Position of the Steinheim interglacial sequence within the marine oxygen isotope record based on mammal biostratigraphy

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ABSTRACT

Since the recovery, in 1933, of a *Homo heidelbergensis* skull from the interglacial *Antiquus*-Schotter in sediments of the River Murr, the site of Steinheim (Germany) has been regarded as an iconic hominin locality for the Middle Pleistocene of Europe. Based on the morphology of the specimen, stratigraphical considerations and the characteristics of the associated faunal assemblage, the Steinheim skull has generally been assigned to the Holsteinian Interglacial. Over the last decades, developments in the knowledge of the complexity of the Pleistocene glacial–interglacial cycles have rendered this date increasingly problematic.

Analyses of caballoid horse remains from the site using log ratio diagrams and principal components analysis reveal striking morphological differences with German horse remains from sites attributed to the Holsteinian or marine isotope stages (MIS) 11 and 9. The morphology of the Steinheim horses is similar to that of horse specimens from MIS 9 sites in southern France, and to a lesser degree there are similarities with MIS 9 horses from northern France and British MIS 11 and 9 horse fossils. This indicates that during the Anglian/Elsterian glacial, European horse populations were split into two lineages. During MIS 11, the western lineage is present in the British Isles and at Steinheim, whereas the German Holsteinian samples belong to the eastern lineage. A date in different substages of MIS 11 is a further possible source of morphological variation between these assemblages. By MIS 9, a degree of admixture had taken place between the eastern and western lineages.

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1. Introduction

Since the end of the 19th century, gravel deposits of the River Murr near the village of Steinheim (Fig. 1) in Germany have been commercially exploited in various pits. The up to 17 m thick Pleistocene sediments produced many fossil remains, including a nearly complete skeleton of *Mammuthus primigenius* in 1910 (Berckhemer, 1933a). Most of the material was collected by quarry workers (Wahl et al., 2009). Systematic collecting from 1923 onwards by the Württemberger Naturaliensammlung Stuttgart (now Staatliches Museum für Naturkunde Stuttgart) led to the recovery of a hominin skull in 1933 (Berckhemer, 1933b; Weinert, 1936). The cranium is attributed to an advanced *Homo heidelbergensis* or stage 2 'pre-Neandertal' (Dean et al., 1998; Street et al., 2006). The Steinheim site has generally been correlated with the German Holsteinian Interglacial (e.g. Schreve and Bridgland, 2002). However, recent advances in the understanding of Pleistocene stratigraphy increasingly render this correlation problematic. A detailed study of late Middle Pleistocene horse remains from the Steinheim hominin site is presented here, shedding new light on the dating of the site and its correlation with other late Middle Pleistocene sites.

2. The Steinheim site

The Steinheim area is slowly subsiding, and sedimentation of the River Murr is thought to have been relatively continuous during the late Middle Pleistocene (Adam, 1954). Fluvial sedimentation was cyclical, with incision taking place during cold stages, followed by deposition of cold-stage fluvial sediments and soil development during the subsequent warm period. The earlier parts of the cold stages are represented by loessic cover sediments (Bloos, 1977).

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Fig. 1. Location of the sites mentioned in the text.

The Steinheim fossil locality was found on the fluvial terrace below the terrace containing a shell fauna typical of the Cromerian Complex (Schreve and Bridgland, 2002). Three fluviatile sequences are deposited on the Keuper bedrock in lateral succession (Bloos, 1977, Fig. 2).

The Middle Pleistocene fauna was recovered from the lowermost fluvial complex (Schotterkomplex I, see Table 1). Initially, two faunal assemblages were recognised, an older, temperate *Antiquus-Trogontherii*-fauna and a younger, cold-climate *Primigenius*-fauna (e.g. Soergel, 1911; Berckhemer, 1933a). Based on preservation characteristics and oral information from quarry workers and collectors, Adam (1954) hypothesised that the fossil assemblage represented four fossiliferous layers within this sedimentary complex. He named these assemblages after the evolutionary characteristics of the elephant remains contained in them. The lowermost layers, the Ältere Mammut-Schotter or *Trogontherii*-Schotter, were only temporarily accessible and produced a small temperate fauna. The second faunal assemblage also represents temperate conditions, which indicates that Schotterkomplex I comprises at least two fluvial cycles. This fauna is referred to as the Waldelefanten-Schotter or *Antiquus*-Schotter fauna, since it is the only assemblage from Steinheim containing *Palaeoloxodon antiquus* (Adam, 1954). The hominin skull is thought to originate in this layer (Berckhemer, 1933b). Cold-adapted species make their entrance in the upper part of the *Antiquus*-Schotter, although some interglacial species continue to be present in the lower part of the next fossiliferous layer, the Haupt-Mammut-Schotter or *Trogontherii-primigenius*-Schotter. This layer is thought to have

been situated in cold-climate gravels (Adam, 1988). Finally, a small cold-adapted faunal assemblage was recovered from the Jüngere Mammut-Schotter or *Primigenius*-Schotter. Small mammal remains have not been recovered from the site.

Table 1
Composition of the large mammal faunas recovered from the site of Steinheim (after Adam, 1954, pp. 133–139).

Fossiliferous layer	Family	Species
Jüngere Mammut-Schotter (*Primigenius*-Schotter)	Proboscidea	*Mammuthus primigenius*
	Perissodactyla	*Coelodonta antiquitatis*
Haupt-Mammut-Schotter (*Trogontherii-primigenius*-Schotter)	Carnivora	*Canis lupus*
		Ursus spelaeus
		Panthera cf. *leo*
	Proboscidea	*Mammuthus trogontherii*
		Mammuthus primigenius
	Perissodactyla	*Equus steinheimensis*
		Coelodonta antiquitatis
	Artiodactyla	*Cervus elaphus*
		Megaloceros giganteus
		Bison priscus
Waldelefanten-Schotter (*Antiquus*-Schotter)	Rodentia	*Castor fiber*
	Carnivora	*Ursus spelaeus*
		Meles meles
		Panthera cf. *leo*
	Proboscidea	*Palaeoloxodon antiquus*
	Perissodactyla	*Dicerorhinus kirchbergensis*
		Dicerorhinus hemitoechus
	Artiodactyla	*Sus scrofa*
		Cervus elaphus
		Capreolus capreolus
		Megaloceros giganteus
		Bos primigenius
		Bison priscus
		Bison cf. *schoetensacki*
		Bubalus murrensis
Ältere Mammut-Schotter (*Trogontherii*-Schotter)	Proboscidea	*Mammuthus* cf. *trogontherii*
	Perissodactyla	*Equus* cf. *mosbachensis*
		Dicerorhinus kirchbergensis
	Artiodactyla	*Cervus elaphus*
		Bison priscus

3. Correlation with other sites in Germany

Since numerical dating methods produce inconclusive results for this part of the Pleistocene (Millard, 2008) and pollen and sedimentary evidence is of limited value in comparisons over large geographical areas (De Beaulieu et al., 2001), much emphasis has been placed on the use of faunal assemblages in correlating late Middle Pleistocene sites. Based on faunal composition, the Steinheim skull layer has been grouped with sites such as Bilzingsleben II, Heppenloch, Stuttgart-Bad Cannstatt (Bunker), Kärlich H and Schöningen II, which are all attributed to the Holsteinian Complex (Adam, 1975; Wagner, 1995; Urban, 1995a; Mania, 1997; Mania and Thieme, 2007). However, over the last decades it has become apparent that many sites previously attributed to the Holsteinian Interglacial (sensu stricto) in actuality represent several temperate
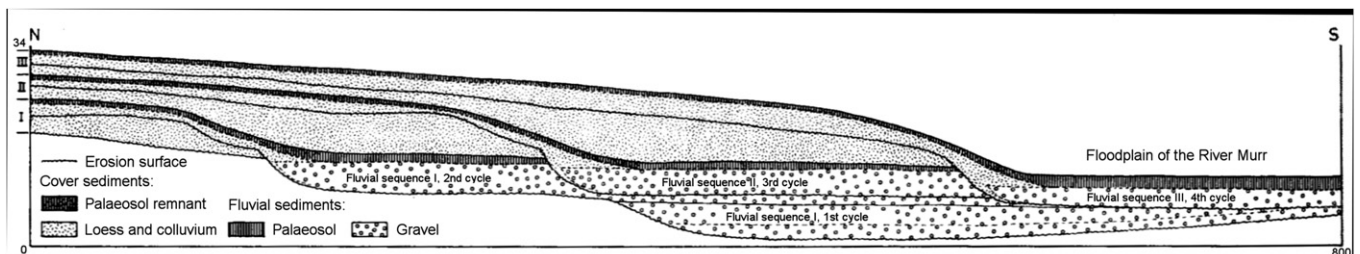

Fig. 2. Terrace stratigraphy of the River Murr near the Steinheim site (modified after Bloos, 1977).

stages (Urban, 1995b; Schreve and Bridgland, 2002; Gibbard and Van Kolfschoten, 2005). It is therefore increasingly problematic to see these sites as a homogeneous group dating from the same temperate phase. Because the Steinheim Antiquus-fauna has been correlated with these supposedly Holsteinian sites, any changes in the numerical and relative dates ascribed to these sites will affect the dating of the Steinheim skull.

The numerical dating evidence for Kärlich H is inconclusive and contested, with TL and Ar—Ar dates ranging between ± 200 and 400 ka (e.g. Zöller et al., 1988; Van den Bogaard and van den Bogaard, 1989; Bittmann, 1992; Gaudzinski et al., 1996). The Holsteinian date for the Heppenloch site was based on the fact that the Heppenloch faunal assemblage differs from those of Eemian and Cromerian age and shows similarities to the faunas from Swanscombe and Steinheim (Adam, 1975). The Bunker site at Stuttgart-Bad Cannstatt is dated to the Holsteinian based on its position in the terrace stratigraphy of the River Neckar, although numerical dates obtained with U-series, TL and ESR methods vary between 150 and 500 ka (Grün et al., 1982; Wagner, 1984).

The Bilzingsleben II site is located on a terrace of the River Wipper. The terrace is part of a terrace complex which also includes the Bilzingsleben I terrace (Bridgland et al., 2004). The Bilzingsleben I deposits consist of late-glacial and interglacial fluviatile sediments and travertine containing temperate molluscan and mammalian faunas, capped by a loess layer (Mania, 1989, 1993). Sediments on the terrace above the Bilzingsleben I/II terrace are correlated with the Elsterian ground moraine found further north. This is thought to represent the first of the two Elsterian ice advances that occurred in eastern Germany, correlated with marine oxygen isotope stage (MIS) 14 (Cepek, 1986; Mania, 1997), leading to a possible date for the Bilzingsleben I terrace in MIS 13 (Bridgland et al., 2004). However, Mania (1997) hypothesises the presence of another interglacial between the Elsterian terrace and Bilzingsleben I. Bilzingsleben I and II are then regarded as representing two substages of the Holsteinian and are both correlated with MIS 11 (e.g. Mania, 1989). Skull fragments and teeth attributed to at least three adult and one juvenile Homo erectus were recovered from the Bilzingsleben II site (Mania and Mania, 2005). The Bilzingsleben skull is generally considered to differ morphologically from the Steinheim and Swanscombe (see Section 4.2) skulls, and is often grouped with remains from sites predating the Holsteinian, such as Mauer, Petralona and Vértesszöllös, although the specific affinities remain unresolved (Arsuaga et al., 1997; Dean et al., 1998; Street et al., 2006).

At the Schöningen site, three laterally overlapping temperate channel fills (Schöningen I—III) have been documented between Elsterian and Saalian (Drenthe phase) ground moraines (Mania, 2007). The site is famous for the wooden spears and other wooden implements found at the Schöningen 13II-4 locality (Thieme, 1997, 1999). The Schöningen I temperate sediments have been correlated with the Holsteinian Interglacial based on vegetation succession (Urban, 1995a, 2007a; but see Urban et al., 2011). The unique characteristics of the Schöningen II and III pollen assemblages led to the formulation of the Reinsdorf and Schöningen Interglacials respectively (Urban, 1995b), the latter of which is thought to be a local equivalent of the Dömnitz Interglacial (Thieme, 1999). The sediments of Schöningen I have been dated with TL at the Schöningen 13I site to ca. 350 ka, while the Schöningen II sediments at the Schöningen 13II site were dated to 250—350 ka (Richter, 2007). If the Holsteinian is the continental counterpart of MIS 11, a correlation which is highly debated in itself (Geyh and Müller, 2005; Urban et al., 2011; but see Desprat et al., 2005; Ashton et al., 2008; Koutsodendris et al., 2010), and the Drenthe ground moraine represents MIS 6 (Gibbard et al., 2005), the Schöningen II and III channel fills could correlate with MIS 9 and 7 respectively (Urban, 1995a). Some researchers argue, based on similarities in the

sedimentary sequences and the evolutionary signature of the small mammal fauna, that the Bilzingsleben II and Schöningen II sites are contemporaneous (Mania, 1995, 1997, 2007; Van Kolfschoten, 2007). Others emphasise differences between the pollen and mollusc assemblages (Jechorek, 2000; Mania and Mai, 2001; Urban, 2007b), large and small mammal faunas (Musil, 2002; Huyghebaert, 2003; Van Asperen, 2004) and stone artefacts from the sites (Jöris and Baales, 2003), although these may be partly due to the fact that the Bilzingsleben II site represents the interglacial maximum, while the main Schöningen II assemblage (spear site, Schöningen 13II-4) dates from the late interglacial phase or an interstadial following the main interglacial (Urban, 2007b). However, horse remains from the Schöningen 12 site, deposited during the interglacial optimum, are similar in size and shape to the Schöningen 13II-4 specimens (Van Asperen, 2004).

The composition of the faunas from these sites clearly indicates a date in the first half of the late Middle Pleistocene (i.e. between the Elsterian and the Drenthe phase of the Saalian). However, at present it is unclear what the temporal order of these sites is, and how they relate to the marine oxygen isotope record. There are many similarities in the composition of the faunal assemblages from these sites. It is therefore necessary to undertake more detailed biostratigraphic analyses to understand the temporal order of these assemblages.

4. Material and methods

The caballoid horse lineage is one of the few large mammal lineages that show clear evolutionary and ecomorphological changes over the late Middle Pleistocene (e.g. Eisenmann, 1991; Van Asperen, 2010, 2011). Horses survived in Central Europe during both glacials and interglacials. The skeletal elements which are most likely to undergo morphological changes due to climatic or evolutionary pressures, the dentition and lower limb bones, are often well-preserved. Some faunal assemblages from sites dating from this period contain large numbers of horse remains. They therefore provide a potential avenue to explore the affinities of the Steinheim faunal assemblage.

4.1. The Steinheim horses

The exact provenance of most of the Steinheim fossil horse remains is unknown. The majority of the fossil assemblage as a whole is thought to originate in the temperate-climate Antiquus-Schotter and the cooler-climate Trogontherii-primigenius-Schotter. The earliest study of horse remains from Steinheim identified Equus sp. in the older (Antiquus) faunas, and Equus cf. germanicus in the younger (Trogontherii-primigenius) faunas (Soergel, 1911). The site produced the type specimens of Equus steinheimensis Von Reichenau 1915. This species was defined based mainly on dental characteristics of a limited number of remains present in the older faunas (Von Reichenau, 1915). Adam (1954) recognised two caballoid species from the site: Equus cf. mosbachensis in the Trogontherii-Schotter and E. steinheimensis in the Trogontherii-primigenius-Schotter.

In a morphological and metrical study, Forstén (1999) questioned these descriptions. She noted that Soergel and Von Reichenau only had small samples at their disposal, and that the dental characteristics they identified as differentiating E. steinheimensis from other known caballoids do not reflect the dental traits of the sample as a whole. She furthermore argued that the homogeneity of the horse material suggests the horse assemblage represents a short period of deposition, although she did not rule out the possibility of evolutionary stasis. She regarded E. steinheimensis as a separate species based on its small size.

Forstén's conclusion that the Steinheim material is homogeneous was confirmed in a study of the variability of modern and Pleistocene caballoid samples (Van Asperen, in press). This implies that the material either represents a discrete horizon within the Steinheim deposits or reflects rapid sedimentation for the entire sedimentary sequence. Alternatively, a longer period of morphological stasis occurred within the caballoid horse lineage. The latter suggestion seems unlikely in the light of the high frequency and amplitude of climatic fluctuations during the Pleistocene (Petit et al., 1999), which led to size and shape variation in caballoid horses (Van Asperen, 2010). The occurrence of discrete assemblages of warm-adapted and cold-adapted species, as well as progressive evolution displayed by the elephant samples (Wahl et al., 2009), seems to rule out rapid deposition of the entire faunal assemblage. The fresh state of the horse remains, with no clear signs of rolling or abrasion, indicates that these fossils have not been extensively reworked from a discrete deposit elsewhere. It is therefore most likely that the Steinheim horse sample originated in a limited part of the sedimentary sequence.

4.2. Material

Previous research has shown that horse dental elements do not vary sufficiently to distinguish between sites dating from various late Middle Pleistocene glacial and interglacial phases (Van Asperen, 2010). Bones of the upper limbs are not preserved in sufficient numbers to provide reliable information about horse size and shape. In contrast, metapodials and phalanges underwent evolutionary and ecomorphological changes over this period, and as a consequence their morphology differs between regions and climatic phases (Van Asperen, 2010). This study therefore focuses on the often well-preserved lower limb elements.

Besides the sample from Steinheim, horse remains from the German sites Bilzingsleben II, Heppenloch, Stuttgart-Bad Cannstatt (Bunker), Kärlich H and Schöningen II were analysed. Furthermore, horse remains from British sites attributed to the Hoxnian/MIS 11 and MIS 9 were examined. The Hoxnian sites (Hoxne, Swanscombe and Clacton-on-Sea) are correlated with MIS 11 based on their stratigraphic position immediately above sediments deposited during the Anglian glaciation, when a major remodelling of the British river systems took place (Bridgland et al., 1985; Gladfelter et al., 1993; Bridgland, 1994; Schreve, 2000, 2004; Ashton et al., 2008). Because of the severity of the Anglian and the pronounced warm character of the Hoxnian, these periods are usually correlated with MIS 12 and MIS 11, respectively (Shackleton, 1987; various authors in Bowen, 1999; Gibbard et al., 2005). The Hoxnian is commonly correlated with the continental Holsteinian. At the Hoxne site, thermoluminescence dating on burnt flints from Stratum C yielded dates of 210 ± 20 to 300 ka (Gladfelter et al., 1993, p. 210). Teeth from the same layer were dated by U-series/ESR to $404 +33/-42$ ka and 437 ± 38 ka (Gladfelter et al., 1993, p. 211; Grün and Schwarcz, 2000, p. 1153). Several analyses revealed morphological similarities between the Steinheim skull and the rather less complete Swanscombe skull (Weiner and Campbell, 1964; Arsuaga et al., 1997; Dean et al., 1998). Thermoluminescence dating of

a sediment sample of the Upper Loam at Swanscombe produced a date of 202 ± 15.2 ka, whilst Lower Loam sediment samples were dated to 228 ± 23.3 ka (Bridgland et al., 1985, p. 32). U-series dating on bone from the Clacton Channel deposits produced a date of $245+35/-25$ ka (Szabo and Collins, 1975, p. 681).

The Grays Thurrock site is located on the second of the Lower Thames river terraces, correlated with MIS 9 (Bridgland and Schreve, 2001). The MIS 9 sites at Wolvercote and Pershore have been correlated with the Grays Thurrock Thames terrace primarily on the basis of terrace stratigraphy (Ashton, 2001). The British terrace stratigraphy has been corroborated by faunal data and amino acid dating (Schreve, 1997; Penkman et al., 2011).

Several faunal assemblages from French sites have been correlated with MIS 9. The stratigraphic sequence in a loess pit near Achenheim, in the northeast of France, has been studied intensely and functions as a type sequence for the late Middle and Late Pleistocene of the loess regions of northwest Europe (Heim et al., 1982). Unit 20a, a soil complex with several humic horizons, is correlated with MIS 9 (Heim et al., 1982; Vollbrecht, 1997). Loess samples from this layer were dated with thermoluminescence to 244 ± 31 and 265 ± 35 ka (Buraczynski and Butrym, 1984, p. 203). Horse data for this unit from Cramer (2002) were included in the analyses.

In southern France, levels 5 and 6 in the Orgnac 3 cave were dated with U-series and ESR to 309 ± 34, $288-45/+82$ and $374-94/+165$ ka, and attributed to MIS 9 (Moncel et al., 2005, p. 1284). Level 2 was correlated with early MIS 8 based on an ESR/U-series date of 298 ± 55 ka for volcanic minerals related to the Mont-Dore-Sancy volcano (Moncel et al., 2005, p. 1284). The fauna from Lunel-Viel caves 1 and 4 is thought to date from the Mindel-Riss Interglacial, since it contains several species of early Pleistocene affinity, such as *Ursus deningeri*, *Dicerorhinus etruscus* and *Bison* cf. *schoetensacki* (Croitor et al., 2008). Evidence of the use of the Levallois technique on artefacts recovered from both southern French sites (Bonifay, 1968) provides an argument in favour of a younger date, with one of the earliest appearances of this technique in the middle of the MIS 9 deposits at Orgnac 3 (Moncel et al., 2011). Horse remains from both sites are investigated here (Orgnac 3: Boulbes, unpublished data; Lunel-Viel: Eisenmann, unpublished data). The horse remains from Orgnac 3 have been identified as *Equus* cf. *steinheimensis* based on similarities with the Steinheim, Achenheim Units 20d-20a and Lunel-Viel horses (Forsten and Moigne, 1998).

4.3. Methods

Only leg bones with fully fused epiphyses were used in this study. Horses display very little sexual dimorphism or adult age variation, and sex and age can therefore be assumed not to be an important factor in the analyses (Van Asperen, in press). Measurements (Table 2) on the metapodials were taken according to Eisenmann (1979) and measurements on the first phalanges follow Dive and Eisenmann (1991). All measurements were taken with vernier callipers and recorded to one tenth of a millimetre. Summary statistics for the different samples can be found in the supplementary information (Tables S1–S4).

Table 2
Measurements taken on the metapodials (Eisenmann, 1979) and first phalanges (Dive and Eisenmann, 1991).

Measurement	Metacarpal	Metatarsal	First phalanx
V1	Greatest length	Greatest length	Greatest length
V3	Breadth of the diaphysis	Breadth of the diaphysis	Breadth of the diaphysis
V4	Depth of the diaphysis	Depth of the diaphysis	Breadth of the proximal epiphysis
V5	Breadth of the proximal epiphysis	Breadth of the proximal epiphysis	Depth of the proximal epiphysis
V6	Depth of the proximal epiphysis	Depth of the proximal epiphysis	Supra-articular distal breadth

Table 2 (continued)

Measurement	Metacarpal	Metatarsal	First phalanx
V7	Breadth of the articulation with the magnum	Breadth of the articulation with the ectocuneiform	Greatest length of the trigonum phalangis
V8	Breadth of the anterior articulation with the hamatum	Diameter of the articulation with the cuboid	–
V10	Supra-articular distal breadth	Supra-articular distal breadth	Medial supra-tuberosital length
V11	Breadth of the distal epiphysis	Breadth of the distal epiphysis	–
V12	Greatest depth of the distal epiphysis	Greatest depth of the distal epiphysis	Medial infra-tuberosital length
V13	Smallest depth of the medial condyle	Smallest depth of the medial condyle	–
V14	Greatest depth of the medial condyle	Greatest depth of the medial condyle	Breadth of the distal epiphysis

Overall differences in size and shape between the samples included in the study were analysed using log ratio diagrams, in which the logs of measurements are plotted against a standard (Simpson, 1941). In log ratio diagrams, the vertical distance between the different measurements expresses their relative sizes (the ratios of their dimensions), while the vertical distance between values for the same measurement is indicative of absolute size differences (Simpson et al., 1960). Differences between samples in the ratios of the measurements give information about shape differences between the various samples. The standard for comparison, the reference line of the diagram, is formed by a sample of *Equus hemionus*, as this is the species most commonly used as a standard for log ratio diagrams of horse remains (e.g. Dive and Eisenmann, 1991; Eisenmann, 1979, 1991).

To further investigate patterns of variation, the measurements were log-transformed to ensure normality and homogeneity of variances, and analysed by principal components analysis (PCA) of the correlation matrix. PCA performs a linear transformation of the original variables into new variables that are linear combinations of the old variables, where each new variable successively accounts for as much of the total variance in the original variables as possible (Davis, 2002). The PCAs were performed with the Predictive Analytics SoftWare Statistics (PASW) package version 18.0. In the analyses on metapodial variables, V8 was excluded because of the high degree of measurement error in this variable. Results will be presented in detail for the metacarpals and summarised for the metatarsal, anterior and posterior first phalanx samples.

The log ratio technique and PCA both have advantages and disadvantages. The log ratio technique gives a good overview of the variation per measurement, but it is difficult to judge how important these variations are. Principal components analysis gives a better indication of the most important sources of variation, though it can be difficult to interpret the results because the technique combines the variation on several measurements into an overall factor loading. These techniques are therefore here used in conjunction, so that results from the use of one technique validate and strengthen those of the other technique.

5. Results

5.1. Metapodials

From the log ratio diagram of the metacarpals (Fig. 3) it is apparent that the Steinheim material is most similar in size and shape to the southern French samples. The Orgnac MIS 9 and MIS 8 specimens are here pooled for better legibility, as apart from a slightly larger size the MIS 8 specimen are identical in morphology to the MIS 9 specimens. The Achenheim specimens are larger, with a relatively deep proximal epiphysis (V6) and broad proximal articular surface (V7), characteristics which also occur in the British MIS 11 samples. The German material is clearly larger. The Holsteinian samples are relatively robust (V3, 5—8) but distally (V10—14) similar to the other samples, whilst the Schöningen 13II-4 specimens are characterised by a shallow proximal epiphysis and

high relief on the distal epiphysis (V12—14). The British MIS 9 samples stand out because of their small size, but are similar in shape to the Schöningen specimens. V10 is large relative to V11 in the Holsteinian, Schöningen 13II-4 and British MIS 9 samples. The Steinheim fossils are intermediate in this regard, whilst V10 is smaller relative to V11 in the British MIS 11 material and the samples from the French sites. This trait has evolutionary significance as V10 decreases relative to V11 throughout the late Middle Pleistocene (Eisenmann, 1979).

In a PCA on the metacarpals ($n = 38$), the factor loadings are positive for all variables on PC1, indicating variation in size (Table 3). The single German Holsteinian specimen, from Bilzingsleben II, is much larger than all other specimens, and the Schöningen 13II-4 specimens are also relatively large (Fig. 4a). The Steinheim material clusters with the remaining samples which are of smaller absolute size. PC2, with positive loadings on length (V1) and proximal depth (V6) and negative loadings on diaphyseal breadth (V3) and depth (V4), indicates the relatively robust diaphyses and short lengths of the southern French specimens. This serves to distinguish these specimens from the British material and the Steinheim and Schöningen 13II-4 samples. The deep proximal epiphyses and broad
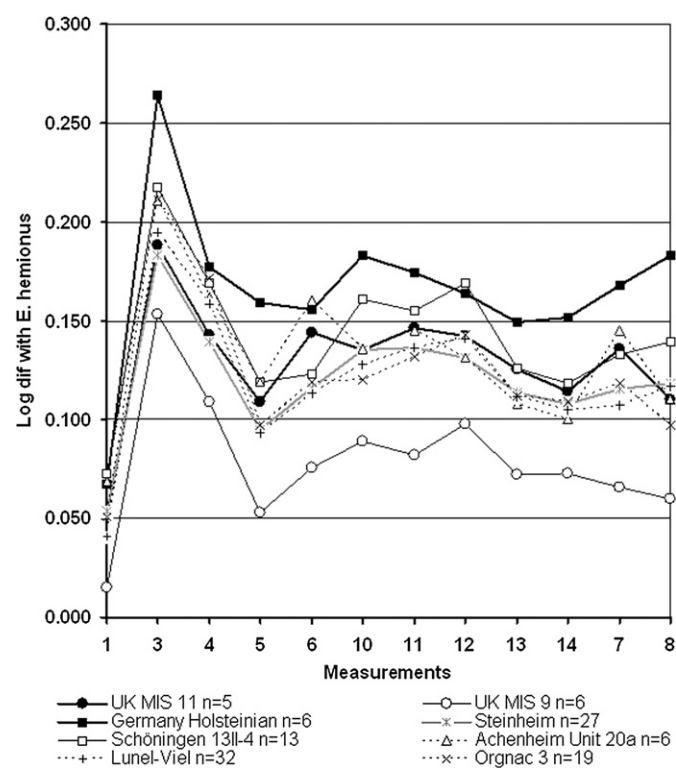

Fig. 3. Log ratio diagram comparing the mean values for the Steinheim metacarpals with those of various contemporaneous samples; reference line: *Equus hemionus* (UK MIS 11: Swanscombe, Clacton and Hoxne; UK MIS 9: Grays Thurrock and Pershore; German Holsteinian: Kärlich H, Bilzingsleben II and Heppenloch).
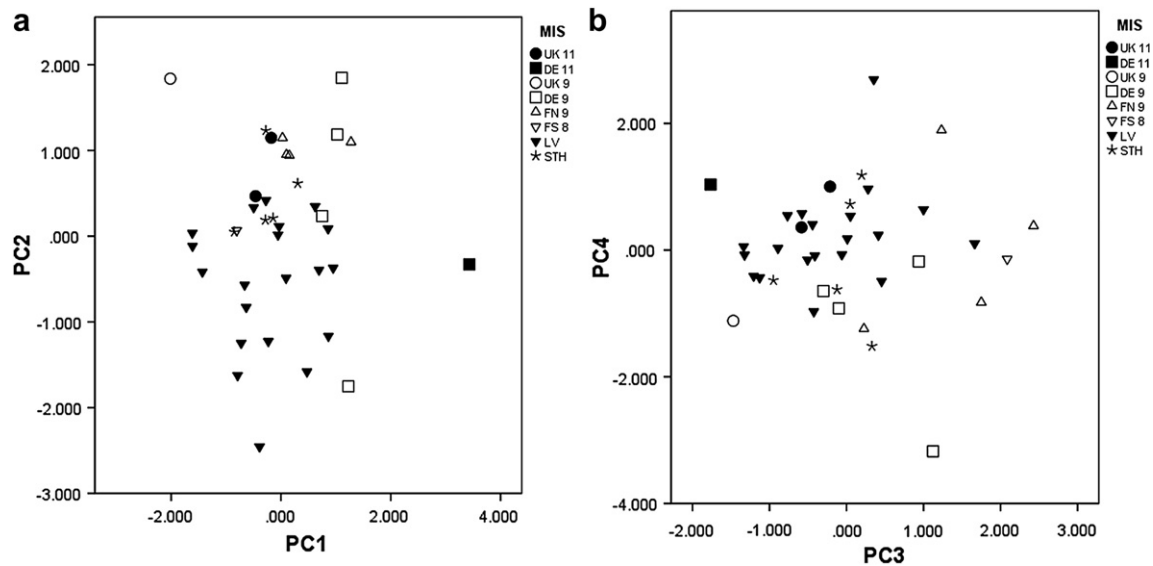
Fig. 4. Results of the principal components analysis of the metacarpals; a. PC2 plotted against PC1; b. PC4 vs. PC3 (UK11: Hoxne and Swanscombe; DE11: Bilzingsleben II; UK9: Grays Thurrock; DE9: Schöningen 12 and 13II-4; FN9: Achenheim Unit 20a; FS8: Orgnac 3; LV: Lunel-Viel; STH: Steinheim).

proximal articular surfaces of the Achenheim material are reflected in their high scores on PC3, while the shallow proximal epiphyses of the Schöningen sample leads to relatively low scores on PC4 (Fig. 4b).

Table 3
Factor loadings for the variables obtained in principal components analysis of the metacarpals and eigenvalues of each eigenvector with associated percentages of variance explained (%var).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
V1	0.624	0.598	0.195	−0.400	0.182	0.119	0.067	−0.003	0.013	0.030
V3	0.842	−0.408	0.126	−0.020	0.136	−0.004	0.188	−0.225	−0.015	−0.041
V4	0.765	−0.367	0.293	0.038	0.387	0.056	−0.127	0.151	0.026	0.007
V5	0.926	−0.038	0.101	−0.129	−0.173	−0.176	−0.130	0.049	−0.130	−0.006
V6	0.694	0.307	0.348	0.534	−0.084	0.020	0.072	0.014	0.010	0.070
V10	0.915	−0.162	−0.025	−0.104	−0.202	0.158	−0.116	−0.121	−0.040	0.152
V11	0.899	−0.120	−0.073	−0.034	−0.277	0.225	0.012	0.090	0.145	−0.107
V12	0.888	−0.127	−0.286	−0.075	−0.026	−0.112	0.222	0.188	−0.031	0.082
V13	0.802	0.156	−0.476	0.117	0.190	−0.115	−0.101	−0.082	0.145	0.049
V14	0.864	0.218	−0.312	0.180	0.115	0.121	−0.029	−0.012	−0.174	−0.121
V7	0.902	0.142	0.230	−0.077	−0.112	−0.249	−0.031	−0.045	0.073	−0.092
Eigenvalue	7.661	0.903	0.735	0.533	0.419	0.227	0.153	0.143	0.098	0.075
%var	69.7	8.2	6.7	4.9	3.8	2.1	1.4	1.3	0.9	0.7

The log ratio diagram and PCA on the metatarsals follow similar trends as in the metacarpals. The Steinheim metatarsals are most similar to the French material, though in this case they are more similar to the Achenheim remains than to the more robust (V3, 4) southern French samples (Fig. S1). The British MIS 11 specimens have very slender diaphyses, though proximally and distally they are more robust than the Steinheim sample. The British MIS 9 specimens are of small size and are especially slender distally and relatively broad proximally. The latter features also characterise the Schöningen sample, which shows similar shapes though absolute size is larger and comparable to the large-sized, robust German MIS 11 material. In the relative size of V10−V11, the Steinheim samples is similar to the British MIS 9 remains and the French samples, whilst V10 is larger relative to V11 in the Holsteinian, Schöningen 13II-4 and British MIS 11 samples.

These patterns are reflected in the PCA ($n = 47$), where PC1 and PC2 together provide a good separation between large-sized and/or distally robust specimens (DE11, UK11, DE9) from the smaller, more slender samples (STH, LV, UK9; Table S5, Fig. S2a). As in the metacarpals, PC2 separates the southern French specimens with more robust diaphyses from the other samples, including the Steinheim material. The Steinheim specimens are distinguished somewhat from the other samples by PC4 and PC6 (Fig. S2b), reflecting a relatively shallow proximal epiphysis (V6).

5.2. First phalanges

The main morphological differences between the anterior first phalanx samples occur in the depth of the proximal epiphysis (V5) and in the ratio between V10 and V12 (Fig. S3). The latter feature has evolutionary significance; over the Middle and Late Pleistocene, an increase in the supra-tuberosital length (V10) relative to the infra-tuberosital length (V12) has been documented (Dive and Eisenmann, 1991). The functional significance of this is thought to lay in a change in the way in which the weight of the animal is divided over the anterior and posterior limbs (Dive and Eisenmann, 1991). Both in size and in morphology, the Steinheim specimens are most similar to the French samples. The British and German samples are evolutionarily less advanced. The MIS 11 samples are less advanced than the MIS 9 samples, and for both periods, the

German specimens are more advanced than the British specimens. The German material is furthermore characterised by relatively deep proximal epiphyses.

The PCA ($n = 31$) confirms these observations, with V5, 10 and 12 being the most important factors in the principal components (Table S6). Differences in absolute size are expressed on PC1, while PC2 reflects evolutionary differences between the samples (Fig. S4a). The Steinheim sample is differentiated from the other samples mainly on PC2, and a comparison with the log ratio diagram reveals this is mainly due to different proportions between V5 and V10. This is related to the overall slenderness of the Steinheim specimens, which is also expressed in its loadings on PC3 and PC4 (Fig. S4b). The low loading of the Lunel-Viel sample on PC3 is caused by a relatively large supra-articular distal breadth (V6) in these specimens. PC4 documents the deep proximal epiphyses of the German MIS 9 specimens.

Morphological patterns in the posterior first phalanges are similar to those observed in the anterior first phalanges (Fig. S5). Size differences are somewhat larger due to the larger size of the German specimens, which are also relatively robust. In the PCA ($n = 35$), this is visible in the high loadings for these samples on PC1 and the low loadings of the Schöningen specimens on PC5 (Table S7, Figs. S6a and b). The Steinheim sample is most similar to the British MIS 9 sample, but evolutionarily less advanced than the German and British MIS 9 material, which is reflected in the loadings on PC2 and PC3.

6. Discussion

The log ratio diagrams and principal components analyses reveal similar patterns of variation. Overall, the Steinheim horse specimens are relatively small and slender. Small body size and slender limbs are correlated with forested, humid temperate environments in equids (Van Asperen, 2010), both as an adaptation to thermoregulatory demands (James, 1970) and to facilitate movement and predator avoidance in densely vegetated habitats (Bro-Jørgensen, 2008). Although horses can survive on a low-quality diet, they need a high and relatively diverse food intake (Salter and Hudson, 1980; Duncan et al., 1990) and small body size may reflect a limited availability of food or a high proportion of less-digestible browse in the diet (Janis, 1988). Based on these ecomorphological adaptations, it seems more likely that the Steinheim horse sample originated from the temperate *Antiquus*-Schotter than from the *Trogontherii-primigenius*-Schotter, deposited in a cooler climate. Pollen and faunal evidence indicates that both the MIS 11 and MIS 9 interglacials were characterised by temperate, humid, forested environments in western Europe (e.g. De Beaulieu and Reille, 1995; Von Koenigswald and Heinrich, 1999; Bridgland and Schreve, 2001; Nitychoruk et al., 2005) and a date for the Steinheim site in either of these interglacials is therefore feasible.

Importantly, for all skeletal elements examined here, a clear contrast between the Steinheim specimens and those from other German sites dated to the Holsteinian or MIS 9 is observed. The Steinheim remains are most similar in the log ratio diagrams to the southern French MIS 9/8 and British MIS 11 and 9 samples, with which they also cluster in the PCAs. In the metatarsals and first phalanges, similarities occur with the Achenheim Unit 20a sample. These morphological patterns suggest the presence of a connection between the southern French horse populations and the populations of northwest Europe through migration or gene flow, whilst a degree of isolation seems to have occurred between western and eastern populations. The European horse lineage could have split into an eastern and a western population by being forced to retreat to refugia located in southern and eastern Europe during the severe

glacial phases of the Anglian/Elsterian, which in much of northern Europe is the southernmost-reaching glacial (Clark et al., 2004; Ehlers et al., 2004). Horse populations migrated to northwest Europe from these refugia during the oceanic MIS 11 and/or 9 interglacials.

This still leaves open the question of whether the Steinheim sample dates from MIS 11 or MIS 9. The British MIS 11 samples morphologically belong to the western lineage, and their small size, a trait even more strongly characteristic of the British MIS 9 horses, may be due to the more temperate, humid conditions prevailing in the British Isles compared to the continent (Van Asperen, 2010). They are clearly differentiated from the German Holsteinian samples, although sample size is small for both geographical areas. This suggests that animals belonging to the western lineage were present in northwest Europe by MIS 11, although it is not clear where the source area of these populations was located since at present no horse remains dating from MIS 11 are known from southern and central France. The Holsteinian samples from the sites Kärlich H, Heppenloch and Stuttgart-Bad Cannstatt (Bunker) can be interpreted as the westernmost representatives of the eastern European lineage. A correlation with MIS 11 seems most likely for these sites based on stratigraphy, faunal composition, similarities with the Bilzingsleben horse remains and differences with the MIS 9 specimens from Schöningen and Achenheim Unit 20a. Although the Bilzingsleben, Kärlich and Schöningen sites are located at some distance from the Steinheim site, the same cannot be said of the Heppenloch and Stuttgart-Bad Cannstatt (Bunker) sites, which are located at a distance of 50 and 16 km respectively from the Steinheim site. If these sites were contemporaneous with the Steinheim site, it is highly unlikely that genetic isolation could have differentiated the Steinheim horses from the Heppenloch and Cannstatt populations, since the topography of the area is not conducive to the development or maintenance of reproductive isolation in a highly mobile species with dispersing subadults (Boyd and Keiper, 2005). The presence of horses affiliated to the eastern lineage in these sites speaks against an MIS 11 date for Steinheim. However, the MIS 11 interglacial was characterised by a long temperate peak followed by a series of three colder phases interspersed with warmer phases with boreal or temperate forests in northwest Europe (Bassinot et al., 1994; Desprat et al., 2005; Nitychoruk et al., 2005; Urban, 2007b). It is therefore possible that Steinheim dates from a different temperate substage of MIS 11 than the other Holsteinian sites. There are indications that in the British Isles, faunas were fully temperate during at least the first two temperate substages of MIS 11 (Schreve, 2004; Ashton et al., 2008). The lack of a detailed chronostratigraphic framework for northwest continental Europe currently prevents similar conclusions to be drawn for this area, but temperate MIS 11 sites could date from different substages.

The close similarities between the Steinheim horse remains and the Orgnac 3 and Lunel-Viel samples could imply that the Steinheim assemblage dates from MIS 9 to early MIS 8. The MIS 9 to early MIS 8 date for these French sites is based on numerical dating at the Orgnac 3 site and the presence of the Levallois technique (Bonifay, 1968; Moncel et al., 2005, 2011). However, since no sites are known in the region dating from MIS 11, and the Lunel-Viel fauna contains several species of early Pleistocene affinity, the attribution of these sites to MIS 9/8 remains to some degree preliminary. Based on their ecomorphological characteristics, it seems unlikely that the Steinheim specimens date from the early glacial of MIS 8. It is not clear how soon changing environmental conditions would lead to observable morphological changes, but it is likely that significant cooling would rapidly cause morphological adaptation as ecomorphological traits

are plastic to some degree. However, the number of specimens in the Orgnac 3 sample dating from MIS 8 is very limited and unlikely to influence the results presented here. It should be noted that while the French specimens are morphologically most similar to the Steinheim fossils of all samples included here, they also differ in some respects, most notably in the higher robusticity of the metapodial diaphyses.

Although they are much smaller in absolute size, the British MIS 9 remains share morphological traits with the Schöningen and Achenheim MIS 9 specimens. Further similarities between the Achenheim Unit 20a specimens and those from Schöningen 13II-4 could indicate that by MIS 9, the western and eastern populations were undergoing a degree of admixture. The absence of such traits, as well as the size and shape differences documented between the Steinheim and Achenheim Unit 20a assemblages, could point to an MIS 11 date for the Steinheim assemblage.

7. Conclusions

To date, numerical dating and the use of pollen and sedimentary evidence have not produced reliable correlations with high resolution for many archaeological and palaeontological sites dating from the late Middle Pleistocene. Biostratigraphy has long been used as an alternative approach. The famous Steinheim skull site has been correlated with a number of German Holsteinian sites based on faunal composition, but these correlations, as well as correlations between the other German Holsteinian sites, now appear problematic in the light of increased knowledge of the complexity of the Pleistocene glacial–interglacial cycles. Because caballoid horses underwent both evolutionary and ecomorphological changes over the course of the late Middle Pleistocene, a study of their abundant remains sheds light on these dating problems.

The Steinheim horse remains are most similar to southern French MIS 9 samples, and to a lesser degree to northern French MIS 9 specimens and British MIS 11 and 9 samples. Broader morphological patterns in northwest European horse remains dating from the first half of the late Middle Pleistocene seem to indicate that the extreme glacial conditions of the Anglian/Elsterian (MIS 12) forced horse populations into southern and eastern refugia, leading to a split in the lineage. During MIS 11, this led to the presence of populations with different morphological signatures in northwest Europe, where the British samples represent the western lineage and the eastern lineage is present in the German samples. Most likely, the Steinheim horse sample, and by implication the Steinheim skull, which was found in layers dating from the same temperate stage as the horse remains, dates from a different substage of MIS 11 than the German Holsteinian samples, as the close proximity of some of these sites to the Steinheim site would not have allowed for a prolonged period of reproductive isolation. A date in MIS 9 cannot currently be excluded, but seems unlikely in the light of evidence of admixture of the western and eastern lineages in the British and northern French MIS 9 horses.

Although this study has focused on a single site, the implications of the trends documented here give a glimpse of the way in which Quaternary animal populations were connected geographically and temporally. Often long-term trends are reasonably well-known on a regional scale or for particular animal species, and knowledge has advanced to a level where it is now possible to integrate such data across the European continent. With regards to faunal assemblages, a crucial link that needs to be forged is that between northwest and central European samples on the one hand, and material from glacial refugium areas further south and east on the other.

Renewed investigation of assemblages that were collected over the last centuries, coupled with research on new sites and faunal material, has the potential to refine and adjust ideas regarding the age and context of famous specimens such as the Steinheim skull. Many well-known, rich fossil assemblages have been published in detail during the previous century, but are currently understudied. If examined in the light of current knowledge and new paradigms, they will prove to be a rich source of new information. Detailed study of other species or animal groups, such as proboscidean, rhinocerotid and bovid lineages, on a supra-regional scale could resolve the present uncertainties regarding the dating of the Steinheim skull. Given the increasing number of large, well-documented and carefully excavated fossil assemblages, it is of paramount importance to study such specimens against the wider background of continent-wide distributions and movements of animals and hominin groups.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2012.10.045.

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