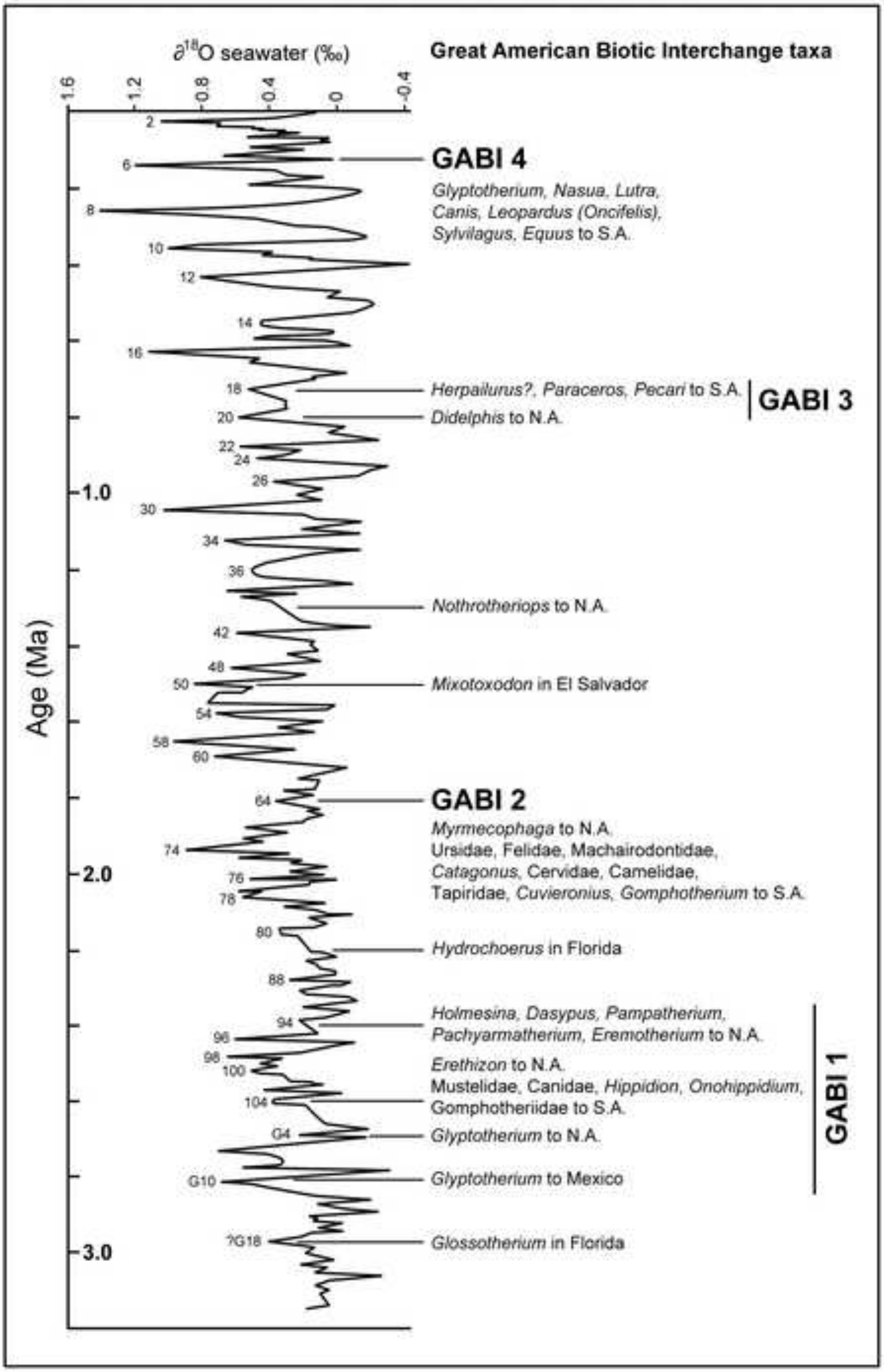

StPElbeuf
Beeches Pit
Lower tufa
Upper tufa
Arrest
Hitchin
Vernon
1
2
St Acheul
Boileau
Acheulean level
● forest
⊗ open ground
△ mesophilous
☐ hygrophilous
100
80
60
40
20
0
Marsh
Pioneer forest
Deciduous forest
Maximum forest
Humid open forest
80
60
40
20
0
Z1A
Z2A
Z2B
Z2C
Z3D
Z3E
Z3B
Z4B
R. elephantium
P. polita
H. limbata
H. obvoluta
A. pura
P. elegans
R. filograna
S. doliolum
C.septemspirale
A. acieformis
P. similis

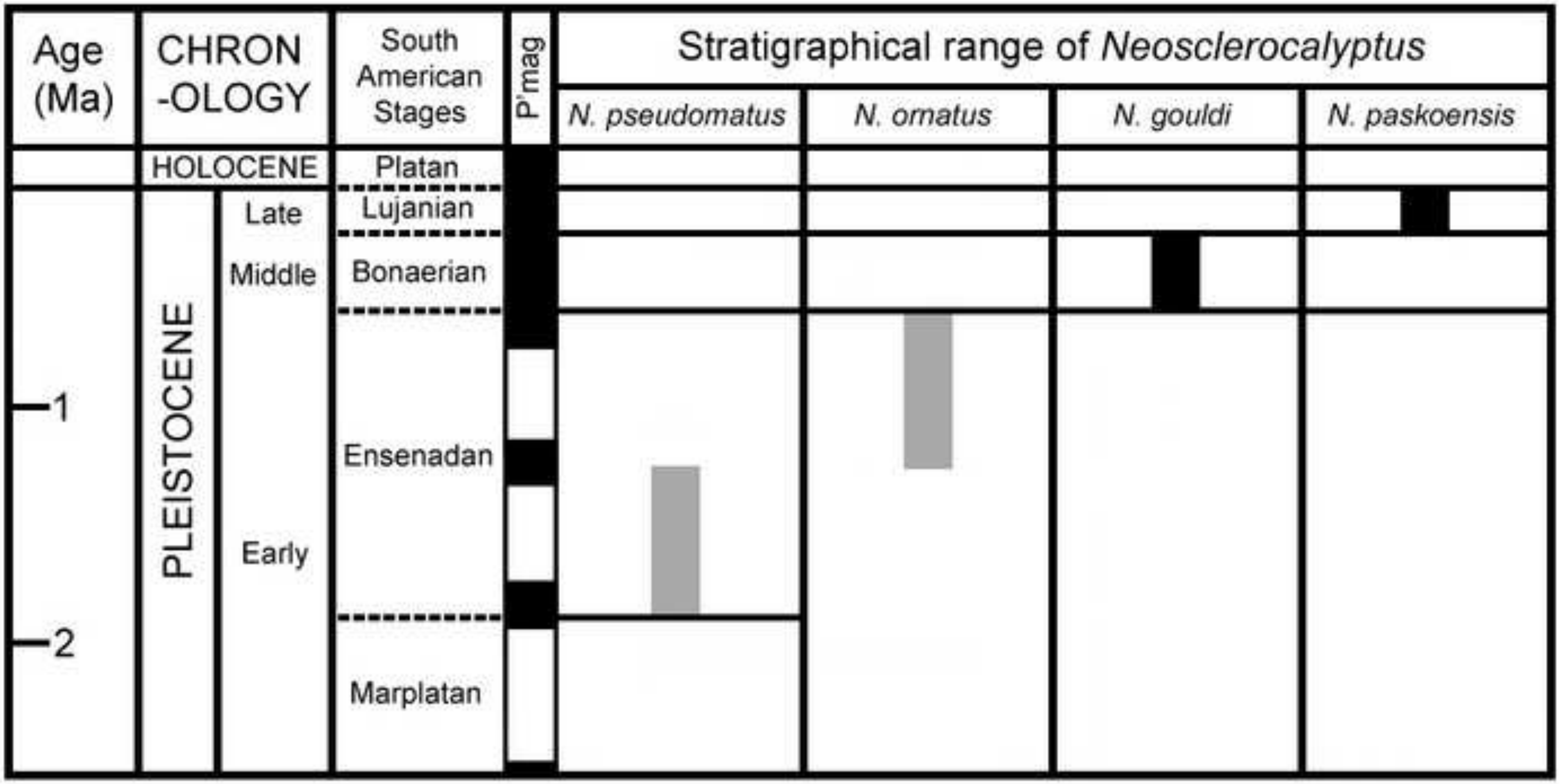


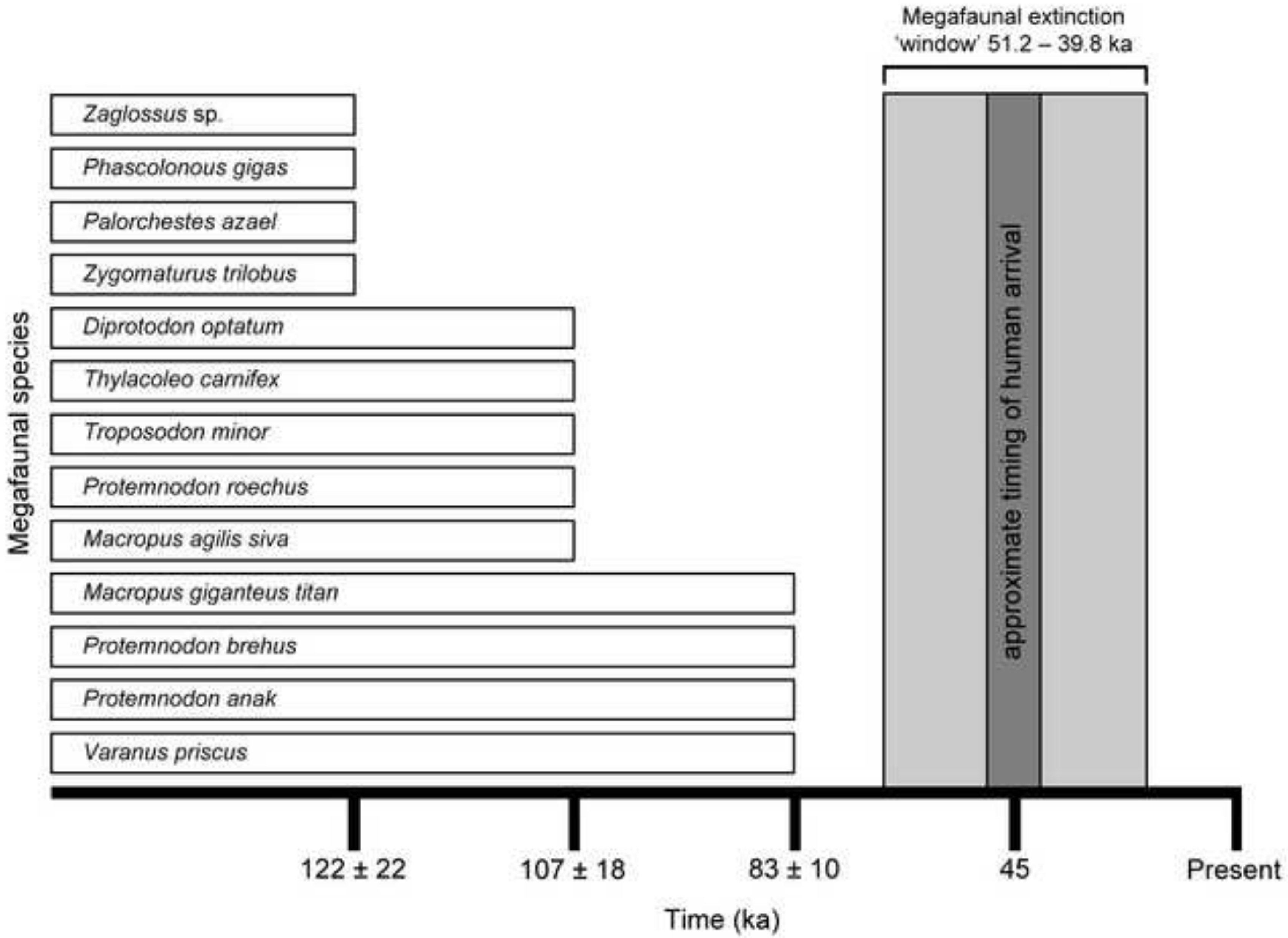
Marine Isotope Stage	Palaeo-magnetism	Chronology	Glacial/Interglacial Stage		Key Deposits		Large Mammal Assemblages	Elephant phylogeny	Small Mammal Assemblages		Small Mammal Localities	First Appearances of Notable Species
1		HOLOCENE										
2		LATE PLEISTOCENE	Valdai Glaciation	Late Valdai	Till, loess Trubchevsk palaeosol Till, loess		MAMMOTH	Mammuthus primigenius	SUNGIRIAN		Tabinki Yudinovo Khotylevo 2 Eliseevichi	Dicrostonyx torquatus
3				Middle Valdai	Bryansk, Alexandrova, Shestkik palaeosols						Arapovichi Sunge Troitsa 2	
4				Early Valdai	Loess Krutitsk palaeosol Loess						Betovo Kabazi 2 (III/3) Gadzach	Dicrostonyx gulielmi
5			Mikulino Interglacial		Salyn palaeosol		Shkurlatian		Shkurlatian		Malukino Chernianka Mikhailovka 5 Shkurlat Eltigen Novonekrasovka	Arvicola terrestris Microtus (Terricola) subterraneus
6		MIDDLE PLEISTOCENE	Dnieper Glaciation	Moscow Stage	Till, loess		CHOZARIAN		CHOZARIAN		Pavlovka-on-Desna Kobylaki Zhukevichi Alpatevo Spasskoe Volgino Strigovo Chekalin (fluvio-glacial layer) Yagodnoe	Dicrostonyx simplicior
				Kursk Interstadial	Kursk palaeosol							
				Dnieper Stage	Till, loess							
7			Warming		Romny palaeosol							
8			Cooling		Orchik loess							
9			Kamenka Interglacial		Kamenka palaeosol						Priluki Plavni Uzunlar Rasskazovo Chernyi Yar	Lagurus lagurus Arvicola chosaricus
10			Cooling		Borisoglebsk loess						Topka	
11			Likhvin Interglacial		Inzhavino palaeosol		TIRASPOLIAN	Mammuthus trogontherii trogontherii	TIRASPOLIAN		Chekalin Gunki Chigirin Ver. Emancha Nerava Rybnaya Sloboda Otkaznoe Uzman Tiraspol (inzh. soil) Mikhailovka 2 Smolenskii Brod	Arvicola cantianus
12			Oka Glaciation		Oka Till, loess						Chekalin (Oka glacial layer) Mikhailovka 2	Dicrostonyx simplicior okaensis
13			Muchkap Interglacial	Konakhovka optimum	Vorona soil complex						Tiraspol (Vorona soil) Kuznetsovo Pekla Volchaya Vershina Posevkino Perevoz Suvorovo (upper layer) Kamyshevakha	Microtus (Stenocranius) gregalis
				Podrudnyansk cooling								
				Glazovo optimum								
14			Don Glaciation		Till, loess						Troitsa 1 Bogdanovka	
15			Late Ilinka Interglacial		Rzhaksa soil complex	Vorotynsk palaeosol					Tiraspol (fluvial) Suvorovo (lower layer) Moiseevo 3 Klepki	
16			Cooling			Loess					Korostylovo 1 Uryv 4 Nagornoe 2 Novokhopersk	
17			Middle Ilinka Interglacial			Ternovka palaeosol					Ilinka 2 and 1 Veretie Trosnianka Berezovka Zapatino	Lagurus transiens Microtus (Terricola) arvaloides
18			Cooling			Loess						
19			Early Ilinka Interglacial			Trotsk palaeosol					Troitskoe Pokrovka Ilinka 4	
20-28		EARLY PLEISTOCENE	Cooling		Pokrovka loess						Litvin Uryv 3	Microtus (Stenocranius) gregaloides
			Balashovsk Interglacial		Balashovsk palaeosol		TAMANIAN	Archidiskodon meridionalis tamanensis	TAMANIAN	Petropavlian	Shamin Karai-Dubina Log Krasnyi Petropavlovka	Microtus arvalinus Microtus oeconomus Microtus (Stenocranius) hintoni
			Cooling		Troianovsk loess					Morozovian	Port-Katon Morozovka	Terricola (Pitymys) sp.
29-31			Interglacial		Klistansk palaeosol					Kairian	Korotoyak (Ostr.) Zapadnye Kairy Ushkalka Kolkotova	Prolagurus pannonicus
32			Cooling		Loess					Nogaisian	Nogaisk Tarkhankut Chishmikioi	Allophaiomys pliocaenicus
?			Warming		Khadzhimus palaeosol		PSEKUPIAN (Late Phase)	Archidiskodon meridionalis meridionalis	ODESSAN (Late Phase)		Khadzhimus Maleknu	Prolagurus ternopolitanus

Figure


Indian subcontinent
mainland SE Asia
insular SE Asia
Upper Pleistocene
Middle Pleistocene
Lower Pleistocene
Modern Fauna
Equus sivalensis BIZ
?
Narmada skull
?
Blade Technology
Soanien core tools & flakes
Large Flake Acheulian
Modern Rainforest Fauna
Stegodon-Ailuropoda Fauna
Homo sapiens
Homo erectus
?
(pre-) Hoabinian core tools and flakes
Flakes & core tools
Elephas-Homo sapiens Fauna
Stegodon-Homo erectus Fauna
Homo sapiens
Homo erectus
Flake Industry
?
Acheulian
0.01
0.1
1.0
2.0
3.0


∂¹⁸O seawater (‰)
Great American Biotic Interchange taxa
1.6
1.2
0.8
0.4
0
-0.4
Age (Ma)
1.0
2.0
3.0
2
6
8
10
12
14
16
18
20
22
24
26
30
34
36
42
48
50
54
58
60
64
74
76
78
80
88
94
96
98
100
104
G4
G10
?G18
GABI 4
Glyptotherium, Nasua, Lutra, Canis, Leopardus (Oncifelis), Sylvilagus, Equus to S.A.
Herpailurus?, Paraceros, Pecari to S.A.
Didelphis to N.A.
GABI 3
Nothrotheriops to N.A.
Mixotoxodon in El Salvador
GABI 2
Myrmecophaga to N.A.
Ursidae, Felidae, Machairodontidae, *Catagonus*, Cervidae, Camelidae, Tapiridae, *Cuvieronius*, *Gomphotherium* to S.A.
Hydrochoerus in Florida
Holmesina, Dasypus, Pampatherium, Pachyarmatherium, Eremotherium to N.A.
Erethizon to N.A.
Mustelidae, Canidae, *Hippidion*, *Onohippidium*, Gomphotheriidae to S.A.
Glyptotherium to N.A.
Glyptotherium to Mexico
Glossotherium in Florida
GABI 1


Age (Ma)
CHRON -OLOGY
South American Stages
P'mag
Stratigraphical range of *Neosclerocalyptus*
N. pseudomatus
N. ornatus
N. gouldi
N. paskoensis
HOLOCENE
Platan
PLEISTOCENE
Late
Lujanian
Middle
Bonaerian
Early
Ensenadan
Marplatan
1
2


Megafaunal extinction 'window' 51.2 – 39.8 ka
Megafaunal species
Zaglossus sp.
Phascolonous gigas
Palorchestes azael
Zygomaturus trilobus
Diprotodon optatum
Thylacoleo carnifex
Troposodon minor
Protemnodon roechus
Macropus agilis siva
Macropus giganteus titan
Protemnodon brehus
Protemnodon anak
Varanus priscus
approximate timing of human arrival
122 ± 22
107 ± 18
83 ± 10
45
Present
Time (ka)

Highlights

- Research over the last decade into biostratigraphical data recorded in fluvial archives is reviewed
- Consideration of biogeography and palaeoclimatic evidence is also included
- This emphasizes the disparities in research priorities and fossil preservation on a global scale