Progress in faunal correlation of Late Cenozoic fluvial sequences 2000–4: the report of the IGCP 449 biostratigraphy subgroup


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Abstract

Vertebrate and invertebrate faunal biostratigraphy is a well-tested method for establishing relative chronologies for fluvial sequences that has proved useful in many parts of the world. The robust bones and teeth of large mammals are commonly found in fluvial deposits, whereas small vertebrates can be readily recovered through systematic sieving of calcareous sediments, as can molluscs, the other major faunal group that has been used for biostratigraphical analysis of fluvial sequences. Because of their rapid and quantifiable rates of evolution, extinction, body mass change and dispersal during the Late Cenozoic, mammals are especially useful for ordering the fragmentary terrestrial sequence of interglacials and glacialis, and proposing correlation with the global marine climatostratigraphic record. Other groups (e.g. reptiles and amphibians, ostracods) are as yet only in the initial stages of development as a dating tool, whereas some (e.g. fish, birds) still require substantial development in order to fully explore their utility. As part of IGCP 449, vertebrate and molluscan assemblages have made important contributions to datasets from a number of areas, notably northern France, central Germany, the Czech Republic and the Ukraine. Further south, mammalian assemblages have proved useful in separating discrete periods of climatic change in Iberia and Syria. At greater distances from the core area of fluvial biostratigraphical archives, significant contributions have come from South America (Uruguay River), South Africa (Vaal) and Australia (Riverine Plain and Lake Eyre drainage basin).

1. Introduction

There is a long tradition of studying fossils found in fluvial deposits and of using these fossil assemblages for relative dating (e.g. Kennard and Woodward, 1897; Kennard, 1924; Zeuner, 1945, 1946; Pike and Godwin, 1953; Sutcliffe, 1964; Kerney, 1971; Kahlke, 1975). A subgroup of IGCP participants undertaking this type of research was formed at the inaugural meeting in Prague (April 2001) and has compiled data on faunal assemblages from fluvial sequences in different parts of the world. Many different types of fossils can be found in fluvial sequences, from tree trunks and large animal bones in coarse gravels to pollen and other microfossils in fine-grained sediments. Although palynological studies have been of great importance since the first interglacials were defined (e.g. West,
1956, 1957, 1980; Zagwijn, 1973; Turner, 1975) the resolution of pollen sequences in fluvial sequences is rarely sufficient for reliable age control (cf. Turner, 1985; Thomas, 2001), a problem that led to much historical controversy between palaeobotanists and other palaeontologists about the number and identity of interglacials in NW Europe (cf. Sutcliffe, 1964, 1975; Shotton, 1983; Bowen et al., 1989; Bridgland, 1994; Gibbard, 1994; Preece, 1995a, 1999; Schreve, 2001a). In essence, those working with animal fossils, particularly molluscs and mammals, were able to distinguish a greater number of interglacials and interstadials within the Middle and Late Pleistocene than the palynologists. With increasingly convincing correlation between the marine oxygen isotope record and terrestrial sequences such as those in river valleys, and supported by geochronological methods wherever possible, it is the version of the Quaternary based on mammals and molluscs that has become for many the status quo (cf. Bowen et al., 1989; Bowen, 1999; Schreve, 2001a,b; Bridgland and Maddy, 2002).

Both vertebrate and molluscan fossils are better preserved in areas of calcareous ground water, which generally coincide with limestone bedrock outcrops. Thus, fluvial deposits overlying the Chalk of NW Europe are often highly fossiliferous, whereas those in adjacent areas overlying non-calcareous Tertiary sands and clays are largely barren. Similarly, the Permian Muschelkalk outcrops in Central Germany coincide with abundant preservation of molluscan and vertebrate fossils in the fluvial terraces of rivers such as the Neckar, Ilm and Wipper, often within subaerial travertines interbedded with the fluvial sediments (Bridgland et al., 2004; see Figs. 1 and 2). Again, fluvial deposits on non-calcareous crystalline rocks, sand(stone)s and clays are generally lacking in useful fossils. The IGCP project has facilitated comparison of such records over wide areas, as will be demonstrated in this paper, which seeks to review and compare the more significant faunal records examined.

In the core area of IGCP 449, NW and Central Europe, the use of mammals and molluscs for biostratigraphy is well established (e.g. Lozek, 1964a,b; Stuart, 1982; Horacek and Lozek, 1985; Horacek, 1990; Kolfschoten, 1990, 2000; Kovanda et al., 1995; Preece, 1995a, 1999; Meijer and Preece, 2000), with mammalian assemblages proving particularly useful for distinguishing the four main post-Elsterian/Anglian interglacials (Schreve, 2001a; Bridgland and Schreve, 2001, 2004; Schreve and Bridgland, 2002; Bridgland et al., 2004). In pre-Elsterian contexts, a combination of mammalian and molluscan signatures has been used to unravel the complexity of short-lived warm events within the Cromerian Complex (Kolfschoten and Turner, 1996; Preece and Parfitt, 2000; Stuart and Lister, 2001). Distinctive taxa have also proved useful in distinguishing certain episodes, for example the presence in MIS 11 of Retinella (Lyrodiscus) elephantium, an extinct member of the Zonitidae belonging to a genus today restricted to the Canary Islands (Rousseau, 1992; Rousseau et al., 1992;
2. Correlation within NW & C. Europe

Inevitably (given the pedigree of research and plethora of sites, both new and historical) this, the core area of IGCP 449, has provided the bulk of the biostratigraphical data compiled by the subgroup. A number of previous IGCP 449 reviews have used mammalian biostratigraphy as a means for correlating fluvial deposits within NW and central Europe (Schreve and Bridgland, 2002; Bridgland and Schreve, 2004; Bridgland et al., 2004), based on comparison with the succession of British Mammal Assemblage Zones (MAZs) established by Schreve (2001a, b). This was based on four discrete mammalian groupings considered to represent the four post-Anglian interglacials, with an additional subdivision of the penultimate stage thought to reflect pulses of faunal turnover at the sub-Milankovitch level. The groupings are correlated with MIS 11/Hoxnian Interglacial (Swanscombe MAZ), MIS 9 (Purfleet MAZ), MIS 7 (Ponds Farm MAZ and Sandy Lane MAZ) and MIS 5e/Ipswichian Interglacial (Joint Mitnor Cave MAZ see Currant and Jacobi, 2001). The principal mammalian characters of each grouping are indicated in Table 1 and Fig. 1. They have been matched to the four interglacial members within the Lower Thames terrace staircase (Bridgland, 1994; Bridgland and Schreve, 2001, 2004; Schreve, 2001a, 2001b; Bridgland et al., 2004). Furthermore, the development of high-precision MC ICP MS uranium-series age-estimates at correlated sites has allowed the testing and confirmation of ideas concerning small-scale environmental change and faunal turnover at the isotopic substage level (Candy and Schreve, 2007). For further details the reader is referred to the above references.

2.1. Britain and Germany

Key Lower Thames sites published during the course of IGCP 449 include three localities attributed to MIS 9: Barling (Bridgland et al., 2001), Purfleet (Schreve et al., 2002) and Hackney Downs (Green et al., 2005), and two attributed to MIS 7: Aveley (Bridgland et al., 2003a; Schreve, 2001a, 2004) and Lion Pit tramway cutting, West Thurrock (Schreve et al., 2006). Data from these sites both test and reinforce the biostratigraphical model erected by Schreve (2001a; Fig. 1, Table 1).

Distinctive molluscan assemblages also occur within the Lower Thames sequence and can further assist in constraining the age of these deposits (Table 1). In the Swanscombe interglacial deposits, attributed to MIS 11, an important feature of the molluscan record is the appearance, part-way through the sequence there, of an exotic, central and southern European suite of Mollusca, typified by species such as *Theodoxus serratiliniformis*. 

Fig. 2. Transverse section through the terrace sequence of the River Wipper in a single meander core at Bilzingsleben, Thuringia (the uppermost two terraces are projected from a nearby area). Mammals from Bilzingsleben II after Fischer et al. (1991). Correlations with marine Oxygen Isotope Stages are suggested and the positions of the deposits correlated with the Elsterian (Elster 1) and Saalian glaciations are indicated. Modified from Bridgland et al. (2004).
<table>
<thead>
<tr>
<th>Site</th>
<th>Key sites in the Thames</th>
<th>Mammalian signature</th>
<th>Molluscan signature</th>
<th>Archaeological signature</th>
</tr>
</thead>
</table>
| Swanscombe   | Key sites in the Thames | - FAD in Britain of *Stephanorhinus hemitoechus*, *Stephanorhinus kirchbergensis*, *Megaloceros giganteus*, *Bos primigenius* and *Equus hydruntinus*  
- Unique appearance of *Ursus spelaeus* and *Dama dama clactoniana*  
- LAD in Britain of *Talpa minor*, *Trogontherium cuvieri*, *Oryctolagus cuniculus* and *Microtus (Terricola) subterraneus*  
- Presence of *Arvicola terrestris cantiana* with mean SDQ 140. Archaic 'Mimomys fold' present at low to medium frequency (<40%)  
- Important absences: *Crocuta crocuta* and *Hippopotamus amphibius* | - Presence of *Theodoxus danubialis* present from pollen zone iii onwards  
- Corbicula fiuminalis present from pollen zone iii onwards | - Early interglacial characterised by Clactonian flake and core industry  
- Later parts of interglacial characterised by Acheulean handaxe industry |
| MAZ MIS 11   | Key sites elsewhere Hoxne|                                                                                                                                                      |                                                                                                                                                                  |                                                                                           |
| Purfleet     | Key sites in the Thames | - FAD in Britain of *Ursus arctos* and *Dama dama cf. dama*  
- Reappearance in Britain of *Crocuta crocuta*  
- Presence of the morphotype 'Neomys browni'  
- LAD in Britain of *Macaca sylvanus*  
- Presence of *Arvicola terrestris cantiana* with mean SDQ 130. Rare 'Mimomys fold'  
- Important absence: *Hippopotamus amphibius* | - Absence of *Theodoxus danubialis* in the Thames  
- Corbicula fiuminalis present from pollen zone ii onwards | - Early interglacial characterised by Clactonian flake and core industry  
- Later parts of interglacial characterised by Acheulean handaxe industry  
- Final interglacial characterised by Middle Palaeolithic Levallois industry |
| MAZ MIS 9    | Key sites elsewhere Cudmore Grove|                                                                                                                                                      |                                                                                                                                                                  |                                                                                           |
| Ponds Fm MAZ, | Key sites in the Thames | - Early interglacial predominantly woodland episode  
- Presence of *Palaeoloxodon antiquus*, *Crocidura* and *Equus ferus*  
- Presence of *Arvicola terrestris cantiana* with mean SDQ 120. 'Mimomys fold' absent | - Corbicula fiuminalis present from pollen zone ii                                                    | - Hominins present but record currently too sparse to attribute to industry               |
| MIS 7e/7c    | Aveley                  |                                                                                                                                                      |                                                                                                                                                                  |                                                                                           |
| Sandy Lane   | Key sites in the Thames | - Later interglacial predominantly open grassland episode  
- Abundance of late morphotype of *Mammuthus trogontherii*, later replaced by *M. primigenius*  
- Abundance of *Equus ferus*, *Stephanorhinus hemitoechus*, *Bos primigenius* and *Cervus elaphus*  
- Presence of *Arvicola terrestris cantiana* with mean SDQ 120  
- Presence of large-bodied *Microtus oeconomus*  
- LAD of *Stephanorhinus kirchbergensis* and *Apodemus maastrichtiensis*  
- Important absences: *Dama dama*, *Hippopotamus amphibius* | - Presence of *Theodoxus danubialis* present from pollen zone ii                                 | - Early interglacial characterised by Clactonian flake and core industry  
- Later parts of interglacial characterised by Acheulean handaxe industry  
- Final interglacial characterised by Middle Palaeolithic Levallois industry |
| MAZ MIS 7a   | Aveley                  |                                                                                                                                                      |                                                                                                                                                                  |                                                                                           |
| Stanton Harcourt Crayford | Key sites elsewhere, Ilford, Marsworth Lower Channel|                                                                                                                                                      |                                                                                                                                                                  |                                                                                           |
Joint Mitnor Cave MAZ, MIS 5e

Key sites in the Thames Trafalgar Square Brentford

Key sites elsewhere Barrington

Joint Mitnor Cave

Mammalian signature

- Presence of Hippopotamus amphibius
- Abundance of Palaeoloxodon antiquus, Dama dama and Stephanorhinus hemitoechus
- Presence of Arvicola terrestris terrestris with mean SDQ 110.
- Absence of Stephanorhinus kirchbergensis and Equus ferus

Molluscan signature

- Corbicula fluminalis absent from Britain

Archaeological signature

- Levallois industry

The archaeological signature of each episode and important correlative sites elsewhere are also listed.

(...)

(= danubialis), Corbicula fluminalis, Belgrandia marginata and Unio crassus (Kennard, 1938; Kerney, 1971). Termed 'Rhenish', this suite has been attributed to a connection with the Rhine, perhaps related to a fall in sea level that reconnected Britain and mainland Europe, following brief separation early in the interglacial (White and Schreve, 2000). A molluscan assemblage containing T. serratiniformis has also been noted in the highest terrace of the post-Elsterian River Wipper (Fig. 2), in central Germany, correlated with the Holsteinian (Mania, 1995).

In contrast to the mammalian record, the molluscan signature of the MIS 9 interglacial in some NW European fluvial sequences is not readily separable from that of MIS 11, although the timing of the appearance of the bivalve C. fluminalis has been cited as a criterion for distinguishing these episodes in the Thames system. This distinction requires the co-occurrence of a detailed pollen zonation in order to position the sequence in terms of pre temperate, early temperate, late temperate and post-temperate pollen biozones (i, ii, ii and iv, respectively; cf. Turner, 1970). During MIS 9, C. fluminalis appears in Zone ii at sites such as Barling, in the lowermost Thames valley north of Southend-on-Sea, whereas it is unknown before Zone iii in the MIS 11 sequences at Swanscombe and Clacton (Bridgland et al., 2001) (Table 1). New work during the IGCP 449 period at Hackney Downs, in East London, recorded a rich molluscan assemblage including a number of biostratigraphically significant species, dominated by C. fluminalis and Belgrandia marginata and including Pisidium clessini and Unio crassus, the last-named known in western Europe only prior to MIS 8 (Preece, 1999; Keen, 2001). Similarly Paladilhia radigueli, a hydrobiid with brackish affinities that was present in older interglacials, also makes its last appearance in MIS 7 assemblages (Preece, 1995a) (Table 1). Deposits of this age also have a coleopteran fauna that is highly distinctive, not only in its species composition, but also in its indication of summer temperatures no warmer than those of the present, in marked contrast to the exotic southern European suite of species invariably found in Last Interglacial (MIS 5e) and MIS 9 deposits (Keen et al., 1999; Coope, 2000, 2001; Gao et al., 2000; Bridgland et al., 2001; Green et al., 2005). Some of the key evidence in this cited work is from rivers flowing into the basin of the Wash in eastern England, including the Nene, the Great Ouse and the Cam, all of which have fossiliferous sites within their Pleistocene sequences (see also Worssam and Taylor, 1969; Bridgland and Schreve, 2001).

Ipswichian Interglacial (MIS 5e) molluscan assemblages are characterised by the presence of species indicative of climates warmer than the present day (ca 2 3°C higher) and, in the UK, of a more continental climate (Keen, 1990; Keen et al., 1999). B. marginata is widespread but C. fluminalis is apparently absent (Table 1), despite apparently suitable environmental conditions and its reputation as a rapid coloniser. Its absence from the UK and the Netherlands during MIS 5e therefore appears a genuine occurrence (Meijer and Preece, 2000).
Following on from the recognition of increased palaeo-climatic complexity in the Cromerian Complex, based on the number of temperate episodes recognised in the stacked sequences in boreholes from the Netherlands (Zagwijn, 1985, 1996), the molluscan and mammalian biostratigraphy of the early Middle Pleistocene has also been thoroughly overhauled (Preece and Parfitt, 2000; Preece, 2001; Stuart and Lister, 2001). Although many of the British sites that have provided evidence for this more complex record are in fluvial or fluvio-estuarine contexts, they are generally isolated one from another in separate systems and represent only very short windows of time as opposed to preserving more complete interglacial sequences. Examples, giving a flavour for the wide distribution of these localities, are Sugworth, Oxfordshire, in the Upper Thames (Shotton et al., 1980), Little Oakley, Essex, in the pre-diversion Thames-Medway (Bridgland et al., 1990), and West Runton, Norfolk, in an early river flowing north, perhaps to an offshore ‘Ancaster River’ (Rose et al., 2001).

Although it is to be anticipated that certain species may have a longer chronological range on the continent than in Britain, for example *Ursus spelaeus*, which disappears from Britain after MIS 11 but is present on the European mainland until the last cold stage (Weichselian), pan-European comparisons have shown that the key biostratigraphical indicators that underpin the British mammalian scheme can aid correlation more widely. Thus, for instance, mammalian assemblages from the Ilm terrace travertine sequence at Weimar-Ehringsdorf, central Germany (Fig. 3), and from the later part of the Tourville Formation in the Seine valley of western France, bear close comparison to the two MIS 7 MAZs defined in the Lower Thames at Aveley (Schreve and Bridgland, 2001; Bridgland et al., 2004; Table 2). All three localities have yielded a diagnostic late form of *Mammuthus trogontherii*. In addition, distinctive Middle Pleistocene malacofaunas are well established in central Europe, notably the late Middle Pleistocene *Helicigona banatica* faunas from travertines in Thuringia (e.g. Thieme and Maier, 1995; Mania, 1995).

Molluscs have provided the raw material for the successful use of amino acid analysis as a geochronological method, first by determination of a leucine/isoleucine ratio from whole shells of particular species (Miller et al., 1979; Bowen et al., 1989, 1995) and later, in work that is still progressing, separating out the intra-crystalline amino acids and using several individual ones for age estimation (Penkman et al., 2007, this volume). The Thames and Avon
Table 2
Presence/absence data of selected biostratigraphically important mammals from selected post-Anglian/Elsterian western and central European late Middle and Late Pleistocene interglacial sites mentioned in the text, with their suggested Mammal Assemblage-Zone (MAZ) grouping (Britain only) and proposed correlation with the marine isotopic record.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Suggested correlation with MI record</th>
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<tbody>
<tr>
<td></td>
<td>11</td>
</tr>
<tr>
<td>Site/MAZ</td>
<td></td>
</tr>
<tr>
<td>Swanscombe MAZ (1)</td>
<td>X</td>
</tr>
<tr>
<td>Račinéves Medzhybozh (2)</td>
<td>X</td>
</tr>
<tr>
<td>Bilzingsleben (3)</td>
<td>X</td>
</tr>
<tr>
<td>Purfleet MAZ (4)</td>
<td>X</td>
</tr>
<tr>
<td>La Celle (5)</td>
<td></td>
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<tr>
<td>Ponds Fann (6)</td>
<td></td>
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<tr>
<td>Ehringsdorf (7)</td>
<td></td>
</tr>
<tr>
<td>Biache-St-Vaast (7)</td>
<td></td>
</tr>
<tr>
<td>Montières Sandy Lane (8)</td>
<td>X</td>
</tr>
<tr>
<td>Ehringsdorf (4)</td>
<td>X</td>
</tr>
<tr>
<td>Trafalgar Square</td>
<td>X</td>
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</tbody>
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<thead>
<tr>
<th>Taxon</th>
<th>Suggested correlation with MI record</th>
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<tr>
<td></td>
<td>11</td>
</tr>
<tr>
<td>Taipa minor</td>
<td></td>
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<tr>
<td>Trogontherium cuvieri</td>
<td></td>
</tr>
<tr>
<td>Ursus spelaeus</td>
<td></td>
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<tr>
<td>Dama dama clactoniana</td>
<td></td>
</tr>
<tr>
<td>Oryctolagus cuvieri</td>
<td></td>
</tr>
<tr>
<td>Microtus (Terricola) subterraneus</td>
<td></td>
</tr>
<tr>
<td>Arvicola t. cantiana (= mosbachensis)</td>
<td></td>
</tr>
<tr>
<td>Macaca sylvanus</td>
<td>X</td>
</tr>
<tr>
<td>Stephanorhinus kirchbergensis</td>
<td>X</td>
</tr>
<tr>
<td>Equus ferus</td>
<td></td>
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<tr>
<td>Stephanochoerus hemitoechus</td>
<td></td>
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<tr>
<td>Homo sp.</td>
<td></td>
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<tr>
<td>Ursus arctos</td>
<td></td>
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<tr>
<td>Dama dama dama</td>
<td></td>
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<tr>
<td>Crocuta crocuta</td>
<td></td>
</tr>
<tr>
<td>Mammuthus trogontheri (late form)</td>
<td></td>
</tr>
<tr>
<td>Coudodonta antiquigaliata</td>
<td></td>
</tr>
<tr>
<td>Arvicola terrestris</td>
<td></td>
</tr>
<tr>
<td>terrestria</td>
<td></td>
</tr>
<tr>
<td>Hippopotamus amphibius</td>
<td></td>
</tr>
<tr>
<td>Hippopotamus incognitus</td>
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</table>

X = confirmed presence; ? = tentative attribution.

Data from (1)Schreve (2001a); (2)Tyráček et al. (2001); (3)Rekovets et al. (2007); (4)Schreve and Bridgland (2002); (5)Schreve (2001a); (6)Auguste et al. (2003); (7)Auguste (1995a); (8)Currant and Jacobi (2001). All other data, this paper.
terraces have formed important relative frameworks for these studies (Maddy et al., 1991; Bowen et al., 1989, 1995; Penkman et al., this volume).

2.2 France

In France, as in Britain, molluscan biostratigraphy has previously formed the basis for comparison with amino acid dating (Bates, 1993; Chausse et al., 2000; Limondin-Lozouet 2001). The Retinella (Lyrodiscus) assemblage, generally recorded from tufas, is, as noted above, considered to represent part of MIS 11. As well as the aforementioned exotic R. (L.) elephantium, this faunal grouping contains several extinct gastropods like Zonioides sepultus, Aegopinella bourdieri, Aegopis acieformis, and species occurring well beyond their modern range such as Macrogastra ventricosa, Platyla similis, P. polita, Rutherenia filograna, Nemiatella pauli, Hygromia limbata and Ema montana. Although not directly representative of fluvial environments, the ‘Lyrodiscus fauna’ is an important marker within the Seine and Somme terrace sequences, occurring in tufas at St-Pierre-les-Elbeuf and Vernon in the Seine valley and at Arrest and St. Acheul in the Somme valley (Rousseau et al., 1992; Antoine and Limondin-Lozouet, 2004; Limondin-Lozouet and Antoine, 2006). The presence of tufa at St. Acheul, type locality of the Acheulean Palaeolithic industry, is an important discovery made during the course of IGCP 449 (Antoine and Limondin-Lozouet, 2004). The recognition of this distinctive assemblage within a well-dated fluvial sequence provides an important link to British localities at Hitchin (Kerney, 1959) and Beches Pit, West Stow (Preece et al., 2006, 2007), both yielding tuftas now interpreted as Hoxnian (MIS 11) but occurring outside major fluvial systems.

During the course of IGCP 449 a new research group called SITEP was initiated in Northern France. It is focused on the study of Pleistocene interglacial tufa deposits from MIS 11 to MIS 5 with the aim of characterizing each temperate period using a multi-proxy approach and appropriate means of dating. Early results have been obtained at two sites, La Celle in the Seine valley and Caours in the Somme valley, respectively attributed to MIS 11 and MIS 5 by radiometric measurements (Antoine et al., this volume). Not only did tufa accumulation prove to be several metres thick at both localities but both sequences were also found to contain evidence for human settlement, in the form of flint artefacts and modified mammalian remains. Molluscs, which are abundant throughout these calcareous formations, allow the reconstruction of landscape evolution in relation to climatic change. The successions begin with wet open-ground assemblages corresponding to pioneer biotopes during early interglacial times. Development of the forest environment is then emphasised by the appearance and spread of shade-loving taxa, allowing at their maximum the identification of the climatic optimum phase. The last stage is characterized by a return to open-ground molluscs, indicating drier biotopes and probably a decline of climatic conditions. The molluscan data from both La Celle and Caours can be characterized by a set of species extinct or beyond their modern range. At La Celle the ‘Lyrodiscus fauna’ is clearly identified and occurs within the optimum interglacial phase that also includes the Acheulean industry (Limondin-Lozouet et al., 2006). The characterization, at high resolution, of faunal succession within the MIS 11 interglacial offers strong future possibilities of correlation between the Seine and Thames sequences (see Schreve 2001b for details of British MIS 11 mammalian faunal turnover). The importance of Caours as a site indicating human occupation of the Somme valley in the Last Interglacial is discussed elsewhere in this volume (Mishra et al., this volume).

In Northern France many fluvial sequences representative of temperate climatic conditions have yielded assemblages of large mammals. The oldest such evidence was recovered at Saint-Prest (Normandy) in sandy deposits of a very old terrace of the Eure river. The fauna, recently revised by C. Guérin et al. (2003), comprises Mammuthus meridionalis depereti, Stephanorhinus etruscus ‘brachycephalus’, Equus stenonis, Alces carnitorum, Megaloceros verticornis, Cervus cf. elaphus, aff. Dama sp., Bison schoetensacki, Hippopotamus major, Trogontherium cuvieri bosvilleti and Pachycrocuta brevirostris. This fauna, attributed to the Bavelian and considered to correlate with MIS 23 to 20, is thus one of the oldest fluvial mammalian assemblages in NW Europe. The assemblage bears strong similarities to that from Untermaßfeld (central Germany), where fluviatile sands of the River Werra have been dated by geological, palaeomagnetic and biostratigraphical evidence to approximately 1.07Ma (MIS 31, immediately above the onset of the Jaramillo polarity subzone) (Kahlke, 2001).

Amongst the mammalian assemblage from the Carpenter quarry at Abbeville (Somme valley), the fauna from the lower part of the white marl is the most interesting from a biostratigraphical point of view. The taxa include Mammuthus meridionalis, Palaeoloxodon antiquus, Stephanorhinus etruscus ‘brachycephalus’, Hippopotamus incognitus, Sus scrofa mosbachensis, a stenonid horse, Equus mosbachensis, Homotherium latidens, Megaloceros verticornis, Bison cf. priscus and Bos primigenius (Auguste, 1995a, 1995b). This mammalian association is of early Middle Pleistocene age, although there are notable differences with the type Cromerian fauna from West Runton defined by Stuart (1975, 1981). In particular, the presence of hippopotamus suggests a period of climatic conditions warmer than at present. An episode with relatively elevated temperatures has been recognised within the Cromerian Complex on the east coast of Britain, in fluvi-oestuarine sediments of MIS 17 or 15 age at Pakefield (Parfitt et al., 2005), but West Runton itself has yielded no evidence of temperatures any warmer than at present (Stuart and Lister, 2001). The first appearance of H. incognitus in Northern France is
noteworthy, since the species subsequently appeared regularly during temperate phases in the area.

Two sites have yielded important information on the evolution and migration of large mammals after MIS 12. The first is Cagny-la-Garenne in the Somme valley, where fluvial levels I and H yielded several important taxa including *Bos primigenius*, *Equus* sp., *Canis lupus mosbachensis* and *Cervus cf.* *elaphus*. The horse is similar to caballine equids described by Eisenmann (1991) from British sites such as Hoxne, Clacton and Swanscombe, all three attributed to the Hoxnian (MIS 11) interglacial. The second site is at La Celle (see above, Table 2), also attributed to MIS 11, where remains of *Cervus elaphus*, *Equus* sp. (again similar to the Hoxnian caballine horse), *Macaca sylvanus* and *H. incognitus* (the first record of this species from this interglacial) were recovered from the tufa sequence during a survey carried out in 2003. In Northern France, *H. incognitus* appears again as part of the fauna of the MIS 7 interglacial at Montières (Boutmy-Muchembled quarry), in fluvial deposits of the Somme river (Auguste, 1995a). Hippopotamus is not thought to have reached Britain during either the MIS 11 or MIS 7 interglacials (Schreve, 2001a), despite its apparent presence on the adjacent continent during both episodes. Conversely, hippopotamus is absent from Last Interglacial deposits at Caours, in a tributary of the River Somme, despite being very common in British assemblages from the Eemian/ Ipswichian (Kolfschoten, 2000).

The interglacial corresponding with MIS 9 has also been recognised at several sites in Northern France. At Cléon, in the Seine valley, it is characterized by the appearance of *Stephanorhinus hemitoechus* (Auguste et al., 2003; Table 2). The fauna preserved within the fluvial levels here includes *Cervus elaphus*, *Bos primigenius*, *S. hemitoechus*, *Equus* sp. and *Palaeoloxodon antiquus*. It is correlated with the fauna of Tourville-la-Rivière (lower part of the Tourville Formation) and allocated to the Domnitz interglacial, attributed to MIS 9.

Moving into the MIS 7 interglacial, sites with mammalian faunas become more numerous and allow the tracking of migrations on a large scale. The site of Biache-Saint-Vaast (Pas-de-Calais) offers a very detailed biostratigraphical record thanks to the preservation of large numbers of bones (>20000 anatomically and specifically identified remains) from 20 species within a well understood chronological sequence (Tuffreau and Somme 1988; Auguste, 1995a). Many large mammals were recovered from the fluvial levels (Auguste, 1995a): *Canis lupus* cf. *mediterraneus*, *Vulpes vulpes*, *Felis silvestris*, *Panthera spelaea*, *Ursus arctos*, *Ursus deningeri* cf. *hercynicus*, *Aonyx antiqua*, cf. *Martes martes*, *Sus scrofa* scrofa, *Cervus elaphus elaphus*, *Megaloceros giganteus* giganteus, *Capreolus capreolus* capreolus, *Bos primigenius* trolechoerus, *Equus* cf. *taubachensis*, *Equus hydruntinus*, *Stephanorhinus hemitoechus*, *Dicerorhinus mercki* (= *Stephanorhinus kirchbergenensis*), *Palaeoloxodon antiquus* and *Castor fiber*. The detailed and exhaustive study of this material has underlined the complexity of MIS 7, with at least two episodes of temperate faunas during this period, the first at the beginning of the stage around 250000 years BP (type fauna: Biache) and the second at the end of the stage around 200000 years ago (type fauna: Tourville-la-Rivière) (Auguste, 1995a; Auguste et al., 2003). The presence of two discrete mammalian faunal assemblages within MIS 7 directly parallels the British record (Schreve, 2001a, b), with the older of the two assemblages attributed to MIS 7c or 7e and the younger attributed to MIS 7a (Candy and Schreve, 2007) (Table 2). It has yet to be determined whether amino-acid racemisation can detect this level of resolution (see Penkman et al. this volume) but samples of *B. tentaculata* opercula are currently being processed with this aim.

Deposits of the Last Interglacial (MIS 5e) are relatively rare in continental Western European fluvial sequences, so the newly excavated site of Caours (Somme Valley) is of particular importance. Several levels of human settlements with a Middle Palaeolithic industry and a very characteristic mammalian assemblage were observed in this tufa sequence. The identified taxa comprise *Bos primigenius*, *Cervus elaphus*, *Dama cf. elationiana*, *Capreolus capreolus*, *Sus scrofa*, cf. *Aonyx antiqua*, cf. *Palaeoloxodon antiquus*, *Stephanorhinus* sp. and *Canis lupus*. The mammalian fauna is dominated by forest species typical of temperate periods and reinforces the climatic interpretation deduced from the molluscan communities. An Eemian age also conforms to the position of the site within the Somme terrace staircase and is upheld by ESR dating (Antoine et al., 2006, this volume; Table 2). In summary, the multiproxy evidence derived from tufa deposits now makes an important contribution to understanding of the northern French river terrace sequences, given that they combine rich molluscan and mammalian faunas with the means for geochronological measurements. The recent discovery of many new tufa sites has substantially assisted in this aim and happily the famous tufa at St-Pierre-les-Elbeuf, thought to have been completely quarried away, was rediscovered towards the end of the IGCP 449 period, allowing new investigation of this important Seine deposit.

3. Extending eastwards from central Europe

As part of the IGCP 449 Inaugural Meeting (Prague, April 2001), a field excursion was led to the Czech site at Račíněves, which lies within the terrace sequence of the River Vltava (= Elbe). Previous interpretations of this site had recognised a supposed Holsteinian soil near the base of a loess sequence above the fluvial beds and from this had been proposed a late Cromerian Complex age for the Račíněves interglacial deposits, with their fauna and artefacts (Tyráček et al., 2001). With attention drawn to this site by the IGCP visit, consideration of the biostratigraphical implications of the mammalian assemblage led Tyráček et al. (2004) to reassign this interglacial deposit to
the Holsteinian (MIS 11). The Račiněves assemblage has a number of taxa in common with the Swanscombe MAZ, notably the rhinoceroses *Stephanorhinus kirchbergensis* and *S. hemitoechus* and a large fallow deer (*Dama dama*); *Artiocaela terrestris cantiana* (= *A. mosbachensis*) teeth from Račiněves have a characteristic Holsteinian morphology (Tyráček et al., 2001, 2004). The molluscan fauna comprises 22 taxa, including the woodland species *Drebecia banatica* and *Aegopis verticillus*, which, with *Helicodonta obsoluita*, *Ena montana*, *Cochloidina lamina* and *Discus ruderatus*, point to fully interglacial conditions. The absence of *Helicigona čapeki* and *Granaria frumentum*, considered diagnostic of Cromerian Complex interglacials in the Czech Republic (cf. Záruba et al., 1977), supports the view that the Račiněves deposits date from MIS 11 (Table 2). This is the principal biostratigraphical site within the Vltava sequence and as such is an important stratigraphical marker (Tyráček et al., 2004). Elsewhere in this part of Europe fluvial mammalian faunas are relatively sparse and loess palaeosol stratigraphy is the more traditional means for erecting age models for terrace sequences, since the pioneering work of Kukla over 30 years ago (Kukla, 1975, 1978). Nonetheless, the data from Račiněves can provide an important link with another area where biostratigraphical evidence is prolific, the region to the north of the Black Sea and Caspian basins.

### 3.1. Evidence from the Eastern European Plain

Amongst the most impressive Late Cenozoic fluvial records are those left by the south-flowing rivers of the East European Platform, the Dniester, Dnieper, Don and Volga (Matoshko et al., 2002, 2004). Affected in their upper reaches by the major Quaternary glaciations, the Black Sea rivers have been periodically inundated in their lower reaches during marine highstands, a record complicated by the similarly driven separation and reconnection of the Black Sea and Mediterranean. The nature of these sedimentary records varies between an unbroken terrace staircase and the most complete biostratigraphical record (Tyráček et al., 2004). There are important small mammal assemblages from the Upper Don of Lower Pleistocene and Upper Pleistocene and several Lower and Middle Pleistocene suites of the Lower and Middle Dnieper also include fossiliferous deposits. However, information is lacking from many others; nevertheless, they represent the principal means of correlation between the four sequences (see below), as was documented in some detail by Matoshko et al. (2004), who also provide bibliographical details of the primary literature sources.

The biostratigraphical record from the Dniester commences with isolated discoveries of a mammal fauna containing *Hipparion* in the Late Miocene Balta Series, which pre-dates terrace incision (Fig. 4). Overlying these deposits, and also pre-dating the incision, is the latest Miocene/earliest Pliocene Stolnichen Series, presumed to represent the early part of the Moldova fauna (Fig. 4), which has yielded “*Dicerorhinus*” aff. *megarhinus*, *Antilope* sp., *Hipparion* sp., *Gazella* cf. *borbonica*, *G. depedernita* and *Homotherium* cf. *cretalidens*. The molluscs *Plicatibaphia* cf. *wetzleri* is also highly characteristic of this series. Dating of these deposits is complicated, since *G. depedernita* is known to have originated in SE or central Europe by 7.9 Ma during Neogene Mammal Zone (MN) 12 and to have disappeared by around 5 Ma (end of MN 13) at the end of the Miocene (Made et al. 2006) but “D.” *megarhinus* is not replaced until the beginning of the late Pliocene (Zone MN 15, 4.2-3.4 Ma) by its descendant “D.” *jeanwirielti* (Heissig, 1996). The first terrace suite to be formed after the initiation of incision is the Kuchurgan Suite, which contains *Zygolophodon borusi*, *Hipparion gracile* (= *Hippotherium primigenium*), “D.” *megarhinus*, *Promimomys moldavicus* and *Pliomys kowalskii*, representing the Moldova faunal complex of the early Pliocene (Fig. 4). The last two species appear in eastern Europe during the late Ruscian and in the subsequent Runkashiv Suite (Fig. 4). The last two species appear in eastern Europe during the late Ruscian and in the subsequent Runkashiv Suite (Fig. 4). The latter suite was correlated by Matoshko et al. (2004) with the Sokol Suite of the Kinel’ series, defined in the Kama tributary of the Middle Volga. It contains a characteristic molluscan assemblage, with *Viviparus dresselli*, *V. mangikiani*, *V. achatinoides aloganensis*, *Valvata vanciana*, *V. piscinalis*, *Borysthenia naticina*, *Bithynia spoliata*, *B. vukotinovici*, *Lithogyphus rumanus*, *B. vukotinovici*, *Lithogyphus rumanus*,
**Fig. 4.** Generalised transverse profile through the Middle–Lower Dniester sediments (see Fig. 3 caption for sources), showing biostratigraphic and magnetostratigraphic dating evidence. Modified from Matoshko et al., 2004; see Bridgland and Westaway (2007) for MIS correlations.

*Unio* ex gr. *rumanus*, *Potomida sibinensis* and *Psilunio serratoradiatus*. The next terrace is formed by the Vadul-lui-Vode Suite, which has yielded the molluscs *Pristinunio davulai* and *P. procumbens*, along with mammals such as a primitive subspecies of *Mammuthus meridionalis* (sometimes referred to as "*Archidiskodon* gromovi") (Lister and Sher, 2001) and *Equus stenonis*. This Dniester suite is correlated with the Uryv Series of the Upper Don, on the basis of small mammals, and with the Khapry Suite of the Lower Don, from which the Khapry mammal complex is defined (Matoshko et al., 2004). The Khapry Sands are magnetically reversed and are considered to lie within the earlier part of the Matuyama Chron just above the Gauss-Matuyama reversal at 2.5 Ma, whereas the mammalian fauna has been correlated with the Middle Villafranchian (Zone MN 17, ca 2.5–1.5 Ma). The final Pliocene terrace of the Dniester, formed by Rashkiv Suite (Fig. 4), also yields fauna representative of the Khapry mammal complex, including the molluscs *Bogatschevia tamanensis*, *B. bugasiicus* and *Potomida* (*Wentzienella*) *moldavica*. 
The earliest Pleistocene terrace of the Dniester is formed by the Boshernitsa Suite (Fig. 4), in which is found the early Tamanian mammal complex, together with molluscs such as *Bogatschevia sturi*, *Unio sturi var. rodozianki* and *Margaritifera varia*. It is correlated with the middle suite of the Goryanka Series of the Upper Don, which is characterized by small mammals such as *Mimomys ex gr. pusillus*, *M. savini* and *Allophaiomys pliocenicus* of the same faunal complex (Holmovoi et al., 1985). The next Dniester terrace, formed by the Kisnytsia Series, contains molluscs such as *Unio sturi var. caudata*, *Unio sturi var. scutum, Unio (Eolymnium) pseudochasaricus* and *Corbicula apysferonica*, together with mammals of the late Tamanian complex (ca 1 Ma), such as *Mammuthus meridionalis tamanensis*. The last species is considered to represent the 'advanced' form showing enhanced variability towards *Mammuthus trogontherii*, although its broad morphological range suggests it is not a simple intermediate (Lister and Sher, 2001).

The Early Middle Pleistocene transition is best established in the Don, where the most advanced Early Pleistocene faunas occur, characterized by the Petropavlovka fauna, with *Mictotus (Palaeolagus) ex gr. economicus*, the steppe lemmings *Prolagus pannonicus* and *Eolagurus argyropouli* and the vole *Microtus hintoni* (Krasnenkov and Agadjanian, 1975; Alexandrova, 1976; Markova, 1998). A comparable small mammal fauna occurs in the lower Dnieper near Karai Dubina (Markova, 1982). Palaeomagnetic studies have placed the beds with this fauna in the upper part of the Matuyama Chron (Velichko et al., 1983), corroborating a terminal Early Pleistocene age (Matoshko et al., 2004). Although it has been suggested that the Petropavlovka Suite marks a distinctive biostratigraphic substage (Alexandrova, 1976), or that it marks the start of the Tiraspolian biozone (Holmovoi et al., 1985; Rekovets, 1994), or the end of the earlier Tamanian biozone (Markova, 1998), Matoshko et al. (2002, 2004) have regarded it as transitional between the Tamanian and Tiraspolian biozones. An age within MIS 20 for Petropavlovka Suite has been proposed by Iossifova (2001).

The next Dniester terrace suite, the Mihailovska Suite, represents the earliest Middle Pleistocene (Tiraspolian), followed by the Koshnitsa and Kolkotov Suites forming the next two terraces, also of Middle Pleistocene stage (Fig. 4). The Tiraspolian is characterized by the presence of *Mammuthus trogontherii wusti*, *Alces latifrons*, *Cervus elaphus acoronatus*, *Equus aff. suessenbomensis*, *Lagurus transiens*, *Microtus hintoni* and *Mimomys savini*. The molluscan assemblage in the Koshnitsa Suite is similar to that from the Holocene, whereas the later Kolkotov Suite has a subtropical malaco fauna, with *Potomida littoralis, P. kinkelini, Viviparus tirapolitanus* and *V. kagarliticus*. There is a well-established biostratigraphical correlation between the Kolkotov Suite and the Nikopol Suite of the Lower Dnieper, the Muchkap Suite of the Upper Don and the Venedy Series of the Middle Volga (Matoshko et al., 2004).

The succeeding terrace, represented by the Varnitsa Suite (Fig. 4), falls biostratigraphically within the Singil mammal complex. This biozone is named after the Singil Suite of the Caspian Sea, which represents a relatively minor transgression of the Caspian Sea (Matoshko et al., 2004), and marks the *Mimomys Arvicaela* transition recognized throughout Europe (Turner, 1996; Matoshko et al., 2004). The Singil fauna is better known from the equivalent Kryvichi Series of the Dnieper and Volga; in the Middle Dnieper it is characterized by *Arviciaela chosarianus*, *Arviciaela mosbachensis (= terresstri cantiana)*, *Eolagurus luteus*, *Microtus gregalis*, *Microtus arvalis*, *M. economicus*, *Cricetus praegralalis* and *Lagurus lagurus*. In the Upper Don the important *Mimomys Arvicaela* transition seems to occur between the Muchkap and Tafino Suites (Iossifova, 1977; Turner, 1996). The lowest three terraces of rivers on the East European Platform (Speya, Siobodzeya and Parkan suites in the Dniester Fig. 4) are characterized by late Middle/Late Pleistocene mammalian species of the Upper Palaeolithic faunal complex, such as *Coelodonta antiquitatis*, *Megaloceros giganteus ruffi*, *Cervus elaphus*, *Capreolus capreolus*, *Rangifer tarandus*, *Bison priscus* and *Mammuthus primigenius*.

These four east European rivers have provided some of the most important data that has been contributed to IGCP 449, both in terms of their biostratigraphy and more widely for correlation purposes (for their possible correlation with the marine oxygen isotope record see Figs. 4 6). Their contrasting records (Matoshko et al., 2002, 2004), with a terrace staircase in the Dniester, a complex sequence of nested, inset staircases in the Upper Don (Fig. 5) and laterally disposed sediment bodies of various ages within ± 50 m of the modern river level in the Middle Dnieper (Fig. 6), has been linked to crustal type and, being in a similar climatic zone to other European rivers, have helped to establish the importance of this criterion for understanding uplift (Bridgland and Westaway, 2007).

There are other important issues in correlating faunas between these eastern extremities of Europe and the core project area further west. In particular, evidence from the Black Sea area is critical with respect to the recent controversial case advanced in Britain for evidence of glaciation during MIS 16 (the Happisburgh Till), reputedly recorded in relation to the Bytham River sequence of East Anglia (Hamblin et al., 2000; Lee et al., 2004). This has been challenged by other stratigraphers and biostratigraphers, who have pointed to important differences in faunas occurring above and below the Happisburgh Till and those similarly disposed in relation to the long-established early Middle Pleistocene Don glaciation, also widely believed to date from MIS 16 (Pevzner et al., 2001). The Don Till is both underlain and overlain by sediments containing archaic water voles of the genus *Mimomys*, which have rooted molar teeth, whereas the Happisburgh Till overlies sediments with the later descendant form with continuously growing (unrooted) molars, belonging to the genus
Fig. 5. Schematic transverse profile across the Neogene and Quaternary deposits of the Upper Don in the Middle Russian and Kalach Uplands near Voronezh, showing sources of biostratigraphic and magnetostratigraphic age-control evidence (after Matoshko et al., 2004—see that paper for original sources). Palaeomagnetic epochs are: Gil., Gilbert; Gs./Mat., Gauss/Matuyama boundary; Mat., Matuyama; Mat./Br., Matuyama/Brunhes boundary; Br., Brunhes. Modified from Matoshko et al., 2004; see Bridgland and Westaway (2007) for MIS correlations.
**Arvicola.** The transition from *Mimomys* to *Arvicola* has long been regarded as one of the most important biostratigraphical markers in the European Pleistocene. Since it is likely that this evolutionary advancement was perpetuated in the water vole population extremely rapidly (given the rapid reproduction and turnover rate in microtine rodents) and Britain was at that time permanently connected to the European mainland by a land bridge (thereby allowing free movement of terrestrial mammals), it is difficult to see how the Don and Happisburgh glaciations can be of the same age (Banham et al., 2001; Preece and Parfitt, 2007) unless there is
a marked diachronity in the evolutionary transition between Mimomys and Arvicola across Europe.

Correlation across Europe and with the marine oxygen isotope stratigraphy of the Dnieper glaciation (e.g. Matoshko, 1995), is equally controversial. In Central and Eastern European schemes, the Dnieper stage has generally been attributed to MIS 8 (e.g. Šibrava, 1986; Matoshko et al., 2004) but it is also generally correlated with the Saalian glaciation. In the Netherlands, the Saalian is equated with MIS 6 (Zagwijn, 1974; Turner, 2000), although in the type Saale River area in Germany an MIS 8 age might fit better with the biostratigraphical evidence, from the terrace sequences of Saale tributaries such as the Wipper and Ilm (Figs. 1 and 2) and the correlation of these with the semi-stacked sequence at Schöningen (Bridgland et al., 2004). According to Vasiliev (1980), outwash from the successive Dnieper, Moscow and Valdai glaciations feeds into terraces of the Volga, potentially recording ice sheets in MIS 8, 6 and 2, respectively (Matoshko et al., 2004).

A more recent contribution from this area by Rekovets et al. (2007) has documented data from a Middle Pleistocene site at Medzhybozh in the Third Terrace of the Yuzhny Bug, a smaller Ukrainian river flowing to the Black Sea between the Dniester and Dnieper courses. This site combines biostratigraphy with stratigraphical evidence, in which two superimposed alluvial cycles are indicated, the lower of which has yielded Palaeolithic artefacts (see Mishra et al., this volume). The best evidence both for distinguishing the two cycles and for estimating their age comes from biostratigraphy, in particular the evidence from the SDQ index of enamel differentiation in Arvicola (see Heinrich 1982, 1987 for details of methodology). Although challenges remain in directly comparing lineages from different regions, the broad trend across Europe is for SDQ indices to progressively decrease from the early Middle Pleistocene to the present (Kolfschoten, 1990; Maul et al., 1998; Maul and Markova, 2007). In the earlier cycle at Medzhybozh, Rekovets et al. (2007) calculated SDQ values of ~116, whereas in the younger cycle they have fallen to 107, leading them to favour an MIS 11 age for the former (Table 2).

4. Comparison over wider areas

Extension of the approach that has been used in the IGCP 449 core area to more distant regions is hampered by the unsurprising variation of faunal components, as different climatic and geographical provinces are encountered. Northward extension is largely precluded by the paucity of long-timescale records in areas inside the limits of the main Quaternary glaciations. To the south lie areas within the Mediterranean climatic zone, where preservation is frequently better but faunal turnover can often be less pronounced than in higher latitudes, leading to problems differentiating different climatic stages. Notable exceptions occur in the fluvial terraces of Italy, some parts of Iberia and the Levant (see below). Extension eastwards towards Asia runs parallel with the climatic zones and so might be expected to show similar patterns of faunal turnover to the west. This is largely borne out by the recognition of comparable faunal zones in Russia, albeit with different classification systems and with taxonomic uncertainties that require further consideration.

4.1. Evidence from southern Europe

Fossiliferous fluvial deposits occur in many areas of southern Europe, complementing the data that come from cave sites and other environments in that area. In Spain, the oldest dated fluvial terrace corresponds to the 165 m level of the Pisuerga River (Duero basin) that includes the Tarriego de Cerrato fossil locality, with a mammal fauna belonging to the upper Miocene (Santisteban et al., 1997; Mediavilla, 2001). For the Quaternary, there an important Early Pleistocene fauna occurs in bed 3 at Fuente Nueva, in the upper part of the stacked fluvial/lacustrine sequence of the Guadix-Baza basin (Martinez-Navarro et al., 1997). Associated with reported early archaeological material are Mammuthus meridionalis, Stephanorhinus etruscus, Megaceros solhucus, Megantreton whitei, Allophaiomys bourgondiae and Allophaiomys chalinei. Bed 3 is magnetically reversed (Matuyama Chron) and is thought to slightly predate the Jaramillo subchron ~1.1 Ma (Martinez-Navarro et al., 2005). The occurrence of M. meridionalis provides an indication of an Early Pleistocene age for high terraces of several Iberian rivers, notably the 80-85 m terrace of the River Manzanares, a tributary of the Tagus (cf. Bridgland et al., 2006; Santisteban and Schulte, this volume) and at the sequence of sequence of Pinedo, where it appears at the 60 m terrace, in a lower position than the finding of Equus stenonis (~75 m), and where a paleomagnetic measurement places the beginning of the Brunhes Chron at that terrace of the Tagus River (Aguirre, 1964).

Four fossil sites of Early Pleistocene age are located in the Spanish Southern Meseta (Guadiana and Jucar rivers). In the Guadiana River, Valverde-2 has yielded Equus cf. stenonis, Cervidae indet., Bovidae indet. and Elephantidae indet. (Alberdi et al., 1984), dated to 19.1.5 Ma (Mazo, 1999). Valverde-1 faunas are composed of Mammuthus meridionalis, Hippopotamus amphibius major, Equus caballus muschelensis, Eucladoceros diasurnus and Leptobos etruscus (Molina et al., 1974). The site of El Provencio, in the 15.16 m terrace of the former Guadiana River, has yielded Mammuthus meridionalis and Bovidae indet. (Mazo et al., 1990) and it is correlated with the Fuensanta de Jucar site, on the 60 m terrace of the Jucar River and dated to ca 1 Ma, which contains Mammuthus meridionalis, Hippopotamus major and Cervidae indet. (Mazo et al., 1990).

The Middle Pleistocene is substantially richer in terms of faunal preservation and abundance, especially the ubiquity of Palaeoloxodon antiquus, which is characteristic of this period in Spain and elsewhere. The celebrated Torralba archaeological site can be placed between the 22 and 35 m
terraces of the Masegar River (Ebro basin) and the 20-25 m and 30-35 m terraces of the Upper Henares River (Tagus basin). The fauna from this locality is typically late Middle Pleistocene and includes Crocidura sp., Microtus breccien­sis, Arvicola aff. sapidus, Apodemus aff. sylvaticus, Orycto­lagus sp., Canis lupus, Panthera sp., P. antiquus, Equus caballus torralbae, Stephanorhinus hemitoechus, Capreolus sp., Cervus elaphus, Dama cf. dama and Bos primigenius.

In the Duero basin, in the tributary Pisuerga River sequence are a number of important fossil localities. The 165 m terrace of this river includes the Tariego de Cerrato fossil locality, with a mammal fauna belonging to the upper Miocene (Santisteban et al., 1997; Mediavilla, 2001), whereas in the 1820 m and 3035 m terraces, P. antiquus appears in association with Equus sp. and Bos sp. (Santonja and Perez-González, 1984). On the Mediterranean side, P. antiquus appears together with Equus cf. chosariacus, S. hemitoechus, Cervus sp., Crocidura sp., Oryctolagus sp. (Girotti et al., 2003). An important Middle Pleisto­cene sequence is known from the Ponte Galeria Formation, in the Campagna Romana outside Rome. Here, the Brunhes Matuyama boundary is recorded with reverse­polarised lagoonal clays characterised by Helicella (reversed polarity, MIS 22) overlain by normally polarised clays with Venerupis senescens (MIS 19). Micromammalian remains from the Helicella clays at Fontingnano are indicative of cold-climatic conditions and include Preade­crotostonyx sp. and Praegalorus panonicus (Sardella et al., 2003). A succession of named faunal units have subsequently been defined for the Early and early Middle Pleistocene (Galeric Mammal Age) and late Middle Late Pleistocene (Aurelian Mammal Age) (Gliozzi et al. 1997).

4.2. Evidence from the Levant

There are relatively few well-documented fossiliferous pre-Holocene fluvial sequences in the Levant. The Mesopotamian rivers Euphrates and Tigris have readily observable terrace sequences (e.g. Tyracción, 1987; Demir et al., this volume), but there are no records of faunal assemblages in currently accessible reaches in Turkey or Syria. Syria’s second-largest river, the Orontes (Asi), also has a clear terrace record in its middle (Besançon and Sanlaville, 1993; Dodonov et al., 1993) and upper reaches (Bridgland et al., 2003b). The Upper Orontes terraces, although calcareously cemented, are devoid of fossils, but at ~50 m above the river in the Middle Orontes, 100 km NW of Hama, is a rich faunal and Palaeolithic site at Latamneh. This has produced a significant vertebrate fauna, providing the key pinning point for biostratigraphically constraining the ages of Orontes terraces (Bridgland et al., 2003b; Bridgland and Westaway, 2007; Mishra et al., this volume). The assemblage includes Mammutthus trogentherii, Stephanorhinus hemitoechus, Megaloceros verticornis and Equus cf. albibensis (Guérin and Faure, 1985; Guérin et al., 1993). It thus combines a giant deer species that are unknown in Europe after the Elsterian with a rhinoceros that first appears in Europe immediately after that glaciation, in the Holsteinian. The likely correlation with the oceanic oxygen isotope sequence is therefore probably between MIS 13 and 11.
The paucity of faunal remains in post-Holocene fluvial deposits in this region, despite widespread calcareous bedrock, is both a surprise and a disappointment. The fluvial sediments in limestone areas are widely calcited, a phenomenon that is highly characteristic of semi-arid Mediterranean areas (Candy et al., 2004, 2005). The one significant Onontes faunal locality, at Latamneh (see above) is from an area where the gravels remain uncremented, raising the possibility that faunal remains are destroyed during, or in advance of, the formation of the calcite cement.

5. Data from other regions

Thus far this review has considered data that can be compared with those from the core NW/Central European area of IGCP 449. There has also been project activity on distant continents where faunas have minimal or no overlap with that in the core area. Nonetheless, palaeontological data from the fluvial sequences in such areas can be of value for environmental reconstruction and for establishing regional biostratigraphies. Brief details of some of the most important data, entirely mammalian, are given below.

5.1. Sub-Saharan Africa

Mammalian faunas are valuable for gauging the age of the important Plio-Pleistocene hominin fossils and archaeological assemblages from East Africa, such as in the Awash and Omo Valleys in Ethiopia (Jaeger and Wesselnman, 1976; Read, 1997; Geraards et al., 2004). At the southern extremes of the African continent, in the Southern Hemisphere temperate climatic zone, the fluvial sequence of the Vaal-Orange River has been studied over a lengthy period and has yielded mammalian assemblages (Cooke, 1949; Helgren, 1977) that assist with age determination (Klein, 1983; Beaumont, 1999; see Mishra et al., this volume), although many of the fossiliferous sites are from non-fluvial contexts on the valley floor.

5.2. South America

Mammalian biostratigraphy has been applied to fluvial sediments in Uruguay, in a contribution to IGCP 449 and to the subgroup by Ubilla (2004). He described the fossiliferous beds of the Sopas Formation, which outcrop in northern Uruguay between the Uruguay and Negro rivers and have also yielded freshwater molluscs, plants and trace fossils as well as vertebrates. The mammalian assemblage includes highly exotic and extinct taxa such as the capybara Neotherium ariaspoli, the glyptodont Neoryurus rudis, and Antifer ulna and Morenelaphus brachyceres, extinct species of deer (Fig. 7). The assemblage is correlated biostratigraphically with the Lujanian Stage (Late Pleistocene Early Holocene) of the Pampean region of Argentina. Minimum radiocarbon ages (43000 years BP and 45000 years BP; Ubilla and Perea, 1999) along with luminescence dates (43.5±3.6 and 58.3±7.4 ka: Ubilla, 2004) provide corroboration of this interpretation.

The finds from the Sopas Formation have been placed in the context of a mammalian biostratigraphical scheme for the Pliocene to Recent in the Pampean region of Argentina proposed by Cione and Tonni (1999). This scheme provides a framework for regional correlation in South America including mammalian assemblage biozones. As shown in Fig. 7, it envisages three Pleistocene divisions, the Ensenadan, Bonaerian and Lujanian Stages, which are defined by the Tolypeutes pampeanus, Megatherian americanaum and Equus (Amerhippus) neogenus biozones, respectively. According to Cione and Tonni (1999) and Nabel et al. (2000), the Ensenadan spans the Late Pliocene early Middle Pleistocene, whereas the Bonaerian represents the Middle Pleistocene and the Lujanian, with which the assemblage from the Sopas Formation is correlated, is Late Pleistocene Early Holocene. Differences in the fauna from the Sopas Formation in comparison with the typical Lujanian mammal fauna of the fluvial Guerrero Member of the Luján Formation in Buenos Aires province (Prado and Alberdi, 1999; Tonni et al., 1999) were interpreted as a consequence of both temporal differences and, potentially, of distinct biogeographical and climatic phases (Ubilla, 2004). The assemblage from Uruguay indicates warm and humid conditions, whereas that from the Guerrero Member points to a colder and more arid environment. The Sopas Formation has yielded mammals indicative of diverse habitats, however. Amongst the extant species are examples that inhabit fluvial and lacustrine environments with riparian forest, open woodland, savannah and grassland. For more detailed discussion of the well developed biostratigraphical arguments, see Ubilla (2004) and references therein.

5.3. Australia

Fossils from Quaternary fluvial deposits in Australia are of fairly minor significance in a field of study that has been dominated by attention to interactions between aeolian, lacustrine and riverine environments, questions of fluctuating and, indeed, progressively increasing aridity in relation to monsoonal precipitation and a extremely successful programme of TL dating of quartz sands, underpinning the story (Kershaw and Nanson, 1993; Nanson and Price, 1998). On this southern continent, many large animals (mainly mammals, which were smaller than 'megafauna' elsewhere, but including birds) became extinct in the Late Pleistocene. They included the giant wombats Diprotodon and Zygomaturus trilobus, the large kangaroos Procotodon goliath and Simosthenurus, predatory marsupials such as Thylacoleo and the large flightless bird Genyornis newtoni. Their remains have been found in the fluvial sequences of the internally draining Lake Eyre Basin (Nanson et al., 1999) and in its associated lacustrine
and dune (e.g. Magee et al., 1995) deposits. Within the lacustrine and aeolian sequences exposed around Lake Eyre, a geochronological framework has been established using multiple methods (AAR and U/Th) to date *Genyornis* eggshell, coupled with sediment dates (OSL and TL) and $^{14}$C dates of mollusc shell and other organic material (Magee et al., 1995). *Diprotodon* and *Zygomaturus* remains have been found in exposures along Cooper's Creek, dated 180-160 ka (Nanson et al., 1999). Much of the interest in these faunas stems from their significance to the debate about megafaunal extinction and the extent to which humans and/or climate were the cause; that debate is beyond the scope of this paper, but the timing of the disappearance of these animals, which is now well established as earlier than that of megafauna elsewhere, takes on some biostratigraphical potential.
It is clear that regional biostratigraphies based (particularly) on mammalian and molluscan assemblages have a significant role to play in the dating and correlation of Pleistocene deposits. Nevertheless, important questions still remain about the wider, inter-regional validity of biostratigraphical signatures in the light of possible diachronocity of faunal changes across adjacent areas and beyond. These problems are well known to workers in the field and might be that Britain enjoyed a peculiar position, in terms of molluscan faunas noted throughout much of the Pleistocene. Nevertheless, even if the earlier, MIS 12, breach is preferred, there was clearly sufficient time for mammals and molluscs to immigrate before sea-level rise isolated Britain from the continent. A new area under exploration by Dr. Sanjeev Gupta (Imperial College, London) is the palaeogeography of the English Channel, where submarine mapping of this area has revealed the remnants of a huge valley, up to 11 km wide and 50 m deep, running SW from the Straits of Dover. It is the creation of this formidable barrier, as opposed to sea-level rise, which may have forced westward-moving fauna and hominins to trek as far north as the present-day Netherlands in order to be able to circumvent it (Stringer, 2006).

Critical to this debate, naturally, is the question over the timing of the creation of the Straits of Dover with both MIS 12 (Gibbard, 1995) and MIS 6 (Ashton and Lewis, 2002) ages advanced. Nevertheless, even if the earlier, MIS 12, breach is preferred, there was clearly sufficient time for mammals and molluscs to immigrate before sea-level rise isolated Britain from the continent. A new area under exploration by Dr. Sanjeev Gupta (Imperial College, London) is the palaeogeography of the English Channel, where submarine mapping of this area has revealed the remnants of a huge valley, up to 11 km wide and 50 m deep, running SW from the Straits of Dover. It is the creation of this formidable barrier, as opposed to sea-level rise, which may have forced westward-moving fauna and hominins to trek as far north as the present-day Netherlands in order to be able to circumvent it (Stringer, 2006).

It is important to remember that biostratigraphy can provide only a relative means of dating deposits in the absence of geochronological support. One of the most pressing needs, therefore, in the understanding of past fluvial systems is the development of absolute dating techniques that extend back beyond the current limits of radiocarbon. This issue has recently come to the fore during the recent debate over the age of the Happisburgh Till in Britain, with reference to the Mimomys-Arvicola transition. At least four older temperate episodes with the ancestral species, Mimomys savini, have been identified in East Anglia, and two younger episodes characterized by the descendant Arvicola terrestris cantiana (Preece and Parfitt, 2000; Stuart and Lister, 2001). On this basis, it is clear that the Cromerian stratotype at West Runton, along with other M. savini localities such as Pakefield, Sugworth and Little Oakley, must be older than the Arvicola group, although the exact timing of the transition cannot be more precisely established. All that can be said is that by the latest part of the Cromerian Complex (MIS 13), Arvicola is present. However, if the lithostratigraphical arguments are to be believed, the descendant form is present alongside its ancestor for a substantial period (possibly more than one glacial interglacial cycle) prior to MIS 16. Whether this can be accommodated biologically is open to question. A particular problem in this respect is the fact that the Bytham River sequence, to which the date of the Happisburgh glaciation is linked (based on evidence of clasts of till, erratics and heavy minerals from the third youngest terrace) (Lee et al. 2004), has little in the way of independent age control, from either biological or geochronological sources.

The potential of uranium-series dating has been clearly demonstrated with respect to the dating of the tufa deposits in the Somme valley in northern France (see Antoine et al., this volume), since in western and central Europe, tufa formation appears to occur only under fully interglacial conditions. Most recently, high-precision MC ICP MS dating of tufa from the British site of Marsworth has revealed the presence of two distinct phases of tufa formation, during MIS 7e and 7c (Candy and Schreve, 2007). By linking the dating evidence
with that from mammalian biostratigraphy, it has been possible to test previously proposed models of mammalian turnover and environmental change during MIS 7 (Schreve, 2001b) and to date the succession of faunal groupings to isotopic substages.

Whether Quaternary biostratigraphical data can be integrated over even wider areas is clearly doubtful, given that biota will be restricted to climatic zones and faunal provinces. However, areas of overlap between faunal provinces might permit useful progress in this direction and fluvial sequences once again promise to provide valuable templates for such research. These transitional zones are highly significant for understanding patterns of migration and dispersal on a large scale, as well as the rivers themselves providing a corridor for movement into new territories. It is notable that the limited project data from Asia includes a Levantine assemblage that includes species familiar in NW Europe, and which might represent a refugial population. Improved dating of fossiliferous fluvial deposits in transitional zones such as the Levant can potentially shed light on pinpointing the timing of immigration of new taxa, as well as contributing to the identification of glacial refugia, with both southern and eastern European areas (Iberia, Italy, Balkans, Turkey) (Hewitt, 2000), now supplemented by the suggestion of cryptic northern refugia in areas of sheltered topography (Stewart and Lister, 2001). The faunas from southern Africa, South America and especially Australia are, inevitably, highly exotic in contrast to the familiar Eurasian taxa that contribute to knowledge of the core are of the project. The biostratigraphy of the last two regions, in particular, is currently known only at very coarse resolution when compared with Europe. Nevertheless, it is anticipated that future developments in the recovery and dating of new assemblages from fluvial sequences will substantially improve biostratigraphical schemes, thereby allowing inter-hemispheric comparison of environmental impacts on the fauna.

7. Conclusions

The following conclusions may be suggested, based upon the outcomes of the Biostratigraphy theme of IGCP 449:

Where preservation is good, faunal assemblages can provide an excellent means of relative dating of fluvial sequences and for potential correlation with the marine oxygen isotope record. Where this can be calibrated with radiometric dates and other geochronological techniques, their value is further enhanced. In Europe, the system of Neogene Mammal Units in standard use for the Miocene and Pliocene has been updated to include magnetostratigraphical evidence, thereby calibrating the boundaries of individual MN zones and facilitating long-distance correlations. For the Pleistocene, in addition to radiocarbon dating for the Late Pleistocene, Uranium-series dating on associated flowstone or tufaceous material currently provides one of the best geochronological supports for dating the faunal succession.

Mammalian and molluscan biostratigraphies have proved particularly valuable in their application to Pleistocene fluvial sequences across Eurasia and extending into North Africa, wherever populations overlap exists. In more distant regions outside Eurasia, stand-alone schemes can be erected, such as in South America. Ultimately, the development of complementary biostratigraphical models for different continents may provide a means of comparing faunal responses to environmental change on a hemispheric scale.

The Pleistocene mammalian biostratigraphy of western and central Europe is relatively well known, with the traditional biochronological successions based on small and large mammals (Mammal Ages) now supplemented by regional systems of Faunal Units (Italy), Mammal Assemblage-Zones (UK) and Quaternary Mammal zones (western Europe). In conjunction with high-precision dating, it is now possible to attribute individual faunal groupings to the Oxygen Isotope Substage level, thereby allowing faunal change to be assessed with a high degree of resolution.

Local and regional schemes must be erected first, with close attention paid to the taphonomy of the assemblages and taxonomic and identification criteria, before correlation is attempted over a wider scale. This will permit patterns of distributional shifts, body size change, population movement and extinction to be compared, as well as potentially identifying the timing and loci of species origination. This will also allow any inter-regional diachronity in evolutionary trends to be recognised.

The microtine rodent record, in particular the water vole lineage, offers one of the most powerful tools for ordering and correlation of Pleistocene deposits. Establishing the stratigraphical range of *Mimomys pusillus* and the timing of the transition between *Mimomys savini* and *Arvicola terrestris cantiana* (= *mosbachensis*) in different regions are priority questions.

Molluscan biostratigraphical analysis has also permitted the recognition of individual interglacials within the Middle and Late Pleistocene. Extinction and presence/absence data are most significant here, in particular the appearance of diagnostic elements such as *Lyrodiscus* and *Theodoxus serratiniformis* in association with MIS 11 and the widespread absence of *Corbicula fluminalis* from MIS 5e.

References


