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Metric analysis of ungulate mammals in the early Middle Pleistocene of Britain, in relation to taxonomy and biostratigraphy
I: Rhinocerotidae and Bovidae

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ABSTRACT

Rhinoceroses (*Stephanorhinus*) and large bovids (*Bison*, *Bos*) from the early Middle Pleistocene of Britain are analysed with regard to their taxonomy, biometric variation, and possible biochronological significance. The localities considered are West Runton (type Cromerian), Pakefield, Westbury-sub-Mendip, and Boxgrove. The samples include important, previously undescribed material. Among the rhinos, in addition to the common *Stephanorhinus hundsheimensis*, upper dentitions from Pakefield and West Runton provide hints of undescribed taxa with affinity to, but distinct from, *S. etruscus* and *S. hundsheimensis*. At Boxgrove, a further rhino cf. *S. megarhinus* occurs, corroborating the chronological extension of this 'Pliocene' species into the Middle Pleistocene. A small bison referable to *B. schoetensacki* occurs at all sites, but in the Westbury Yellow Breccia (upper interglacial level) it is accompanied by a larger bison which may be *B. priscus*. Dental material from Pakefield provides evidence of additional, smaller bovid species, with features recalling *Leptobos* and *Bubalus*, but their identity is unclear; there is also larger material probably representing *Bos*, which if confirmed would be the oldest record of aurochs in the British Isles.

1. Introduction

The European early Middle Pleistocene is an intensively-studied interval now recognised to comprise four temperate marine isotope stages between the Brunhes/Matuyama boundary and the Anglian/Elsterian glaciation. The relative ordering of key terrestrial localities, and their relation to MIS stages and substages remains, however, a matter of contention (Preece et al., 2009). Several British localities yielding rich mammal faunas have been central to this debate, with small mammals, in particular, providing valuable biostratigraphic markers (Preece and Parfitt, 2000, 2008; Stuart and Lister, 2001; Maul and Parfitt, in press). Large mammals also have potential to contribute to this debate, but the identification of British material, and its variation across sites, is in need of re-study. In the present investigation, a morphological and biometric analysis of rhinoceroses and large bovids from key British localities is undertaken, allowing an assessment of taxonomy, species occurrences, and morphometric variation. Other ungulate mammals (horses, pigs and deer) are considered by Lister et al. (in press).

Four key localities form the core of the present study, between them yielding the richest stratified mammal faunas from the early Middle Pleistocene of Britain. Two are sites of the Cromer Forest-bed Formation: Pakefield (Suffolk) (Stuart and Lister, 2001; Parfitt et al., 2005), and the type Cromerian West Runton Freshwater Bed (Norfolk) (Stuart, 1975, 1996). The others are the Calcareous Member of the cave infill at Westbury-sub-Mendip (Somerset) (Bishop, 1982; Andrews et al., 1999), and the hominid locality of Boxgrove (West Sussex) (Roberts and Parfitt, 1999) (Fig. 1). The smaller assemblages from Little Oakley (Essex) (Lister et al., 1990) and Sugworth (Oxfordshire) (Stuart, 1980) lack sufficient rhinoceros and large bovid material for biometric study. Conversely, abundant material is available from other sites of the Cromer Forest-bed Formation, but the collections are stratigraphically mixed, including Early Pleistocene material (Azzaroli, 1953; Lister, 1993a, 1996, 1998). New, careful excavations at some of these localities have begun to yield stratified large-mammal material

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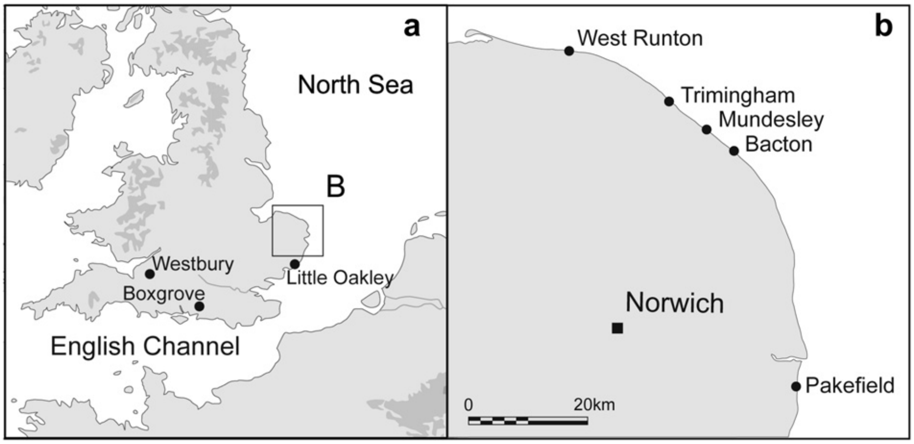

Fig. 1. British early Middle Pleistocene localities discussed in this paper.

(Sidestrand: Preece et al., 2009; Happisburgh: Parfitt et al., 2010) and offer promise for the future.

Two key biostratigraphic questions relate to the chronological ordering of the British localities. First, do large mammal taxonomy and morphometrics support the *Mimomys*/*Arvicola* zonation suggested by small mammals (Preece and Parfitt, 2000, 2008)? Second, can the large mammals shed light on the relative ages of localities within each zone, i.e. West Runton vs. Pakefield in the *Mimomys* zone, and Westbury vs. Boxgrove in the younger *Arvicola* zone? Metric data from some key sites in continental Europe have been incorporated in the graphs for comparative purposes. However, only data and descriptions from the literature are included here. A full integration of rhinoceros and large bovid data between British and continental localities is highly desirable, but would represent a substantial further research effort which is beyond the scope of this paper.

The taxa considered in the present contribution are represented at all four localities, but in rather different proportions. Rhinoceroses are most frequent at Pakefield, followed by West Runton and Boxgrove at roughly equal abundance, while at Westbury-sub-Mendip only the upper dentitions of two individuals are recorded. Bovids are most frequent at Westbury, with the vast majority of upper teeth in the entire study, and roughly 50% of the lower teeth and postcranials. Among the other localities, Pakefield and West Runton are very close in the number of measurable upper teeth and postcranials, but the former is much richer in lower teeth. Boxgrove bovids are represented by only two upper teeth and seven postcranials (three of which are associated).

2. Materials and methods

The authors studied a significant amount of unpublished material, and re-studied previously published specimens. All measurements of British specimens are original, while those from continental Europe are taken from the literature, and are included only where it is clear that measurement methods are similar to those used here. The material from Westbury and Boxgrove is stored at the Natural History Museum, London (NHM). The material from West Runton and Pakefield is distributed in the following collections: NHM, including the major collections of A.C. Savin from West Runton and Pakefield, and R. Mutch from Pakefield; The Castle Museum, Norwich (NCM), including new material from the the 1990–1995 elephant excavation at West Runton; The Cromer Museum (CRM); The British Geological Survey, Keyworth (BGS), The Yorkshire Museum, York (YM), The University Museum of Zoology, Cambridge (UMZC), and the private collection of I. Cruickshanks (Suffolk).

Rhinoceroses and large bovids are described on a site-by-site basis rather than under taxonomic headings, because in many cases the taxa are uncertain and form the subject of study. The characters used for identification, and the measurement methods, are described separately for the two Families. Dental measurements have been plotted on bivariate graphs, with continental samples marked as ranges for comparison. The relatively small number of postcranial elements prevented a size comparison between sites on an element-by-element basis. Instead, ratio diagrams as described by Lister (1993b) were used, standardising the different skeletal elements onto a common scale and combining them in a single graph. The standard of comparison was a single associated skeleton of the living species most closely related to the species considered. Measurements of the standard skeletons are provided in Supplementary information. Raw measurement data of the British specimens plotted in the graphs are also tabulated in Supplementary information, plus additional original measurements for some bones. All measurements are in millimetres.

The measurements used for the ratio diagrams were chosen, for each bony element, primarily to maximise sample sizes. For long bones, however, this was restricted to bone diameters (widths or depths) as these more accurately reflect body mass than do lengths (Scott, 1990). Where both proximal and distal epiphyses of a single long bone were measureable, only one was plotted, to avoid pseudoreplication. The likelihood of isolated bones belonging to the same individual is low, particularly for the fluviatile deposits of West Runton and Pakefield. Such associations cannot be completely ruled out, however, and there are two cases of associated limb bones from Boxgrove (a bovid humerus, radius and metacarpal, and a rhinoceros astragalus and calcaneum). In this case each element has been included in the ratio diagram.

Ideally, in a ratio diagram, different measurements of the same bone, or of different bones of the same individual, should show the same percentage deviation with respect to a chosen standard (i.e. individuals may be larger or smaller but are of the same shape). However, if the standard skeleton differed significantly in bone proportions from the remainder of the sample (either because it belonged to a different species or because it happened to be an aberrant individual), this assumption would be violated. Any differences observed in the percentage ratios of two measures from a single individual provide a benchmark below which a difference cannot be considered significant, in terms of overall body size, when comparing across individuals.

As an example, variation was examined between measurements on *Bison* astragali, comparing lateral depth (Dl) and medial depth (Dm) against a modern skeleton of *B. bison*. In ten specimens (all from Westbury), Dm in all cases gives a lower percentage than Dl. This could be because *Bison* at Westbury is a different species from *B. bison* and has a slightly differently-shaped astragalus. Three *Bison* metatarsals from Pakefield, on the other hand, differed in their proximal to distal ratios by +5.8%, −8.5% and −14.2%. This might reflect mere individual variation in the fossil population, although a difference as high as 20% (14.2 + 5.8) suggests shape variation that could indicate the presence of two species.

Despite its limitations, the ratio diagram remains a valuable method for comparing size variability in limited fossil samples.

The taxonomic identification of specimens or samples varies in its degree of certainty. The term 'sp. aff.' (=species affinis) is used when a specimen has a similarity or close relation with a known species, but is distinct and of unknown specific attribution. For example, '*Stephanorhinus* aff. *etruscus/hundheimensis*' means a species of *Stephanorhinus* which is similar to, or has affinity with, *S. etruscus* and *S. hundsheimensis,* but shows features suggesting an undescribed taxon that requires further taxonomic study. The term "aff." is thus different from 'cf.' (=confer), which is used to indicate that the specimen resembles the named species very closely, but has certain minor features not found on the type specimens. The term is also used where specimens are too incomplete to show all diagnostic features.

3. Localities

Among British localities with rich mammal faunas attributed to the early Middle Pleistocene, those were selected which have been excavated or re-excavated in recent years, and where the available fossil assemblage can be attributed with confidence to an identifiable horizon. This precaution ensures that the mammal faunas at each locality come from a single depositional unit (or, in the case of Westbury, from a series of separately identifiable units), and reduces the possibility of differences in age within each sample.

3.1. West Runton, Norfolk

West Runton has long been known for the rich fossil fauna found in organic detritus muds at the foot of the cliff. This unit, placed within the 'Upper Freshwater Bed' by Reid (1882), is part of the Cromer Forest-bed Formation and was chosen as stratotype of the Cromerian stage by West (1980), who named it the West Runton Freshwater Bed (WRFB). The WRFB rests on marls of the preceding Beestonian stage and is covered by marine sediments and then by Anglian glacial deposits. Pollen studies (West, 1980) placed the WRFB in the early temperate substages of an interglacial vegetational succession (pollen zones Cr I-II). Palaeomagnetic studies (Gibbard et al., in press) interpret its normal magnetization as early Bruhnes chron. The molluscan fauna includes species extinct after the Anglian/Elsterian glaciation and is similar to that of Pakefield (Group 1 of Preece and Parfitt, 2000). The mammal fauna also includes species indicating a pre-Elsterian age, and the evolutionary level of the water-voles (genus *Mimomys* – with rooted teeth) suggests for both WRFB and Pakefield the first half of the Cromerian Complex. However, the WRFB vertebrate fauna differs in some key elements from that of Pakefield, suggesting that they are not contemporaneous (Preece and Parfitt, 2000; Stuart and Lister, 2001). The normal magnetization of the WRFB points to an age not earlier than late MIS 19; Preece and Parfitt (2008), based on the fauna, suggest either MIS 17 or early MIS 15.

Early collections of large mammals (principally by A.C. Savin) have the dark, shiny preservation characteristic of the WRFB, and are often marked as having come from the 'Upper Freshwater Bed'. More recent *in* situ finds include specimens found during controlled excavations in 1990–1995 at the West Runton Mammoth site (Stuart and Lister, in press).

3.2. Pakefield, Suffolk

Pakefield, together with nearby Kessingland, forms part of the southern exposure of the Cromer Forest-bed Formation. Blake (1877, 1890) first described the stratigraphic sequence at Pakefield, composed of ferruginous sands and gravels at the base, overlain by the "Rootlet bed", a compact grey-brown silt with carbonate nodules, later interpreted as an overbank deposit of the ancient Bytham River (Lee et al., 2008). West (1980) described a sequence at Pakefield very similar to that observed by Blake. The gravels and sands under the beach were named bed c by West, and the "Rootlet Bed" bed b [=Lee et al.'s. (2008) Lithofacies B]. A channel cut into the Rootlet Bed is filled with dark, laminated muds and silts (West's Beds g and h). Like that of West Runton, West (1980) interpreted the sequence as the early temperate substages of an interglacial. This sequence is overlain by glacial sands and chalky tills of the Anglian cold stage.

Mammalian fossils were collected at Pakefield through the nineteenth and early twentieth century. The sections subsequently became overgrown with vegetation and have been re-exposed by coastal erosion only in the last 15 years. This has allowed renewed studies of the stratigraphic sequence and important new *in situ* finds from the Rootlet Bed, including human artefacts (Parfitt et al., 2005). The taxonomic composition of the fauna is very similar in the Rootlet Bed and underlying gravels, implying a similar age (Stuart and Lister, 2001).

The deposits at Corton (the stratotype of the Anglian stage, a little to the north of Pakefield), are very similar to those at Pakefield/Kessingland in terms of stratigraphy, pollen spectra, macroflora and mammalian fauna. Stuart and Lister (2001) suggest they are of the same age and probably represent the same floodplain deposit. Pakefield, Kessingland and Corton will hereafter be referred to in the text and figures as 'Pakefield'.

The mammalian remains from the Rootlet Bed and ferruginous gravels are usually matt grey or brown, sometimes with reddish stains and/or pitting. However, a complete horse radius [NHM M6734, Savin 1201] (see Lister et al., in press) and a bovid molar [NHM 6567] are shiny and black. Both are recorded in Savin's catalogue, the horse having been found in 'sandy clay in low near base of cliff', the bovid in 'sandy clay in low, west of village'. This suggests that they had both fallen from the cliff (cf. Lister, 1996), perhaps from the black laminated silts incised into the Rootlet Bed (Parfitt et al., 2005), which recently yielded small vertebrates. However, a different provenance, in terms of horizon or even locality, cannot be excluded.

The Mollusca (Group 1 of Preece and Parfitt, 2000), plus the water-vole *Mimomys savini*, place Pakefield in the earlier part of the Cromerian Complex, together with West Runton. The presence at Pakefield of large mammal species absent from WRFB (*Palaeoloxodon antiquus, Hippopotamus* sp. and *Praemegaceros dawkinsi*) suggested to Stuart and Lister (2001) that Pakefield could be younger than the Cromerian stratotype. However, the subsequent identification at Pakefield of the vole *Mimomys pusillus* (Parfitt et al., 2005), generally restricted to the Early Pleistocene, suggests that Pakefield may instead be older than West Runton. The normal magnetization of the Rootlet Bed points to an age not older than late MIS 19 (Lee et al., 2008); Preece and Parfitt (2008) tentatively suggest an MIS 17 age.

3.3. Westbury-sub-Mendip, Somerset

The Pleistocene cave-infill deposits at Westbury-sub-Mendip were first exposed by quarrying in the late 1960s. They comprise two Members: the Siliceous Member, of Early Pleistocene age, and the overlying Calcareous Member, of early Middle Pleistocene age, the latter yielding most of the fauna. A study of finds up to 1974 was published by Bishop (1982), and a subsequent comprehensive review, including material from later excavations, was carried out by Andrews et al. (1999). The Calcareous Member comprises breccia and conglomerates organised in 19 well-stratified horizons, all attributed to the second half of the early Middle Pleistocene. In particular, the presence of water-vole with un-rooted teeth, *Arvicola terrestris cantiana*, suggests that it post-dates the West Runton type Cromerian. Conversely, species such as the vole *Pliomys episcopalis,* shrew *Drepanosorex savini,* “cat” *Panthera gombaszoegensis*, “dog” *Xenocyon lycaonoides* and bovid *Soergelia elisabethae*, all elsewhere found only in pre-Anglian/Elsterian contexts, suggest that it pre-dates the Hoxnian/Holstenian (Bishop, 1982; Schreve et al., 1999).

The Calcareous Member at Westbury covers several climatic episodes, from the fully temperate unit 11 (Pink Breccia), the mammal fauna indicating broad-leaved deciduous woodland, to evidence of continental conditions in the overlying units 13 (Brown Breccia), 14 (Grey Silty Breccia) and 15/1 (Red Silty Breccia), with steppe-tundra elements but some evidence of wooded habitats and a cool but not severely cold climate, to a second temperate optimum in units 15/2 (Red Silty Breccia) and 15/4 with mixed deciduous woodland and climates warmer than those of Britain today. These are succeeded by sediments laid down under apparent periglacial conditions in units 15/8, 18 (Grey Breccia) and 19 (Yellow Breccia), with an increase in steppe-tundra and montane elements. Although this sequence might represent separate interglacials, Schreve et al. (1999) regard it as more likely that the temperate episodes are separate warm substages within a single interglacial, on the basis of similar mammalian faunas, and evidence for cold, but not periglacial conditions between them. They further note that the small-mammal faunas of both units 11 and 15/2 + 4 are comparable with those of unit 4c at Boxgrove, and may represent parts of the same temperate phase, the periglacial conditions of units 15/8 being correlated with the Anglian (but see below).

3.4. Boxgrove, West Sussex

The sedimentary sequence at Amey’s Eartham Pit, Boxgrove has yielded a rich handaxe industry associated with extensive palaeoenvironmental evidence. Investigations started in the late 1970s, with intensive excavations 1983–92 and 1995–96. The sedimentary sequence shows a progression from beach gravels, to sands deposited in a near-shore shallow marine environment (Slindon Sands), to laminated silts and clays deposited in a large lagoon (Slindon Silts), to a thin palaeosol horizon (Unit 4c) which marks the development of a terrestrial grassland with freshwater ponds. This interglacial sequence is overlain by slope deposits with periglacial features indicating a change to the colder climatic conditions of the Anglian stage. Unit 4c was the principal focus of the excavations and has yielded artefacts, hominin remains, and one of the richest early Middle Pleistocene vertebrate faunas in Europe (Roberts and Parfitt, 1999; Preece and Parfitt, 2000).

Like that of the Westbury Calcareous Member, the mammalian fauna of Boxgrove is placed in the second half of the Cromerian Complex. It is believed to post-date the type Cromerian due to the presence of the water-vole *Arvicola*, and to pre-date the Hoxnian based on the presence of the shrew *Sorex savini*, vole *Pliomys episcopalis,* rhino *Stephanorhinus hundsheimensis* and giant deer *Praemegaceros dawkinsi* (Roberts and Parfitt, 1999). However, the presence at Boxgrove of *Microtus gregalis*, a descendant of *M. gregaloides* recorded at Westbury, suggests that Boxgrove may post-date the Westbury sequence (Preece and Parfitt, 2000). The fauna from the terrestrial deposits is of interglacial character, but it suggests a climate cooler and probably more continental than that of the present day (Parfitt, 1998).

4. Rhinoceroses (Rhinocerotidae)

4.1. Introduction and methods

Three rhinoceros species have been identified in the European early Middle Pleistocene: *Stephanorhinus hundsheimensis* (Toula, 1902)*, S. kirchbergensis* (Jäger, 1939) and *S. hemitoechus* (Falconer, 1868), all assigned to the genus *Stephanorhinus* Kretzoi (1942) by Fortelius et al. (1993). Of these species, only the first has been recorded with certainty in the British early Middle Pleistocene (“Cromerian Complex”), and does not persist through the Anglian/Elsterian glaciation (Parfitt, 1999). On the contrary, *S. kirchbergensis* and *S. hemitoechus*, which are first recorded in the early Middle Pleistocene of Mosbach, Germany (Koenigswald and Tobien, 1987, *fide* Fortelius et al., 1993), appeared in England after the Anglian glaciation (Parfitt, 1999).

European Pleistocene rhinos of the Early and early Middle Pleistocene were formerly all referred to *S. etruscus* (Falconer, 1868); hence Stuart (1982) and Bishop (1982) respectively attributed the rhinoceros from West Runton and Westbury to this species. However, Cromerian Complex rhinos are now generally allocated to S. *hundsheimensis*, *S. etruscus* being confined to the Late Pliocene and Early Pleistocene (Fortelius et al., 1993; Lacombat, 2006, 2007). Parfitt (1998) tentatively proposed an additional rhinoceros species, *Stephanorhinus* sp. A, for material from Boxgrove, together with the more common *S. hundsheimensis*.

Following the pioneering works by Owen (1846), Dawkins (1867, 1868) and Falconer (1868), British Pleistocene rhinoceroses have not been analysed in detail. Studies on Western European rhinoceroses have led to taxonomic confusion and many synonymies have arisen. Lacombat’s (2005, 2006) data are restricted to Mediterranean Europe and the Massif Central (France), wheareas Guérin (1980) and Fortelius et al. (1993) extend to all of Western Europe, England included. However, none of the British specimens was described or identified, although some British localities yielding rhinoceros remains were quoted as part of the samples on which non-metric and metric characters were scored.

Lacombat (2005) agreed with Fortelius et al.’s (1993) recognition of two evolutionary grades of *S. hundsheimensis*, a smaller Early Pleistocene form (comparable in size to *S. etruscus*) and a larger early Middle Pleistocene form, but warned (Lacombat, 2005: 142) that “La transposition de ces stades évolutifs au nord de l’Europe est impossible. Les rhinocéros pléistocènes septentrionaux, de taille plus importante, nécessitent une étude particulière”.

Guérin (1980), Fortelius et al. (1993) and Lacombat (2006) conclude that the dental morphology of the different species of Pleistocene *Stephanorhinus* is extremely similar, *S. kirchbergensis* being the only distinctive species in its larger size and some features of its teeth. Among the other three species there is a wide overlap of tooth size, necessitating qualitative morphological data to discriminate among them. Therefore, both metrical data for the whole sample (teeth and postcranials), and commonly-used morphological characters for the upper teeth were scored. These characters, codified by Guérin (1980) and refined by Lacombat (2006), are (Fig. 2): the presence/absence, position, inclination and continuity of the cingula; the presence/absence and number of internal folds (crochet, crista and antecrochet); the open or closed mediofossette; the angle between the crochet and the metacone; the presence/absence and development of a protocone constriction; and the development of a paracone fold. Beyond these characters, other features of upper teeth seem to be variable in the British sample, and have been scored: lingual outline of proto- and hypocone; width and shape of the lingual valley. The dental terminology used in this work is an English translation of the French one introduced by Guérin (1980) (Fig. 2).

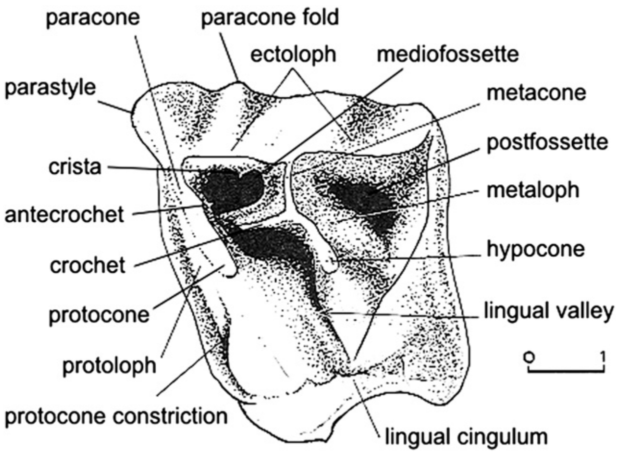

Fig. 2. Nomenclature of rhinoceros upper cheek teeth: left P^4 in occlusal view, modified from Guérin (1980,Fig. 5B).

Among the localities considered, Pakefield is the richest in rhinoceros remains with at least 50 measurable dental remains (from complete dentitions to isolated teeth) and 9 utilizable postcranials. Boxgrove has respectively 9 and 8, West Runton 14 and 8. Westbury has measurable dental remains of only two individuals (a third, represented by three upper premolars, quoted by Bishop (1982) as curated at Bristol City Museum no. 124/1969, has not been seen in this study).

Following Fortelius et al. (1993), tooth lengths and widths (BL, buccal length; MB, mesial breadth; DB, distal breadth; LL, lingual length) were measured at the base of the crown to minimise the influence of wear. In rhinoceroses, wear can result in the loss of mesial and distal cingula and of the enamel layers, affecting even crown base dimensions. BL and MB have been plotted in scatter graphs (Figs. 3 and 4), resulting in broad scatters with little distinction among groups. This could be due to the difficulty of correctly assigning isolated premolars to P3 or P4, and molars to M1 or M2 (Fortelius et al., 1993). However, even when the graphs are re-plotted using only teeth in jaws, or teeth unequivocally associated with others by matching wear facets between them, the distribution is rather irregular. This could at least partly be due to the wide variation in tooth length due to wear. Even within the same individual (hence at an equal wear stage), there is often a notable difference in the length and breadth measurements of the same tooth from the two sides (joined by a line in Figs. 3 and 4).

In addition, sample sizes are small, so it is difficult to assess if observed patterns are meaningful or are due to sample bias. To help overcome this problem, the material was compared with the published metrical ranges of *S. hundsheimensis* from the Continent (from Fortelius et al., 1993 and Lacombat, 2006; dental data by Guérin, 1980 are not comparable because of different measuring technique) (Figs. 3 and 4).

Morphologically, the majority of the rhino teeth in the British early Middle Pleistocene samples conform to the features described by Lacombat (2006) for *S. hundsheimensis*, with the following minor differences:

a) the protocone constriction is always present on the molars (rather than rarely);
b) the paracone fold of the premolars is sometimes strong, rather than thin and slightly prominent;
c) the crochet is sometimes multiple on the premolars rather than always single or double.

However, there are some important exceptions, which will be discussed below.

Postcrania are represented by a much smaller number of remains, preventing any meaningful morphometric comparison except by the use of a ratio diagram (Fig. 5). The standard used was an associated modern black rhinoceros (*Diceros bicornis*) skeleton of unknown sex from Ethiopia, stored at NHM as 1876.2.15.5. The measurements are taken following Mazza (1988). In the ratio diagram for each bony element, the measure representing a highest number of specimens, i.e. mainly distal and some proximal diameters, was chosen.

Postcranial dimensions were compared to Fortelius et al.'s (1993) *S. hundsheimensis* sample which, however, is small (from 2 to 13 of each element), so the comparison is useful only as a rough indication of relative size.

4.2. *Boxgrove*

Rhino teeth from Boxgrove are generally in the small to medium size range of the overall British sample (Figs. 3 and 4), and are of *S. hundsheimensis* morphology, including an associated right and left P^2–M^2 [NHM M82500-10]. By contrast, five plotted postcrania are large, all in the upper half of the ratio diagram (Fig. 5), and often above the range of Fortelius et al.'s (1993) small sample of *S. hundsheimensis*.

One dental specimen, NHM M82482-97, is rather small and, because of its peculiar morphology, is unlikely to belong to *S. hundsheimensis*. It was provisionally named *Stephanorhinus* sp. A by Parfitt (1998). The specimen (Fig. 6) consists of the right complete tooth row (M^1 is fragmentary) and the left roughly complete premolars plus fragments of M^1 and M^3. Apart from the above-listed characters "a–c", which are all represented in this specimen in contrast to the *S. hundsheimensis* sample of Lacombat (2006), it differs in the following features from specimen NHM M82500-10 from Boxgrove and from most of the other British early Middle Pleistocene specimens:

d) protocone of P^2 isolated from ectoloph due to complete lack of the lamina usually joining them;
e) strong protocone constriction on P^3–P^4;
f) low crown and lingual cingulum of premolars;
g) protocones of M^1 and M^2 swollen at their bases and tapering toward the occlusal surface, giving a narrower wear facet and larger medial valley;
h) lingual walls of molar hypocone concave, contributing, with the protocone, to wide lingual valley. M^1 hypocone also bulges at its base;

Of these features, "d and "e" have not been observed in any other British early Middle Pleistocene specimen. However, contrary to Lacombat (2006), Guérin (1980) suggests that the protocone can be isolated in the P^2 of *S. hundsheimensis* (=Guérin's *Dicerorhinus etruscus brachycephalus*), *S. kirchbergensis* (=Guérin's *D. mercki*) and *S. hemitoechus*. Both "e" and "c", among Pleistocene *Stephanorhinus*, are thought to be exclusive to *S. kirchbergensis* (Lacombat, 2006); however, the latter is present in another specimen from Boxgrove (NHM M82534), in M6636 from Trimingham, and in a palate from Pakefield (M18705), all referable on other morphological features to *S. hundsheimensis*. Feature "f" is present only in two specimens from Trimingham (M6636 and M19449). Features "b" plus "g–h" are variably expressed in British early Middle Pleistocene specimens, ranging from the extreme in the Boxgrove specimen (to which M6636 and M19449 from Trimingham are quite close, though they lack P^2 so "d" is unknown), to a more moderate

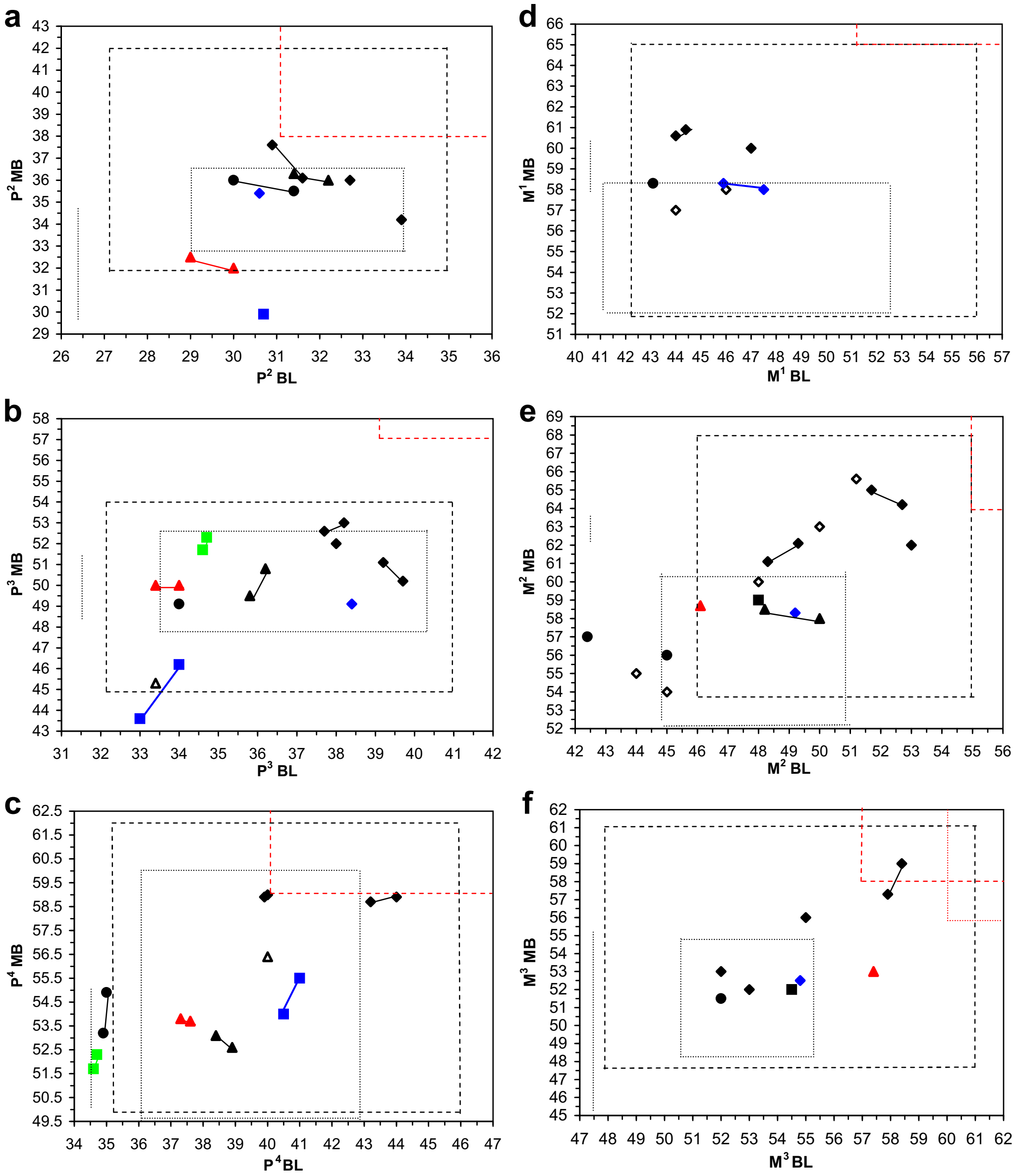

Fig. 3. Biometric comparison of rhinoceros upper cheek teeth. (a) P^2, (b) P^3, (c) P^4, (d) M^1, (e) M^2, (f) M^3. Symbols: ◆ & ◇, Pakefield, *Stephanorhinus hundsheimensis*; ◆, Pakefield, *Stephanorhinus* sp. B aff. *S. etruscus/hundsheimensis*; ■, West Runton, *S. hundsheimensis*; ■, West Runton, *Stephanorhinus* sp. B aff. *S. etruscus/hundsheimensis*; ■, West Runton, *Stephanorhinus* sp. A aff. *S. etruscus/hundsheimensis*; ●, Westbury, *S. hundsheimensis*; ▲ and △, Boxgrove, *S. hundsheimensis*; ▲, Boxgrove, *S.* cf. *megarhinus*. Closed symbols: specimen in tooth row (tooth positions unambiguous); open symbols: isolated teeth (of unsure position in the tooth row). Specimens joined by a line are left and right of the same individual. Associated left and right upper premolars from W. Runton [NHM M19462] appear on both P^3 and P^4 graphs. Ranges of comparative samples: dotted box, *S. hundsheimensis*, Cagnes-sur-Mer, Sainzelles, Vallonnet, Soleilhac (from Lacombat, 2006); dotted line (breadth only), *S. hundsheimensis*, Isernia (from Lacombat, 2006); dashed box, *S. hundsheimensis* (after Fortelius et al., 1993); dotted red line (M^3 only), *S. kirchbergensis* lower range, Prince Cave (from Lacombat, 2006); dashed red line, *S. kirchbergensis* lower range (after Fortelius et al., 1993).

condition in other *S. hundsheimensis* specimens. Features “g-h” are typical of *S. kirchbergensis* (Fortelius et al., 1993: 72 and 117).

In sum, features “a–e” suggest that M82482-97 does not belong to *S. hundsheimensis*. The Boxgrove specimen shares some characters of the molars and premolars with *S. kirchbergensis*, but features “b” and “f” rule out an attribution to that species. The low cingulum and crown of the premolars of M82482-97 (“f”) contrast with their hypsodonty in *S. kirchbergensis* (Fortelius et al., 1993: 72 and 117); the paracone fold of the premolars of M82482-97 is strong (“b”), whereas this fold is “très petit… à peine indiqué…” in *S. kirchbergensis* (Guérin, 1980: 648).

Parfitt (1998: 128) suggests: “The Boxgrove teeth appear to have similarities with the Early Pleistocene species *S. megarhinus* and with an unnamed species of rhinoceros from deposits of probable Late Pleistocene age from Germany (von Koenigswald, 1991)”. Von Koenigswald (1988) identified as *Dicerorhinus megarhinus* a skull and jaw fragments with partial dentition and isolated teeth found at Gross-Rohrheim, and remains from other localities in the Upper Rhine Valley. Fortelius et al. (1993: 118) added some specimens from Meyrargues (Rhône Valley, France), earlier identified as *D. mercki* (syn. *kirchbergensis*) by Bonifay (1961) and later as *D. megarhinus* by Guérin (1980). The species has previously been allocated to *Dicerorhinus*, *Stephanorhinus* and *Lartetotherium*, while Lacombat and Mörs (2008) refer it to *Dihoplus* Hessig 1999. It is provisionally retained in *Stephanorhinus*.

There were no comparative *S. megarhinus* specimens available, but M82482-97 from Boxgrove was compared with published

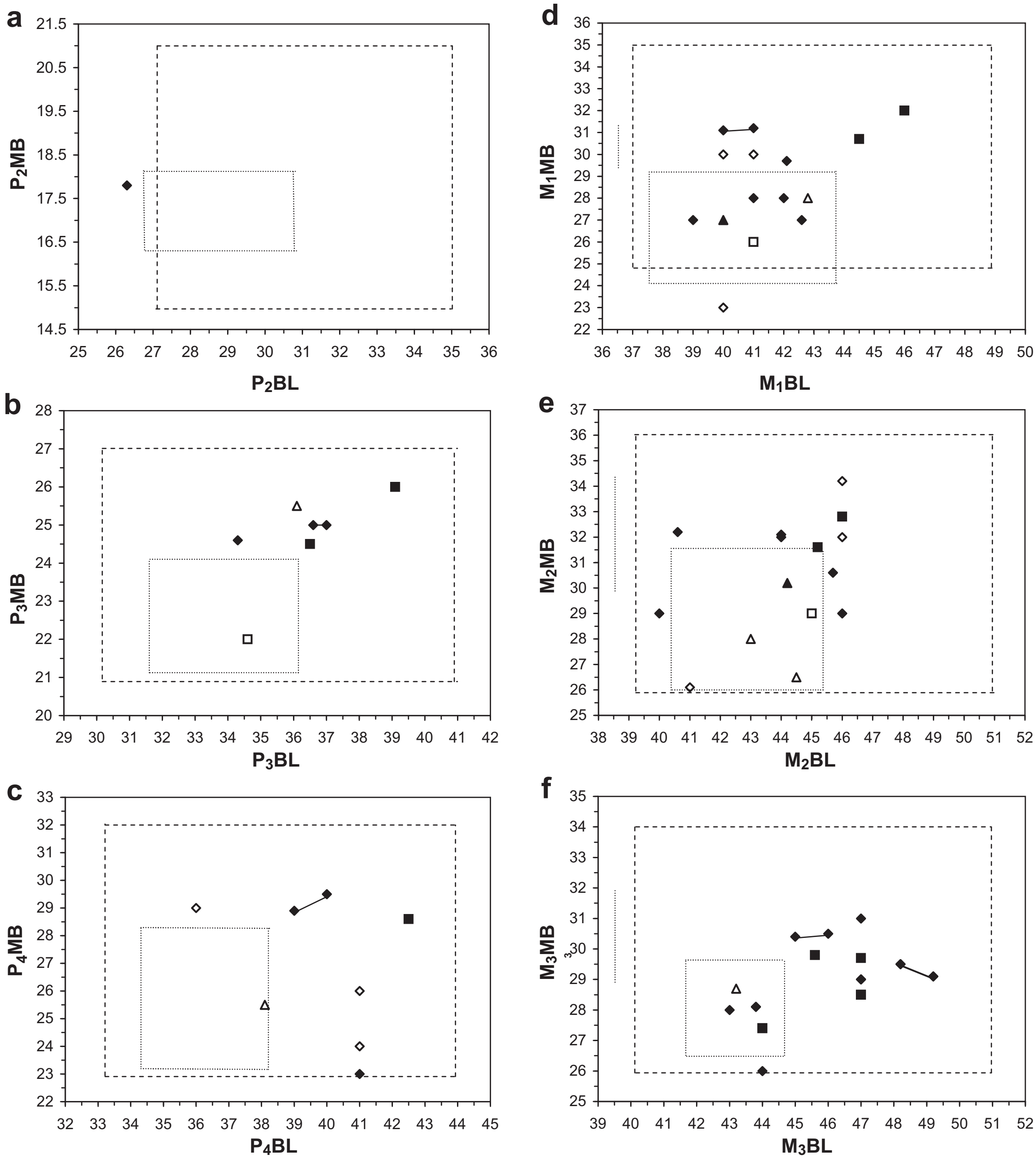

Fig. 4. Biometric comparison of rhinoceros lower cheek teeth. (a) P_2, (b) P_3, (c) P_4, (d) M_1, (e) M_2, (f) M_3. Symbols: ◆ and ◇, Pakefield, *Stephanorhinus hundsheimensis*; ■ and □, West Runton, *S. hundsheimensis*; ▲ and △, Boxgrove, *S. hundsheimensis*. Other symbols and ranges of comparative samples as in Fig. 3 (the range of *S. hundsheimensis* from Lacombat (2006) refers here to Ceyssaguet, Vallonnet, Soleilhac).

pictures and descriptions of that species. Lartet (1867) (fide Guérin et al., 1969) states that the protocone of P^2 is isolated in *S. megarhinus*, and that there are multiple crochets on its P^4. The isolated P^2 protocone is visible also in the '*S. megarhinus*' from the Upper Rhine Valley (von Koenigswald, 1988, Fig. 18) and is confirmed by Guérin (1980: 461), who adds that the protocone constriction is rare but present in the P^3 and P^4 of this species (it is apparently present in the specimen from Meyrargues pictured by Bonifay, 1961, Figs. 2–5). The P^2 protocone is isolated also in *S. jeanvireti* (Guérin, 1980: 461) but in this species the protocone constriction has never been observed on the premolars, and other described features do not correspond to those found in the Boxgrove specimen.

The paracone fold of the premolars ("b"), which is quite strong in M82482-97, is described by Guérin (1980: 461) as being "net … épais… massif…" in *S. megarhinus*. The crochet is multiple (from triple to quadruple) and very complicated in the P^3 and P^4 of the Boxgrove specimen, with smaller spurs splitting and re-joining each other at different heights on the crown. Guérin (1980) states that the crochet can be double in *S. megarhinus* premolars, and in the specimen from Meryrargues (Bonifay, 1961, Figs. 3 and 5) it is double and complicated by the same additional little spurs as in M82482-97. Similarly, in the specimens from Gross-Rohrheim it ranges from double to quadruple and again has small additional spurs (von Koenigswald, 1988, Fig. 18).

Features "g-h", which are typical of Middle Pleistocene *S. kirchbergensis*, are also found in the possibly related *S. megarhinus* (Fortelius et al., 1993). So, the state of features "a, b, c, d, e, g" and "h" in specimen NHM M82482-97 from Boxgrove corresponds to the descriptions for *S. megarhinus*. Moreover, the M^3 morphology

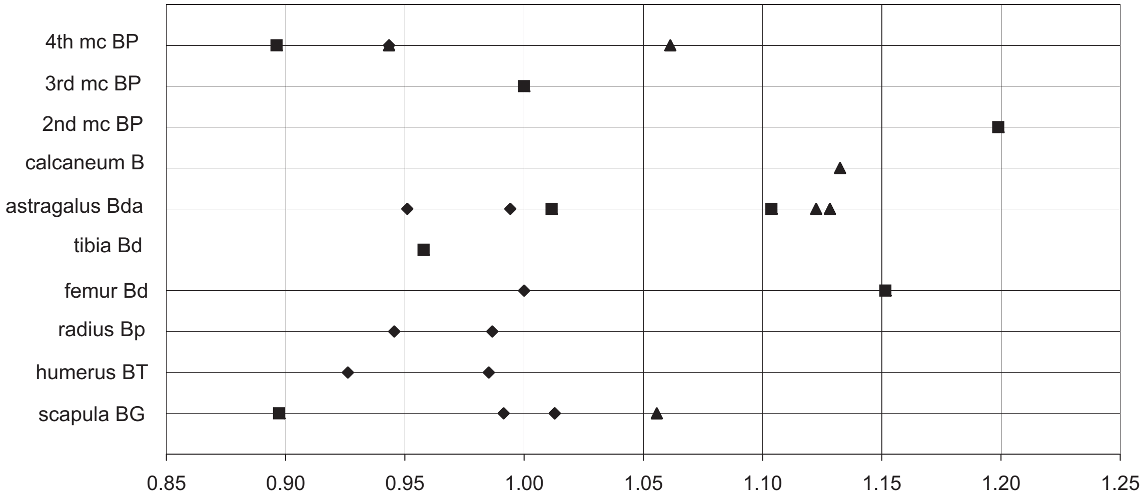

Fig. 5. Biometric comparison of rhinoceros postcranial size. Limb bone measurements (mostly diameters) are plotted as a proportion of the corresponding measurement on a modern *Diceros bicornis* skeleton [NHM 1876.2.15.5] used as a standard. Symbols: ◆, Pakefield, *Stephanorhinus* cf. *hundsheimensis*; ■, West Runton, *S.* cf. *hundsheimensis*; ▲, Boxgrove, *S.* cf. *hundsheimensis*.

corresponds closely to that described by Guérin (1980: 458) for *S. megarhinus* in the large crochet, usual absence of antecrochet, and open mediofossette.

Plotted with other early Middle Pleistocene British specimens (Fig. 3), the premolars of Boxgrove specimen M82482-97 are rather small, while M^3 is proportionally long (Fig. 3). Compared to the ranges given by Lacombat (2006) for *S. hundsheimensis*, this specimen has unusual proportions of P^2 (low MB, high DB, and quite high BL), and a high LL of the P^3. The only measurement outside the ranges given by Fortelius et al. (1993) is the very high LL of M^3. The addition of continental *S. megarhinus* to Fig. 3 is not possible because of differences in published measurement techniques. Therefore, the specimen from Boxgrove was re-measured according to the methods of other authors. This shows that the specimen is smaller than, but relatively close to, the specimen from Meryrargues (Bonifay, 1961), very close to the specimen from Gross-Rohrheim (von Koenigswald, 1988), and within the range, even if at its lower end, of a sample of *S. megarhinus* from French, Italian and Belgian localities (Guérin, 1980, table 89). The specimen from Boxgrove is much smaller than *S. kirchbergensis*, being well below the lower end of the range given by Fortelius et al. (1993) (see Fig. 3) for all molar measurements and for the plotted premolar measurements.

In conclusion, it is believed that specimen NHM M82482-97 from Boxgrove can be attributed to *S.* cf. *megarhinus*, while bearing in mind the stratigraphically unexpected presence of a 'Pliocene' species in early Middle Pleistocene deposits: *S. megarhinus* is otherwise known from the Pliocene (Ruscinian) (Guérin et al., 1969; Guérin, 1980). On the other hand, as pointed out by Fortelius et al. (1993), the multiple records of this form in Late Pleistocene deposits of the Rhône and Rhine Valleys make explanations based on aberrant individuals unlikely.

Among the Boxgrove material in the NHM are three skull fragments: two occipital portions with part of the parietals [M82542 and M82543], and a dorsal portion [M82544] (Fig. 7). These have been

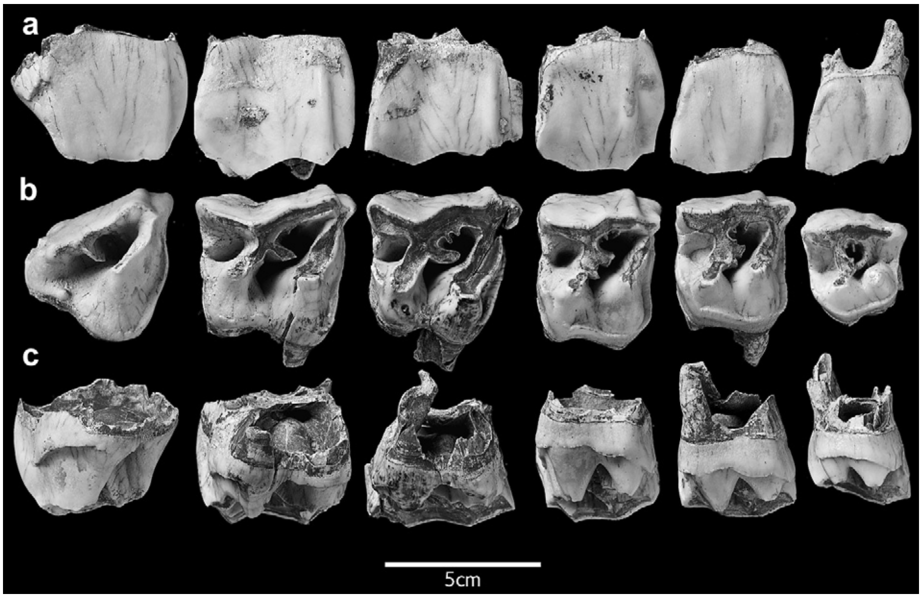

Fig. 6. Associated right upper cheek teeth P^2–M^3 (from right to left), of *Stephanorhinus* cf. *megarhinus* from Boxgrove, NHM M82482-97: (a) labial view; (b) occlusal view; (c) lingual view.

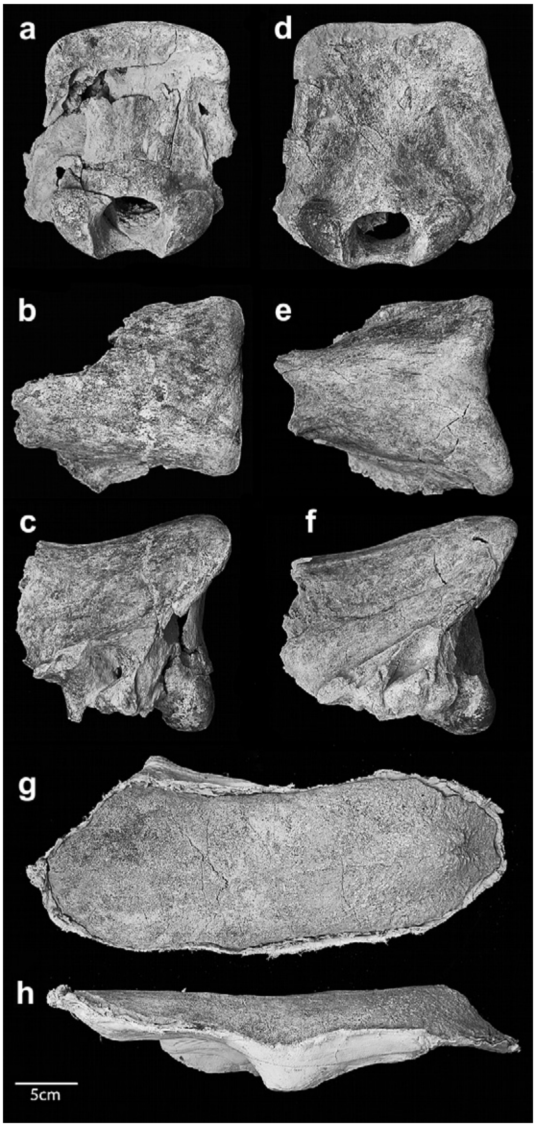

Fig. 7. Rhinoceros skull fragments from Boxgrove: (a) NHM M82543, occipital view; (b) NHM M82543, dorsal view; (c) NHM M82543, left lateral view; (d) NHM M82542, occipital view; (e) NHM M82542, dorsal view; (f) NHM M82542, left lateral view; (g) NHM M82544, dorsal view; (h) NHM M82544, right lateral view.

compared with descriptions of different *Stephanorhinus* species (Zeuner, 1934; Guérin et al., 1969; Guérin, 1980; Loose, 1975).

The occipital crest of M82543, in lateral view, is shorter and less backward-projecting than in *S. megarhinus*, with a less sharp angle between parietals and occipitals, and looks more like *S. hundsheimensis*. The caudal outline of the occipital crest, in dorsal view, is slightly concave as in both *S. hundsheimensis* and *S. megarhinus*, but with the concavity "U" shaped as in *S. hundsheimensis* (Ref. Loose, 1975: plate 4, Fig. 2 rather than "V" shaped as in *S. megarhinus* (ref. Guérin, 1980: plate 12, Fig. b) and lacks the small sagittal lump typical of the latter (Guérin, 1980: 448), again resembling more the former species. The lateral edges of the occipital are too damaged to assess the occipital outline in caudal view.

M82542 has been slightly deformed by sediment weight, resulting in a compression from left dorsal to right ventral. The occipital crest, in lateral view, is a little more elongated and backwardly-directed, resulting in a somewhat sharper angle between parietals and occipitals and greater similarity to *S. megarhinus*. The caudal outline of the occipital crest, in dorsal view, has a "V" shaped concavity as *S. megarhinus* (see above), the degree of concavity being a little enhanced by the deformation of the skull. However, the medial portion of the outline is clearly abraded so that it is unclear whether the small sagittal lump typical of *S. megarhinus* (Guérin, 1980: 448) was present. However, in caudal view, the outline of the occipital is rather dorso-ventrally elongated and rectangular, as in *S. megarhinus* (Guérin et al., 1969, 1980), rather than shorter and more trapezioidal as in *S. hundsheimensis*.

The preserved morphological features of M82542 therefore suggest attribution to *S. megarhinus*, but of the six measurements that it was possible to take on M82542 (measurements 15, 16, 22, 23, 31 and 32 after Guérin, 1980: 47, table 1), only one (measurement 32) is within the *S. megarhinus* range given by Guérin (1980: 450, table 84), all the others being much smaller. This could be at least partly due to the small sample available to Guérin (1980) for *S. megarhinus*, ranging from one to four specimens in the various measures, and so probably not encompassing the species' true size range. The same measurements are even smaller in M82543, but for both Boxgrove specimens are all well within the *S. hundsheimensis* ranges given by Guérin (1980: 634, table 122) (Table 1).

Angles "o" and "m" (Zeuner, 1934) were measured on the two occipital portions. Bearing in mind the large measuring error and ambiguous definition of these angles in different species (Guérin, 1980: 44–45), angle "o" of the two specimens is within the range given by both Zeuner (1934) and Loose (1975) for '*S. etruscus*' (including *S. hundsheimensis*) and *S. kirchbergensis*; unfortunately none of these authors give values for *S. megarhinus*. However, angle "m" is rather acute in the Boxgrove specimens: in M82543 it is just within the range given by Zeuner (1934) for '*S. etruscus*' but below the range given by Loose (1975) for the same species, while in M82542 it is below both Zeuner's and Loose's *S. etruscus* ranges.

In the dorso-nasal portion M82544, the insertion scars of the two horns are about the same size, as in *S. hundsheimensis*, while in *S. megarhinus* the posterior one is larger and with stronger rugosities (Guérin et al., 1969; Guérin, 1980).

In conclusion, M82543 and M82544 probably belong to *S. hundsheimensis*, even if angular measure "m" is below the published ranges of the species. Conversely, the morphology of M82542 apparently rules out attribution to *S. hundsheimensis*, being consistent with *S. megarhinus*, but the size is smaller than in the latter. We therefore speculate that this specimen could match the dental remains M82482-97 (also rather small for *S. megarhinus* – see above), and suggest a tentative attribution to *S.* cf. *megarhinus*.

4.3. West Runton

The West Runton sample spans a range of sizes (Figs. 3 and 4). It includes mandibles with dentitions [NHM M19442; NCM 1925.107] as well as isolated teeth such as a P_3 [NHM M19506] and M_1 [NHM M19507], all referable to *S. hundsheimensis*.

Some morphological peculiarities are present in associated left and right P^3 from West Runton [NHM M19462 (ex Savin 1057)] (Fig. 8). Their dimensions are within *S. hundsheimensis* ranges (Fortelius et al., 1993; Lacombat, 2006), but the teeth are rather broad and short (Fig. 3), notable considering that the specimen was quite young and had not undergone mesio-distal attrition.

The features that distinguish this individual from other British early Middle Pleistocene specimens are:

j) the complete absence of a lingual cingulum (the mesial cingulum is well developed as always, but it disappears

Table 1
Biometric comparison between rhinoceros skulls from Boxgrove and published ranges.

	Linear measures after Guérin (1980)	M82543	M82542	*S. megarhinus* Guérin, 1980	*S. hundsheimensis* Guérin, 1980
15	Occipital crest width (between lateral angles)	153	159	165–200 (*N* = 3)	132–175 (*N* = 9)
16	Occipital face width (between mastoids)		225	243–282 (*N* = 3)	223–254 (*N* = 4)
23	Occipital face height (from top foramen)	148	160	167–190 (*N* = 4)	139–191,5 (*N* = 9)
31	Occipital foramen transverse diameter	56,5	58	72 (*N* = 1)	49,5–63 (*N* = 4)
32	Occipital condyles external width	139	146	127–158 (*N* = 3)	133–146 (*N* = 4)
	Angular measures after Zeuner (1934)			*S. etruscus* + *S. hundsheimensis* Zeuner, 1934 [a]	*S. hundsheimensis* Loose, 1975 [a]
m	Steep foramen axis – parietals	38°	30°	34°–70° (*N* = 8)	42°–55° (*N* = 7)
o	Opisthion + occipital crest – parietals	73°	74°	63°–83°(*N* = 14)	70°–79° (*N* = 7)

[a] Zeuner (1934) and Loose (1975) consider *S. hundsheimensis* within *S. etruscus*; Zeuner does not separate the data but for Loose we used original measures from his Table 12 (Mosbach and Mauer only) that certainly belong to *S. hundsheimensis*.

completely on the protocone to weakly reappear in the region of the lingual valley. From here, a bulging and very oblique ridge extends along the hypocone wall to reach the distal cingulum);

k) the presence of an extremely long and strong crista, about half the length of proto- and metaloph, to which it runs parallel, bearing a mesial bifurcation;
l) the high distal cingulum which encloses, together with the metaloph, a deep and wide postfossette which extends down into the fused bases of the hypo- and metacones. The roots beneath proto-, hypo- and metacones are fused.

Moreover, the paracone fold (feature “b”) is stronger than in other British specimens and creates a right-angle with the mesial portion of the ectoloph rather than the usual gentle bend.

Lacombat (2006) states that *S. hundsheimensis* always has a strong and continuous lingual cingulum (actually continuous in only 90% of specimens according to Guérin, 1980: 646) and a thin and little-prominent paracone fold. So, features “j” and “b” cast some doubt on the attribution of this specimen to *S. hundsheimensis*. Neither Guérin (1980) nor Lacombat (2006) describes the state of features “k” and “l”, but they are unique in the British early Middle Pleistocene sample, so the specimen is here named *Stephanorhinus* sp. A aff. *S. etruscus/hundsheimensis* (see above for explanation of the term ‘aff.’).

Some morphological peculiarities are present in another specimen, CRM 1884.2.1-2 (Fig. 9). This consists of the left and right maxillaries with, respectively, P^2–P^4 and P^2–M^1. The P^2s and P^3s of CRM 1884.2.1-2 are small and extremely narrow, while the P^4s and M^1 are of normal proportions (Fig. 3). The features distinguishing this individual from almost all other British early Middle Pleistocene specimens are:

m) the lingual valley of the P^2s is U-shaped rather than V-shaped and, under it, the lingual cones are partially fused (i.e. in occlusal section they connect through a bent line rather than through an angle);
n) there is a high distal cingulum on all the premolars which, rather than connecting gradually to the lingual cingulum, bends occlusally and makes a strong angle with it;
o) the metaloph of the P^2s is parallel to the distal cingulum rather than to the protoloph and, through a curved ridge, joins the vertex of the above-described angle between distal and lingual cingula.

Features “m–o” are seen in one other specimen examined, NCM 1986.14.1-7 from Pakefield, and will be discussed below.

Another interesting character, found only in CRM 1884.2.1-2, is the presence of a “kerb” on the labial wall along the crown-root edge. This kerb is usually interpreted as a structure where the

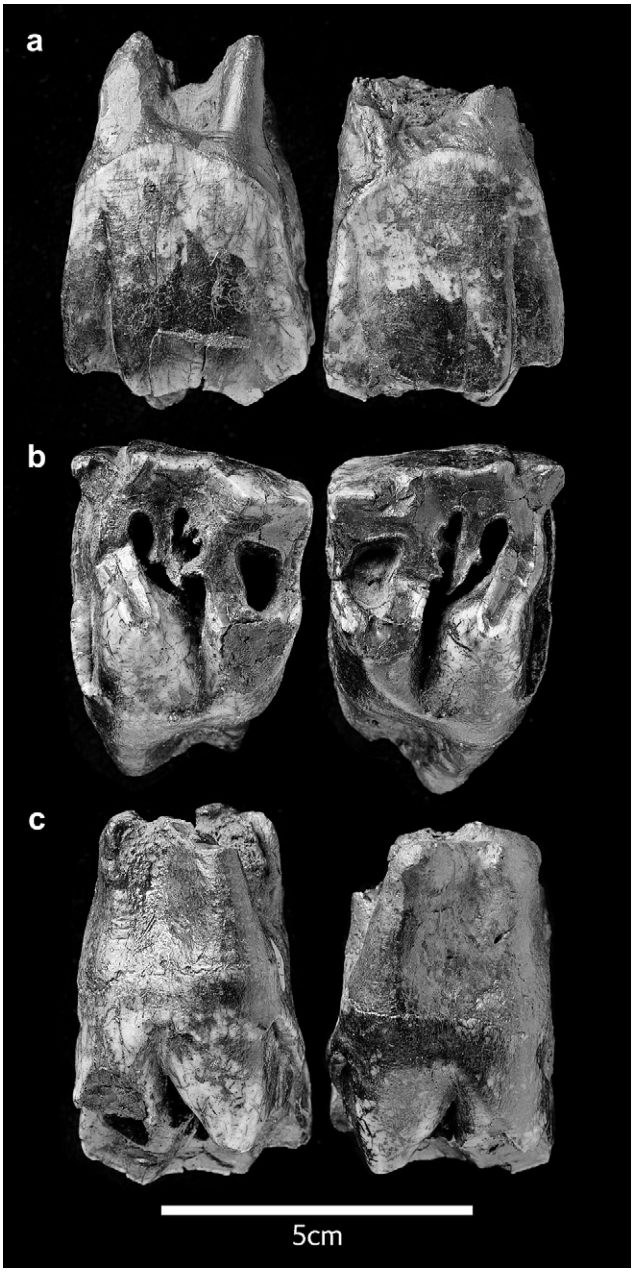

Fig. 8. Associated upper left and right P^3 of *Stephanorhinus* sp. A aff. *S. etruscus/hundsheimensis* from West Runton, NHM M19462: (a) labial view; (b) occlusal view; (c) lingual view.

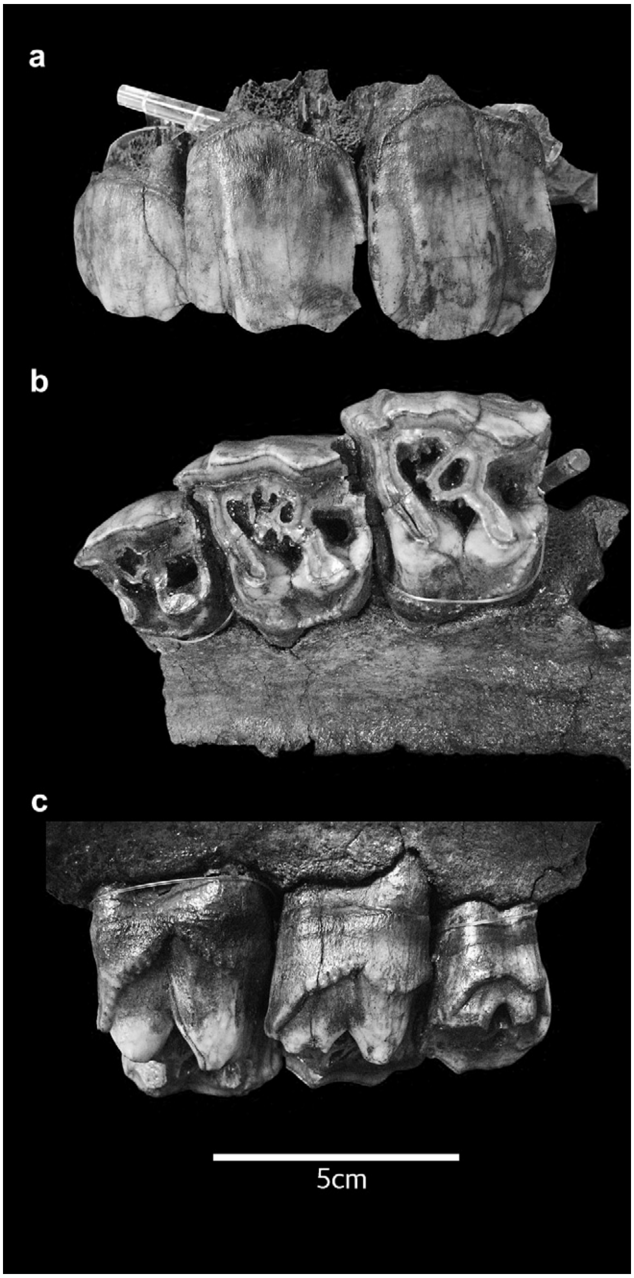

Fig. 9. Upper left P^2–P^4 of *Stephanorhinus* sp. B aff. *S. etruscus/hundsheimensis* from West Runton, CRM 1984.2.1: (a) labial view; (b) occlusal view; (c) lingual view.

cement can grip, being often present in species with abundant coronal cement. In accordance with the presence of the kerb, the basal part of the labial wall in the premolars is flat rather than convex as usual. In M^1, where the kerb is more pronounced, the basal part of the labial wall is concave, but this concavity is shared by several other British upper molars.

Postcranial measurements from West Runton span the ranges of the other British sites (Fig. 5) and of continental *S. hundsheimensis* (Fortelius et al., 1993). Since rhinoceroses lack marked sexual dimorphism, the presence of both large and small specimens within the WRFB could reflect the possible existence of two species. Whether they can be coupled respectively with the more common *S. hundsheimensis* and the morphologically different NHM M19462 or CRM 1984.2.1-2 is currently an open question.

4.4. Pakefield

The dental measurements (Figs. 3 and 4) show a wide size range, Most specimens are referable to *S. hundsheimensis*, including a palate with upper dentition [NHM M18705 (ex Savin 1)], and the four isolated tooth rows of one individual [NHM M19495, M19496, M19439 and M19443; ex Savin 388].

One unusual specimen from Pakefield, described by Newton (1882) (Figs. 1–5, pl. 8, p. 38), consists of an associated left P^2–P^3 and M^1–M^3 [NCM 1986.14.1-5, ex Fick 3915-9] and right M^1 and M^3 [NCM 1986.14.6-7, ex Fick 3920-1]. The individual is young. The P^2 and P^3 have the lowest breadths among the Pakefield specimens, similarly to, but rather higher than, West Runton CRM 1884.2.1-2. The specimen also has the same distinguishing features “a–c” and “m–o” as the West Runton specimen, with which it can thus be grouped, although it lacks the “kerb” on the labial wall along the crown-root edge.

None of these characters is dealt with by Guérin (1980), Fortelius et al. (1993) or Lacombat (2006), so their expression in continental European *S. hundsheimensis* is unclear. However, among the British material, they are present in the Pakefield and West Runton individuals only. Whether such characters are intraspecific variants, or reflect separate taxonomic status, is difficult to say and a larger sample would be needed to study individual variability. For the moment, both CRM 1884.2.1-2 from West Runton and NCM 1986.14.1-7 from Pakefield are here considered *Stephanorhinus* sp. B aff. *S. etruscus/hundsheimensis.*

Among the Pakefield material in the YM, there is a partial skull (without catalogue number) (Fig. 10). This specimen preserves the dorsal surface and a good part of the lateral left side but for the alveolar portion of the maxillary. The nasals and the inter-nasal septum are complete while the occipital preserves only the very dorsal portion.

The six measurements that it was possible to take on this specimen (measurements 3, 5, 9, 15, 22 after Guérin, 1980: 47, table 1, and angle st after Loose, 1975: 4, Fig. 3) are all consistent with *S. hundsheimensis* but show differences from the other *Stephanorhinus* species considered here (see Table 2).

Two of the most diagnostic morphological characters on the skull, the relative position of the posterior edge of the nasal incision and of the anterior edge of the orbit with respect to the tooth row (Guérin, 1980), cannot be considered because of the lack of teeth. However, in accordance with the metric data, the following morphological features described by Guérin (1980) for the early

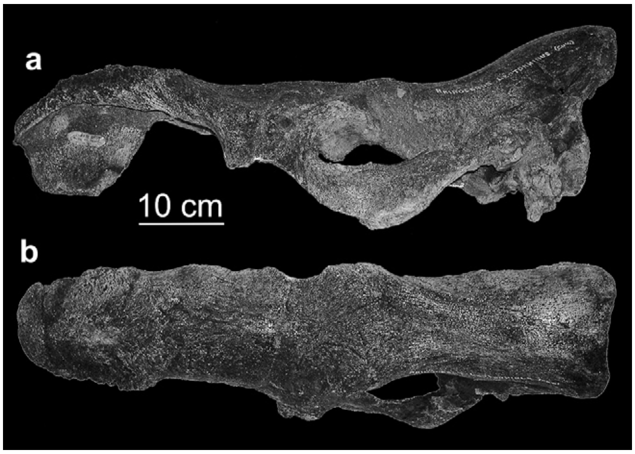

Fig. 10. *Stephanorhinus hundsheimensis* skull from Pakefield (YM, without catalogue number): (a) lateral view; (b) dorsal view.

Table 2
Biometric comparison between rhinoceros skull from Pakefield and published ranges. Ranges for measures 3, 5, 9, 15, 22 after Guérin (1980); ranges for measure *n* after Loose (1975). * Loose (1975) considers *S. hundsheimensis* within *S. etruscus*, so we used the original measures from his Table 12, considering the specimens from Mosbach and Mauer as *S. hundsheimensis* and the specimen from Sénèze as *S. etruscus*.

	Linear measures after Guérin (1980)	Pakefield specimen	*S. megarhinus*	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*
3	Skull length (nasal – occipital)	710	690–808 (*N* = 3)	530–655 (*N* = 11)	605–760 (*N* = 9)	661–786 (*N* = 13)	730–740 (*N* = 2)
5	Skull width (min at the orbito-temporal fossa)	122	110–150 (*N* = 3)	79–126 (*N* = 16)	107–145 (*N* = 8)	107–138 (*N* = 12)	125–149 (*N* = 4)
9	Orbit – nasal opening distance	104	105–125 (*N* = 6)	90–123 (*N* = 19)	81–122 (*N* = 12)	95,5–143 (*N* = 13)	89–133 (*N* = 4)
15	Occipital crest width (between lateral angles)	160	165–200 (*N* = 3)	101–174 (*N* = 12)	132–175 (*N* = 9)	101–160 (*N* = 16)	131–167 (N = 4)
22	Skull width (min at the nasal level)	132	140–212 (*N* = 4)	100–145 (*N* = 17)	114–174 (*N* = 11)	140–183 (*N* = 13)	127–171 (*N* = 4)
	Angular measures after Loose (1975)			*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*
n	Tangent hornbases – parietals	155°		150 (*N* = 1) *	141–160 (*N* = 7) *	143–160 (*N* = 9)	145–155 (*N* = 4)

Middle Pleistocene species of *Stephanorhinus*, evident in the plates by Loose (1975), suggest an attribution to *S. hundsheimensis*:

- The degree of posterior elongation of the occipital crest (Guérin, 1980: 629; Loose, 1975: pls. 3 and 5), lower than in *S. kirchbergensis* and much lower than in *S. hemitoechus*;
- The dorsal outline of the skull, in lateral view, with a small but clear insertion for the posterior horn (Guérin, 1980: 629; Loose, 1975: pls. 3 and 5), this insertion being barely visible in *S. hemitoechus*;
- The inflation of the nasal portion on the attachment of the anterior horn (Guérin, 1980: 631; Loose, 1975: pls. 4 and 6), less pronounced in *S. kirchbergenisis* and lacking in *S. hemitoechus*;
- The less laterally developed zygomatic arches (Guérin, 1980: 631; Loose, 1975: pls. 4 and 6), forming a thinner tempo-orbital fossa than in *S. kirckbergensis* and *S. hemitoechus* (in the latter the braincase is narrower at the caudal end of the zygomatic arch, increasing the width of the temporal fossae);
- The slightly concave caudal outline of the occipital crest, in dorsal view, (Guérin, 1980: 631; Loose, 1975: pls. 4 and 6), this outline being slightly convex in *S. hemitoechus*.

Attribution to *S. megarhinus* should be ruled out as well because of the concave caudal outline of the occipital crest, lacking the little bump typical of this species described by Guérin (1980: 448).

In conclusion, both morphological and metrical data suggest attributing the skull from Pakefield to the most common species at this locality, *S. hundsheimensis*.

Pakefield postcranial measurements are often smaller than the smallest given by Fortelius et al. (1993) for *S. hundsheimensis*, as well as all being in the lower part of the British rhinoceros sample (Fig. 5). Whether this reflects a match to the small lower molars, proportional variation, or sampling error, is unknown.

4.5. *Westbury*

The two upper dentitions from Westbury, right P^2–P^4 plus left P^2–M^2 [NHM M35150 (corresponding to M33773 in Bishop, 1982)], and a crushed M^1–M^3 [NHM M33729], are of small size in all teeth. There are no postcranial specimens from Westbury to check if they were also relatively small. M35150 is of *S. hundsheimensis* morphology.

Schreve et al. (1999: 282) suggest that “a hitherto unrecognised rhinoceros with affinities to ‘*Rhinoceros megarhinus*’ de Christol has been identified at Westbury (Currant, unpublished data). Comparable material is known from Boxgrove and Trimingham (Norfolk)”. Currant (pers. comm., 2009) refers here to specimen NHM M33729 from Westbury, to the above-described NHM M82482-97 from Boxgrove, and to specimen NHM M19449 from Trimingham.

Specimen M33729 from Westbury, three crushed and rather worn right molars, resembles the *S.* cf. *megarhinus* specimen from Boxgrove in swollen protocones (feature “g”) and concave lingual wall (“h”) of M^2 and M^3, features typical of *S. megarhinus* (Fortelius et al., 1993).Most of the other *S. megarhinus* features (“b–e”) cannot be scored because they relate to the premolars. Moreover, the M^3 morphology of the Westbury specimen doesn’t match the description of *S. megarhinus* given by Guérin (1980: 458), since M33729 has a strong antecrochet (usually absent in *S. megarhinus* M^{3}s, as in the Boxgrove specimen) which joins the crochet to give a closed mediofossette (usually open in *S. megarhinus* M^{3}s, again as in the Boxgrove specimen). Therefore, the available data are too weak for specific assignment of this specimen.

As for specimen NHM M19449 from Trimingham (right D$_1$–M$_1$ plus germs of P$_3$–P$_4$), it has been described above how it, together with NHM M6636 (left M$_1$–M$_3$ plus germs of P$_3$–P$_4$) from the same locality, resembles the *S.* cf. *megarhinus* from Boxgrove in several features (“b” and “f–h”). However, multiple crochets (“c”) are present on the premolars only of M6636 (not on M19449), both specimens lack the protocone constriction on the premolars (“e”), and it cannot be known whether the protocone of their P^2 was isolated (“d”) because they both lack P^{2}s. Since the last three features, together with the strong paracone fold of premolars (“b”) and the open lingual valleys of molars derived from features “g” and “h”, are the only features described on Continental material as typical of *S. megarhinus*, the presence of features “b”, “g” and “h” is considered too weak for specific assignment. This also in view of the fact that features “g” and “h” are expressed in different ways in British early Middle Pleistocene specimens, and that feature “f” (low lingual cingulum of premolars), shared with the specimen from Boxgrove, could be partly due to the still-incomplete development of the teeth, with the roots not yet formed.

4.6. *Conclusion (rhinos)*

A taxonomic revision of British Early and Middle Pleistocene rhinoceroses is needed, through a detailed comparison with coeval continental material. This would allow us to assess whether the morphological and metrical variability of the British sample may be considered intra-specific, geographical variability within the species described for the Continent, or as representing different (possibly new) species. In addition to the common *S. hundsheimensis*, the upper dentitions suggest the presence of three possible taxa, one represented by the specimen from Boxgrove [NHM M82482-97] here attributed to *S.* cf. *megarhinus*; and two, of unclear taxonomic status, with affinities to the *S. etruscus*/*hundsheimensis* group, represented respectively by the associated upper P^{3}s from West Runton [NHM M19462], and by CRM 1984.2.1-2 from West Runton plus NCM 1986.14.1-7 from Pakefield.

From an ecological point of view, it would not be surprising if two rhinoceros species were found together in British Early and/or early Middle Pleistocene localities. Two species of rhinoceros can live in the same area without being in competition for food and resources because of their distinct niches (Mazza, 1993). Examples are the present-day white rhinoceros, *Ceratotherium simium*, and black rhinoceros, *Diceros bicornis*, from African savannahs; the late Middle Pleistocene *S. hemitoechus* and *S. kirchbergensis* from several British and continental localities (e.g. Fortelius et al., 1993); the Early Villafranchian *S. jeanvireti* with *S. etruscus* (Guérin, 1972); or the Ruscinian *S. megarhinus* and *D. miguelcrusafonti* (Guérin and Santafé, 1978). There is even a possible instance of three species of rhinoceros living together: *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus* at Mosbach 2 (Fortelius et al., 1993) and at Abîmes de la Fage (Guérin, 1973).

5. Bovids (Bovidae)

5.1. Introduction and methods

The earliest and most primitive true bison to appear in Europe is *Bison menneri* Sher 1997 from the late Early Pleistocene of Untermassfeld (Germany), of very large size but extremely gracile legs (Sher, 1997). *B. shoetensacki* Freudenberg 1914 appeared in Europe in the early Middle Pleistocene at the German sites of Voigtstedt, Süssenborn, and Mauer (Sala, 1986), in Britain (West Runton and Westbury, see below) and in Italy (Venosa, Isernia la Pineta, Slivia) (Sala, 1986), to become extinct before the Holsteinian/Hoxnian interglacial (Parfitt, 1999). *Bison voigtstedtensis* was described as a primitive form of *B. shoetensacki* from Voigtstedt by Fischer (1965), and later considered a separate species by Flerov (1975, 1979). At present it is considered by most authors (e.g. Sala, 1986; Moyà-Solà, 1987; Brugal, 1995) as a subspecies of *B. schoetensacki*, while others recognise its specific status (e.g. van der Made, 1998a,b, 1999). It is included here within *B. schoetensacki*, as originally described by Fischer (1965).

B. priscus Bojanus 1827 appeared in Europe at the end of the early Middle Pleistocene. Sala (1986) suggested that *B. priscus* evolved either from *B. schoetensacki*, or directly from Asian forms. However, he maintained that *B. priscus* replaced *B. schoetensacki* in Europe and that the simultaneous occurrences of the two species recorded in literature are erroneous. Conversely, Sher (1997) suggested the existence of both species at sites such as Mosbach and Mauer (Germany) because of the existence of metacarpals of different proportions, the longer and more slender belonging to the former species, the shorter and more robust to the latter. In accordance with Flerov (1979), (fide Sher, 1997), Sher (1997) believed that short-horned, long-legged bison of relatively light construction (such as *B. menneri* and *B. schoetensacki*) were forest-dwellers, while long-horned, short-legged bison of more robust build (such as *B. priscus*) were adapted to more open spaces. Conversely, Sala (1986: 163) suggested that both *B. schoetensacki* and *B. priscus* "could live in open environments, steppes and prairies as well as in closed environments, forests and woods."

Leptobos Rütimeyer 1877 is a Villafranchian genus of temperate Eurasia and North Africa (Sala, 1986), and has been regarded as close to the ancestry of *Bison* (e.g. Sala, 1986; Douvernois and Guérin, 1989; Geraads, 1992). In Britain, *L. etruscus* has been recorded from the Red Crag Nodule Bed (Stuart, 1982), and the Siliceous Member at Westbury (Gentry, 1999). *Leptobos* is usually considered to have been replaced by *Bison* at the end of the Early Pleistocene, but Brugal (1995) suggests that it could have survived until the beginning of the Middle Pleistocene in some areas of Spain, France and Italy.

The genus *Bubalus* Hamilton-Smith 1827 has been recorded – as *B. murrensis* Berckhemer, 1927 – in several German Middle and Late Pleistocene localities (e.g. Steinheim: Berckhemer, 1927; localities in the Upper Rhine Valley: von Koenigswald, 1988). *B. murrensis* has also been recorded in Romania (Rădulesco and Samson, 1985) and in the Netherlands (Dam et al., 1997) but no *Bubalus* remains have been recorded in the British Isles. An older species of *Bubalus*, *B. marathousae*, has been recorded from the early Middle Pleistocene of Greece (Megalopolis: Tsoukala, 1992).

The genus *Bos* spread from Africa at the end of the early Middle Pleistocene (Martínez-Navarro et al., 2007), being first recorded in Europe at Venosa-Notarchirico (Italy ~0.5–0.6 Ma) by Cassoli et al. (1999) (fide Martínez-Navarro et al., 2007). The older record of this genus at Ponte Galeria (Italy ~0.7–0.8 Ma), as *Bos galerianus* (Petronio and Sardella, 1998), has been questioned by Martínez-Navarro and Palombo (2004) who reassigned it to the Indian genus *Hemibos*. *B. primigenius* has been recorded in the early Middle Pleistocene only in southern and central Europe, reaching northern Europe in MIS 11, the oldest records for Britain being at Clacton (Essex) and Swanscombe (Kent) (Stuart, 1982; Currant, 1989).

The taxonomy of large bovids is traditionally based on cranial and horn characters, but Sher (1997) showed that well-established limb bone characters can be useful as taxonomic markers. However, he stated that "variability of proportions and minor details of structure of large bovine teeth are so wide that even the possibility of discrimination between *Bos primigenius*, *B. priscus* and *B. bonasus* remains a matter of debate." The similarity of described species had already led Groves (1981) to propose *Bison* as a subgenus within *Bos*. This suggestion was followed by Brugal (1985) and Gentry (1999), but has not been accepted by the majority of authors, e.g. Sala (1986), Gee (1993) and Sher (1997), and will not be adopted here.

The position of upper and lower molars was determined following Gentry (1999), and the measurements taken are occlusal length (L) and greatest breadth (B). Since bovid teeth are columnar, variation in length up the crown is relatively minor and occlusal length is often easier to take on tooth rows. These measures were plotted for each upper and lower tooth type (Figs. 11 and 12). The Westbury dental sample is numerically predominant, and the low number of upper teeth and lower premolars from the other localities limits their interpretation.

Postcranial data are plotted in a ratio graph (Fig. 13), where the 1.0 line is based on an associated modern American bison (*Bison bison*) skeleton of unknown sex, stored at NHM as 851.a. For each bony element, the measurement representing a highest number of specimens was chosen.

There are usable horncores only from West Runton and Pakefield.

5.2. Westbury

There is confusion over the identity of the bison at Westbury-sub-Mendip (Calcareous Member). Bishop (1982) recorded *B. priscus*, revised to *B. schoetensaki* by Sala (1986), Gentry (1999) and Preece and Parfitt (2000), but referred again to *B. priscus* by Preece et al. (2009); at Boxgrove Parfitt (1998) recorded *B. priscus*, which was revised to "*Bison* sp., size of *B. priscus*" in Parfitt (1999).

The Westbury sample of teeth has a wide size range (Figs. 11 and 12). Among the levels, only the Yellow Breccia yielded a sample large enough to warrant independent consideration; it spans a wide range of sizes, from the smallest to the largest in the overall sample. Molar sizes have been plotted in Figs. 11 and 12 in comparison with continental samples of *B. schoetensacki* and *B. priscus*, but do not provide a clear basis for taxonomic discrimination.

In the postcranial bones (Fig. 13), it is evident that the specimens from Westbury are the largest among the British localities considered, with a range, in the astragalus Dl, of as much as 0.43 in relation to the standard. Sher (1997) demonstrated that the metacarpal dimensions of Early and early Middle Pleistocene large

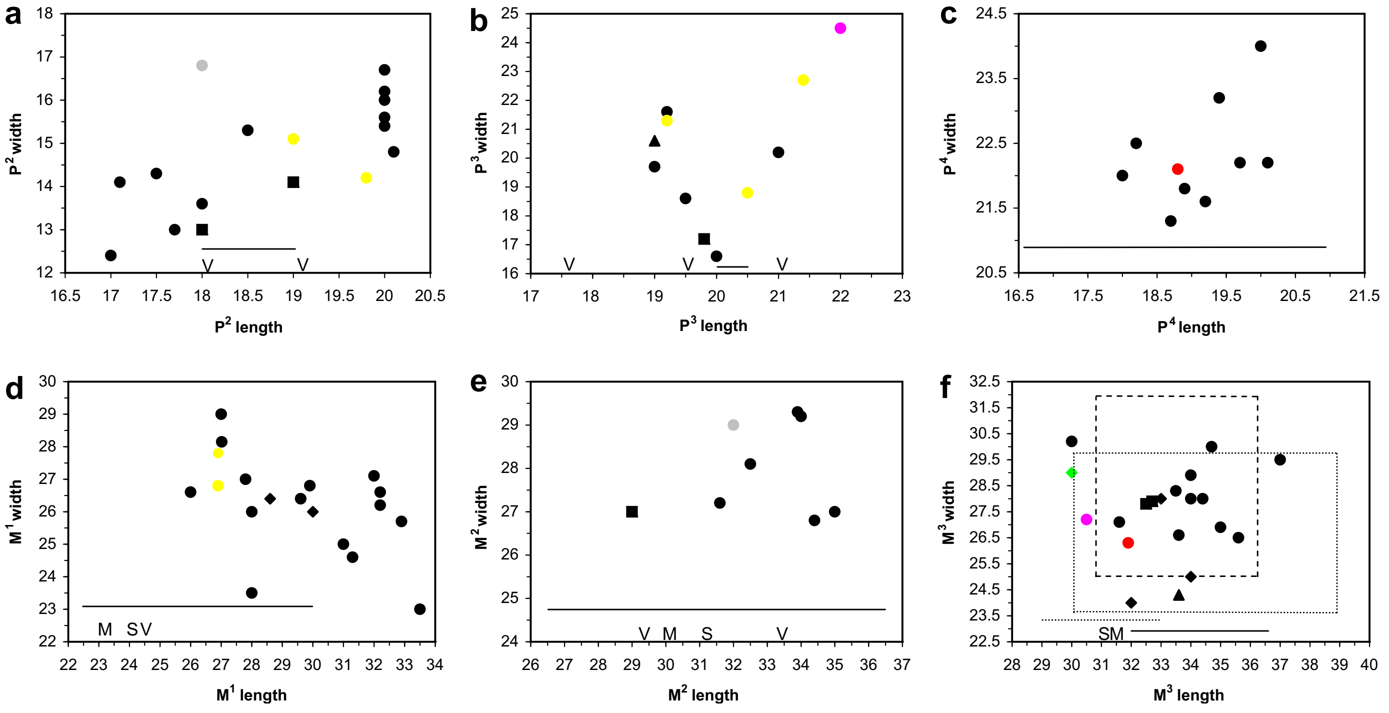

Fig. 11. Biometric comparison of bovid upper cheek teeth. (a) P^2, (b) P^3, (c) P^4, (d) M^1, (e) M^2, (f) M^3. Symbols: ◆, Pakefield, *Bison* cf. *schoetensacki*; ◆, Pakefield, Bovidae indet., NHM M6567; ■, West Runton, *Bison* cf. *schoetensacki*; ●, Westbury, *Bison* unstratified; ●, Westbury, *Bison* Pink Breccia; ●, Westbury, *Bison* Yellow Breccia; ●, Westbury, *Bison* Red Breccia; ●, Westbury, *Bison* Grey Breccia; ▲, Boxgrove, *Bison* cf. *schoetensacki*. Ranges of comparative samples: dotted line (M^3 length only), *B. schoetensacki*, Voigtstedt (from Fischer, 1965); capital letters on the x axis (length only), *B. schoetensacki*, single specimens, "V" Voigtstedt (from Fischer, 1965), "M" Mauer (from Fischer, 1965), "S" Süssenborn (from Flerov, 1969); dotted box (M^3 only), *B. schoetensacki*, Mauer (from Sala, 1986, table 4); dashed box (M^3 only), *B. schoetensacki*, Isernia (from Sala, 1986, table 4); solid line (length only), *B. priscus*, Siberia (from Sher, 1997, table 2).

bovids cluster according to sex and species. Unfortunately, there are only three complete metacarpals from the British early Middle Pleistocene localities: two from Westbury and one from Boxgrove. Sher (1997, Fig. 11) plotted the two Westbury specimens [NHM M33146 and M33758], finding that they are very robust, clustering quite close to the *B. priscus* male sample from Mosbach and distant from the more gracile *B. shoetensacki*. One of the Westbury bones (M33758) is a little shorter, the other (M33146) a little longer and within the sample of the more massive bison of uncertain affinity from Tiraspol (see Sher, 1997: 173–174). The two Westbury specimens are, however, unstratified and fall in the middle of the Westbury range of postcranial bone diameters (Fig. 13).

The wide size range at Westbury might be due to (a) the presence of different species, (b) strong sexual dimorphism in the postcrania (commonly recorded for large bovids, e.g. Brugal, 1995; Sher, 1997), or (c) fluctuation of size with the climate changes through the Westbury Calcareous Member.

Hypothesis (a) is consistent with the observed size variation in the teeth, which are partly within the size range of *B. schoetensacki*, and partly within that of *B. priscus*. Appreciable sexual dimorphism is not recorded for bison tooth size. On the other hand, Gentry (1999) carefully analysed the morphology of all the bison postcranial elements from Westbury and found no evidence for more than one species.

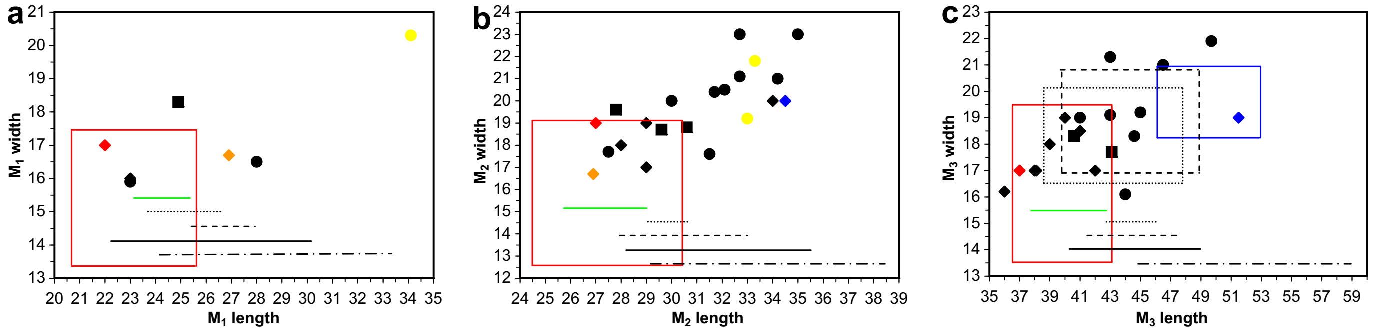

Fig. 12. Biometric comparison of bovid lower cheek teeth. (a) M$_1$, (b) M$_2$, (c) M$_3$. Symbols: ◆, Pakefield, *Bison* cf. *schoetensacki*; ◆, Pakefield, cf. *Bos primigenius* [YM]; ◆ Pakefield, Bovidae indet., BGS 21637 + 21645; ◆, Pakefield, Bovidae indet., NHM M82473; ■, West Runton, *Bison* cf. *schoetensacki*; ●, Westbury, *Bison* level indet; ●, Westbury, *Bison* Yellow Breccia. NHM M82473 has been plotted on both M$_1$ and M$_2$ graphs. Ranges of comparative samples (boxes, length and breadth; lines, length only): solid red box, *Leptobos etruscus*, Senèze (from Douvernois and Guérin 1989, table. 8); solid green line, *B. menneri*, Untermassfeld (from Sher, 1997, fig.5); dotted line, *B. schoetensacki*, Voigtstedt (from Fischer, 1965); dashed line, *B. schoetensacki*, Tiraspol (from Flerov and David, 1971); dotted box (M^3 only), *B. schoetensacki*, Mauer (from Sala, 1986, table 4); dashed box (M^3 only), *B. schoetensacki*, Isernia (from Sala, 1986, table 4); solid line, *B. priscus*, Siberia (from Sher, 1997, fig. 5); dotted/dashed line, *B. priscus*, Ehringsdorf (from Flerov, 1975); solid blue box (M^3 only), *Bos primigenius*, Paglicci Cave (from Sala, 1986, table 4).

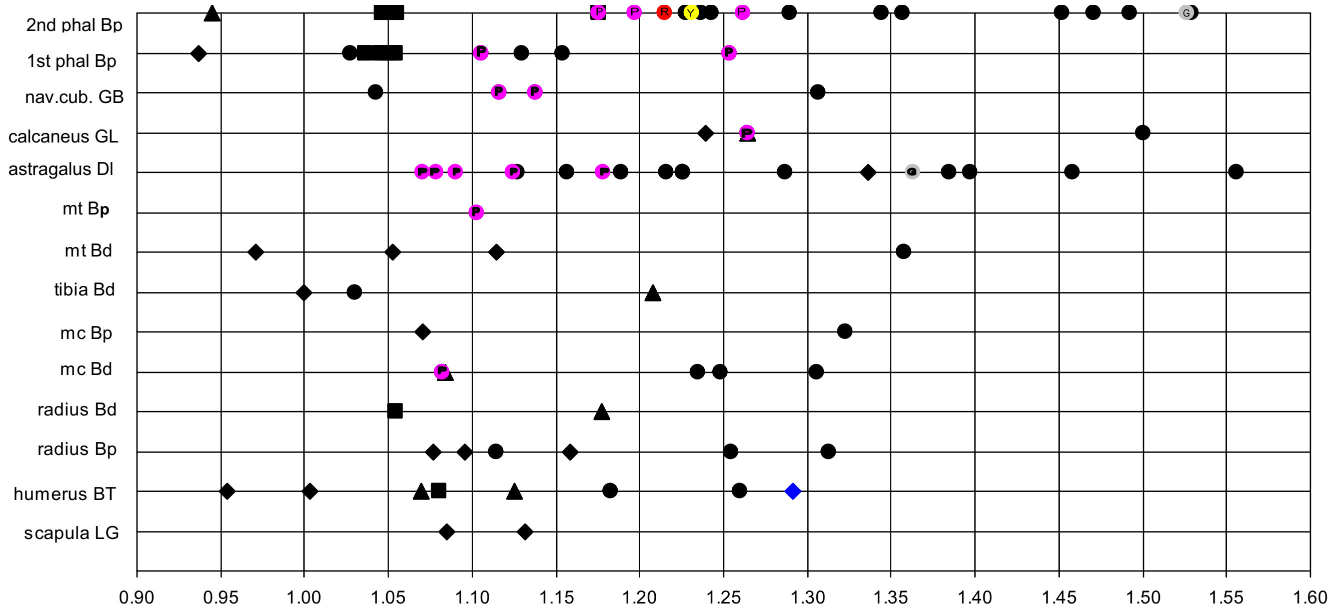

Fig. 13. Biometric comparison of bovid postcranial size. Limb bone measurements (mostly diameters) plotted as a proportion of the corresponding measurement on a modern Bison bison skeleton [NHM 851] used as a standard. Symbols: ◆, Pakefield, Bison cf. *schoetensacki*; ◆, Pakefield, cf. Bos *primigenius*, NHM M6578; ■, West Runton, Bison cf. *schoetensacki*; ●, Westbury, Bison level indet; Westbury, Bison Ⓟ, Pink Breccia; Westbury, Bison Ⓨ, Yellow Breccia; Westbury, Bison Ⓡ, Red Breccia; Westbury, Bison Ⓖ, Grey Breccia; ▲, Boxgrove, *Bison cf. schoetensacki*.

To test hypothesis (b), the Westbury sample was compared with Sher's (1997) data on *B. menneri* from Untermassfeld, a large *Bison* sample that is morphologically homogeneous (Sher, 1997) and accumulated within a relatively short time (Kahlke and Gaudzinski, 2004; Kahlke, 2006). For each measurement (metacarpal Bp and Bd; astragalus GLl and Bd; calcaneum GL and GB; navicocuboid GB; first and second phalanx Bp), the smallest Westbury specimen was expressed as a percentage of the largest, as for Untermassfeld (data in Supplementary information). For most measurements, the difference is greater in the Untermassfeld sample, suggesting that sexual dimorphism in a single species could, in theory, explain the size range observed at Westbury.

To test hypothesis (c), specimens were compared from the different levels of the Calcareous Member, taking stratigraphical information from labels or from Gentry (1999); only about a quarter of specimens are stratified. Bison postcrania are abundant in the Pink Breccia (unit 11), and these are small with respect to the rest of the Westbury sample (Fig. 13). Two plottable teeth from the Pink Breccia ($P^{3/4}$ M48457 and M^3 M43947) are extremely small, while a third (P^3 M48459, Gentry, 1999, Fig. 7.29b) is large; however, the length and width measurements of the latter are inflated by the nearly unworn state of the tooth. Teeth from the Yellow Breccia are more numerous and span a wide range of sizes, from small remains that could correspond to the small bones from the Pink Breccia, to several of the largest specimens from the site. The Pink Breccia, the lowest level of the Calcareous Member (Andrews et al., 1999), was deposited during a temperate phase with broad-leaved deciduous woodland; the Yellow Breccia (level 19), one of the highest, was laid down under apparent periglacial conditions with evidence of steppe-tundra.

In summary, the wide range of measurements in teeth (not markedly sexually dimorphic) as well as bones, together with the correlation of size distribution with stratigraphy, makes it unlikely that sexual dimorphism alone (hypothesis b) can explain the total size range observed among the Westbury bovine remains. Taxonomic and/or stratigraphic heterogeneity (hypothesis [a] and/or [c]) are likely additional factors, and the earlier age of the Pink Breccia could suggest that its small bison was *B. schoetensacki*, while the later Yellow Breccia reflects the immigration of *B. priscus* (whose presence at the site is strongly suggested by metacarpal proportions), with both species co-existing.

5.3. Pakefield

The Pakefield bovid has been recorded as *Bison* sp. by Stuart and Lister (2001) and as *B.* cf. *schoetensacki* by Parfitt et al. (2005).

The sample includes only five upper molars, two M^1 and three M^3, all within the Westbury range for length, although two of the M^3s are narrower (Fig. 11). These, however, fit the breadth range for Mauer *B. schoetensacki* given by Sala (1986). For the more abundant lower molars, the graphs show a generally smaller size at Pakefield, although the majority of teeth still fall within the ranges of both *Bison schoetensacki* and *B. priscus* given by Sher (1997) (Fig. 12).

Two specimens, however, are much larger: an isolated M_2 [NHM M82472], and a nearly complete mandible with M_2–M_3 from the Backhouse collection at YM (Fig. 14). These three teeth are relatively narrow but very long, falling at the upper end of the Westbury range. The clear gap in size with respect to the other Pakefield specimens raises the possibility that they could belong to a different species. The two large specimens are beyond *B. schoetensacki* length ranges given by Sher (1997) and Sala (1986). The M_3 length is 51.5 mm, exceeding any *B. priscus* from Siberia (Sher, 1997) or large *Bos primigenius* from Grays Thurrock (MIS 9) and Ilford (MIS 7)) (Breda, unpublished data); but it is within the range of *B. priscus* from Ehringsdorf (Sher, 1997). Regarding morphology, the isolated M_2 is fragmentary, but the lower jaw (Fig. 14) is well-preserved with typical Rootlet Bed preservation. Some of the features described by Sala (1986) as discriminating *Bos* and *Bison* are either not visible, or are expressed in an intermediate state in this specimen. They are: mesio-distal compression of the two columns of the lower molars (which should be stronger in *Bison*), and ectostylid size (which should be larger and longer in *Bos*). However, the labial re-entrant valley between hypoconid and talonid is quite angular as in *Bison*, rather than more rounded as in *Bos* (Sala, 1986), but the crowns of the molars are columnar as in *Bos* rather than basally inflated as they should be in *Bison* (Merla, 1949; Sala, 1986; Gee, 1991). Gee (1991: 212) also points out that *Bos* M_3s

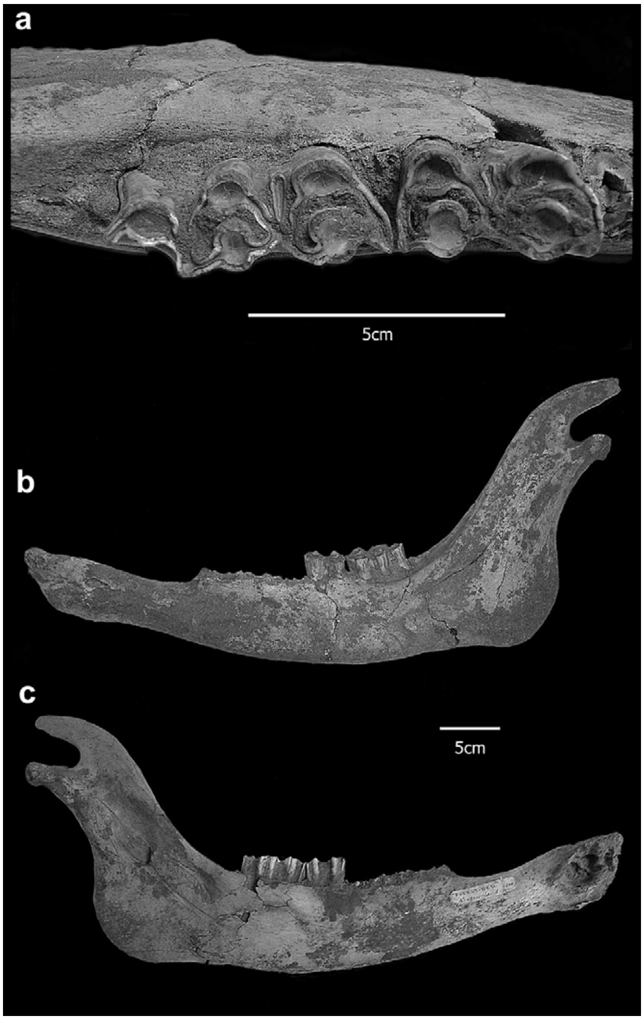

Fig. 14. Left mandible with M_2–M_3 of cf. *Bos primigenius* from Pakefield [YM]: (a) occlusal view; (b) labial view; (c) lingual view.

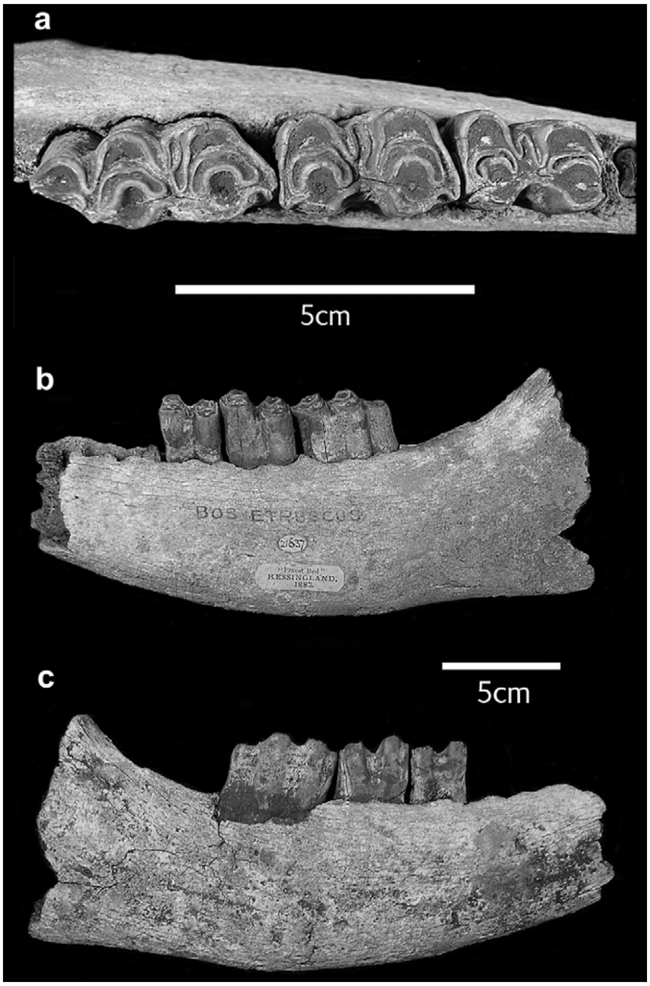

Fig. 15. Left mandibular ramus with M_1–M_3 of indeterminate bovid from Pakefield [BGS 21637 + 21645]: (a) occlusal view; (b) labial view; (c) lingual view.

are relatively narrow with parallel anterior and posterior edges, while *Bison* M_3s have a prominent bulge on the labial side of their anterior lobe and are pinched at their base, somewhat flaring toward the occlusal surface. The specimen is relatively narrow like *Bos*, but a little flaring toward the occlusal surface (visible only in lingual view), like *Bison*. Thus, the identification of this specimen is unclear. However, concerning the shape of the mandible, the region behind M_3 is long and gently sloping, with the ascending ramus backwardly-inclined. This feature is described by Gee (1991: 51–52) (Fig. 2) as typical of *Bos primigenius* in comparison to *Bison,* in which the region behind the third molar is quite short and angled, with a sharply rising ascending ramus.

At the other end of the scale, the smallest specimens from Pakefield are below even the *B. schoetensacki* ranges given by Sher (1997). They are represented by an M_1 [NCM 1918.61 FC4086] and a left mandibular ramus with M_1–M_3 [BGS 21637 + 21645]. This jaw (Fig. 15) was part of the Backhouse collection and bears his label: "Prof. Boyd Dawkins regards this as *Bos etruscus*. I named it so on his authority but have seen no printed notice of such a species". The lengths of M_1 and M_3 (Fig. 12) are below the ranges for *B. menneri* (Sher, 1997), which has smaller lower molars than any later *Bison*, but are close to averages given by Douvernois and Guérin (1989) for *Leptobos etruscus* from Sénèze. The size of these specimens is thus consistent with *Leptobos*. As for morphology, Sher (1997: 112) cautions that dental features are subject to a very wide variation and depend primarily on the stage of wear. Nonetheless, the Pakefield molars show few prominent lingual ribs and a simple pattern of the central cavities, primitive conditions in bovids (Gentry, 1999). The weak metastylid is typical of *L. etruscus* (Douvernois and Guérin, 1989), but the Pakefield specimen lacks the small accessory columns often found on the lingual side of *Leptobos* lower molars (Douvernois and Guérin, 1989). Gee (1991: 268) refers to a lower molar (BGS 21661) from Corton (part of the Pakefield sedimentary complex: Stuart and Lister, 2001), which may represent *Leptobos*. Unfortunately this tooth has not been found during the present anaysis.

A further possible record is a right M_1 or M_2 [NHM M82473; Fig. 16] recently collected from the yellow clay at the top of the Rootlet Bed. It is in the size range of M_1 from Westbury but below the M_2 range (Fig. 12a,b). However, its lingual stylids are strongly developed, so that the divergence, in lingual view, of the mesial and distal edges of the crown is much more pronounced than in the other specimens, inflating the occlusal length measurement. Its identity is uncertain but the well-developed ectostylid precludes an ovibovine (Gentry, pers. comm., 2004). It is strikingly similar to the M_2 of a complete left mandible from the Early Pleistocene of East Runton [NHM M6560] referred to *Leptobos* cf. *etruscus* (Gee, 1991: 268). The similarity lies in the general size and proportion, in the lingually projecting para- and metastylid, and in the occlusally-diverging mesial and distal walls in lingual view. If M82473 were an M_2 it would be close to the *L. etruscus* average given by

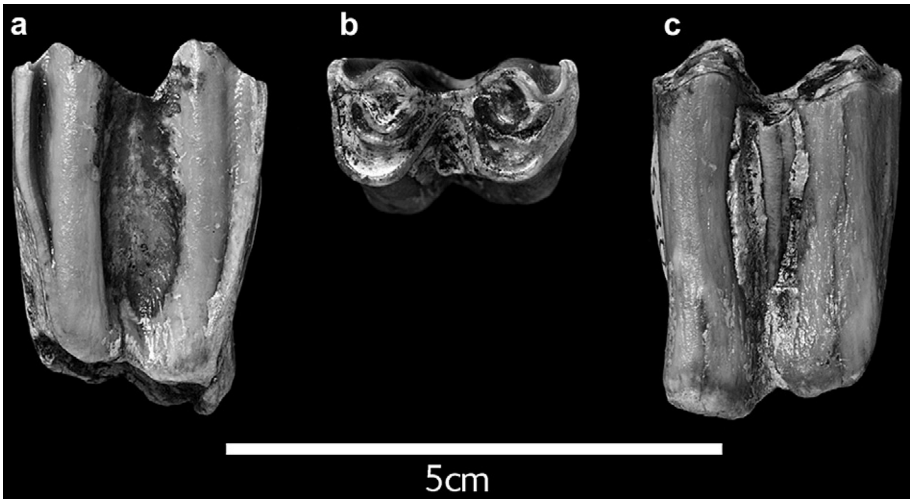

Fig. 16. Indeterminate bovid right M_1 from Pakefield, NHM M82473: (a) lingual view; (b) occlusal view; (c) labial view.

Douvernois and Guérin (1989), although if it were an M_1 it would be well above the length range of *L. etruscus* given by the same authors (Fig. 12a,b).

Another notable Pakefield specimen is a right M^3 [NHM M6567] (Fig. 17). Freudenberg (1914: 86) noted its strongly plicated internal enamel which, according to Piligrim (1939: 260 and 264), is typical of *Bubalus*, with "spurs which project into the central fossettes". Freudenberg (1914) also mentions that the lingual interlobar column is positioned away from the body of the tooth. Notable is the presence of a second lingual interlobar column joined to the mesial lobe. M6567 is more square than other bovid upper molars in this study, being very short (length 30 mm, at the lower edge of *B. schoetensacki* range) but rather wide (breadth 29 mm, toward the upper limit of *B. schoetensacki*) (Fig. 11f). This corresponds to the statement by Piligrim (1939: 254) that the upper molars of *Bubalus* are "but a little longer than broad". Unfortunately there are no *B. murrensis* upper molars described in literature to compare the size and morphology of M6567, so its identification remains unclear.

The postcranial specimens from Pakefield ($N = 16$) are generally the smallest in the study, the only exceptions being a large humerus [NHM M6578] (Fig. 18) and an astragalus [NHM M6584] and calcaneum [NHM M82471] (Fig. 13). The ratio between the diameters of the smallest and largest humeri is 0.74 at Pakefield (data in Supplementary information) and 0.81 at Untermassfeld (data from Sher, 1997). The size range is thus wider in the 3-specimen sample from Pakefield than in the 31-specimen sample from Untermassfeld, suggesting something more than sexual dimorphism in the former. The breadth of the distal trochlea (BT) of M6578 is larger than any *B. schoetensaki* from Isernia or Mauer (Sala, 1986), within the range of the large *Bison* of uncertain affinity from Tiraspol (Sala, 1997), beyond the range of *B. priscus* from North-East Siberia (Sher, 1997) but within those of the same species from Casa Filo, Italy (Sala, 1986) and from the Rhine Valley, Germany (Martin, 1987). Moreover, M6578 is beyond the ranges of *B. primigenius* from Ukraine and Germany (Sher, 1997) but within that of the same species from the Rhine Valley (Martin, 1987). So, in size, it could belong either to *B. priscus* or to *B. primigenius*. Concerning morphology, the characters described by Hiddingh (1984), Sala (1986) and Martin (1987) for discriminating between *Bos* and *Bison* were scored, and M6578 corresponds better to the morphology of *B. primigenus*. The features involved are: the distal extension of the epitrochlea medialis (more distally extended than the trochlea medialis, as in *Bos*, rather than as much as the trochlea

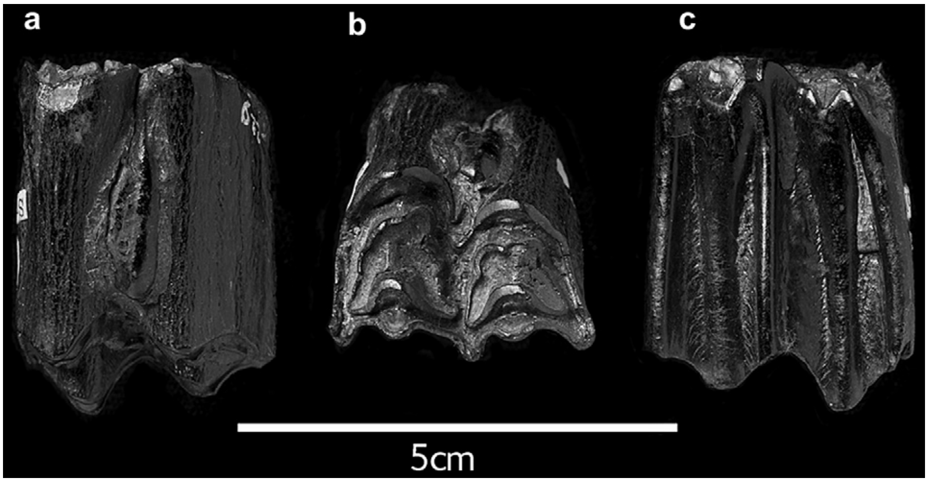

Fig. 17. Indeterminate bovid right M^3 from Pakefield, NHM M6567: (a) lingual view; (b) occlusal view; (c) labial view.

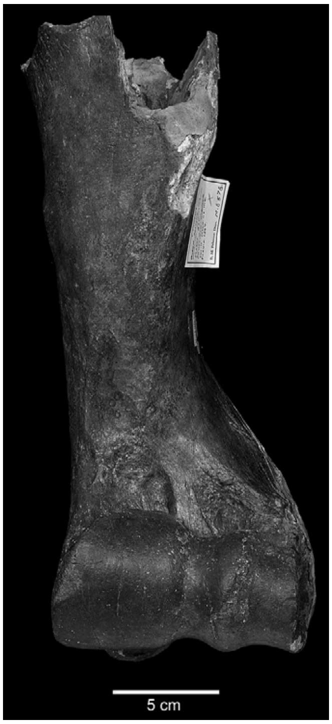

Fig. 18. Left humerus of cf. *Bos primigenius* from Pakefield, NHM M6578: anterior view.

medialis as in *Bison*) and the distal profile of the trochlea (which has marked swellings and depressions as in *Bos*, rather than being smoother as in *Bison*).

Horncore evidence is limited. An adult horncore from the Mutch collection [NHM M82547] (Fig. 19a) is broken at the proximal end but probably close to the base, as open sinuses are exposed inside. The preserved contour length is 23 cm. Its shortness and rather strong curvature are consistent with *Bison schoetensacki* (cf. Sala, 1986). The Backhouse collection [YM] includes a right frontal with base of horn, labelled "*B. etruscus*" (Fig. 19b). The frontal extends behind the posterior edge of the horncore – suggesting *Leptobos* or *Bison*, but not *Bos*. The more lateral, rather than backward direction of the horncore relative to the frontal suggests *Bison* rather than *Leptobos* (Van der Made, pers. comm.). The preserved (incomplete) length of the horncore is approximately 150 mm, basal circumference of horncore 245 mm, dorso-ventral diameter 67 mm, antero-posterior diameter 82 mm. Another horncore [NCM 1918.61.4004] has not been seen.

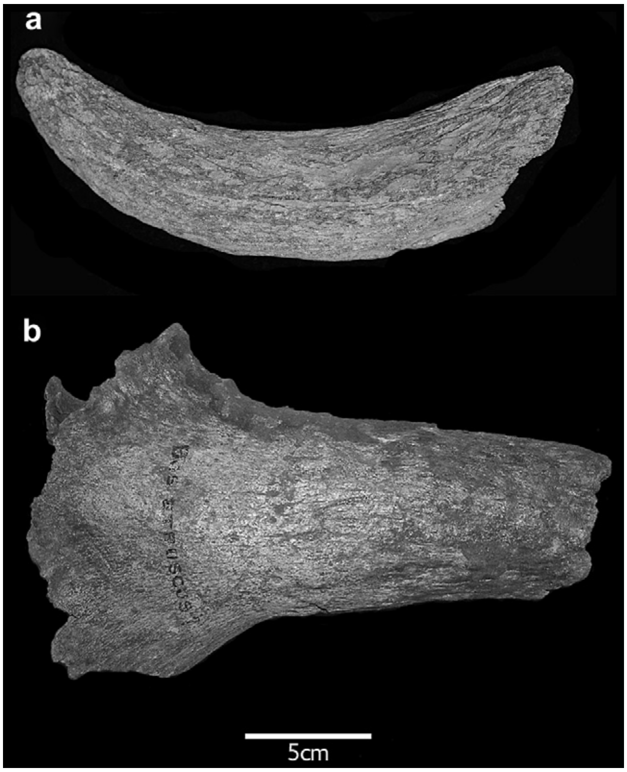

Fig. 19. Horncores of cf. *Bison schoetensacki* from Pakefield: (a) NHM M82547; (b) YM, dorsal view.

In sum, the majority of the Pakefield sample can be referred to *Bison* cf. *schoetensacki*. In addition, the possible presence of *Bos primigenius* is suggested by the large mandible and humerus, while other dental remains have features suggestive of *Leptobos* and *Bubalus*. Further collecting is required to confirm these records.

5.4. West Runton

At West Runton, Stuart (1974, 1982, 1996) and Sala (1986) recorded *B. schoetensacki*. In size, dental remains are generally within the main Westbury and Pakefield ranges (Figs. 11 and 12). Three upper premolars (two P^2 and one P^3) are rather narrow, while, an M^2 is notably short. Postcranial specimens are few ($N = 10$, eight of which are phalanges), but plot within the Pakefield range.

Two partial horncores are preserved at NHM. The more complete [M17249] (Fig. 20) is a left adult horncore broken at the proximal end but probably close to the base as open sinuses are exposed inside. The preserved contour length is 21 cm. Its size and general form are similar to NHM M82547 from Pakefield (above), and are consistent with *Bison schoetensacki*. The second piece [M17250] is an unidentifiable distal tip of a horncore.

5.5. Boxgrove

Dental remains are rare. The single upper molar, M^3 [NHM M82531] (Parfitt, 1999, Fig. 174), is notably narrow, similar to two specimens from Pakefield (Fig. 11f).

Postcranial specimens from Boxgrove are few ($N = 7$), but plot within the Pakefield range. By comparison with Sher's (1997) graph (see above), the single complete metacarpal from Boxgrove [NHM M82529] is about as long as the longest from Westbury but far more slender, clustering with either *B. priscus* female from Mosbach or *B. schoetensacki* from Mauer and Mosbach (Preece et al., 2009).

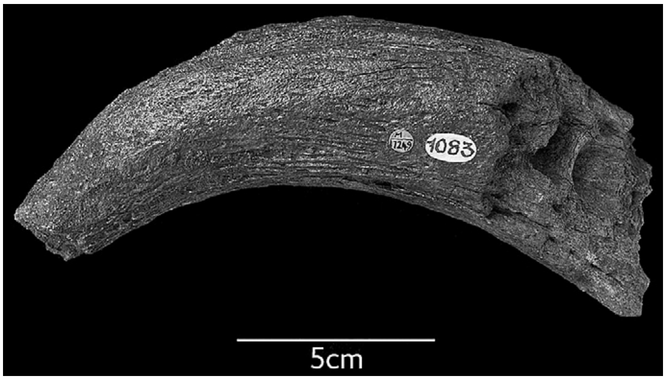

Fig. 20. Horncore of cf. *Bison schoetensacki* from West Runton, NHM M17249, anterior view.

5.6. Conclusion (bovids)

It seems very likely that more than one large bovid was present in the British early Middle Pleistocene. Although the comparison with Untermassfeld indicates that the wide size range of postcrania at Westbury could in theory be encompassed by sexual dimorphism within a single *Bison* species, the pattern of variation between levels suggests possible taxonomic differentiation, with *B. schoetensacki* present in the earlier (temperate) Pink Breccia, and both *B. schoetensacki* and *B. priscus* in the later (colder) Yellow Breccia.

At Boxgrove, sample size is small, but the bovids are more compatible in size with the group of smaller specimens from Westbury, and in fact map very closely in range to the sample from the Pink Breccia. This hint of a stratigraphic correlation between the interglacial at Boxgrove and the earlier temperate stage at Westbury is, however, opposite to the conclusion drawn on the basis of *Microtus* species by Preece and Parfitt (2008), and may have climatic rather than chronological significance.

The bovid remains from West Runton and Pakefield are also generally in the smaller half of the Westbury range (*B. schoetensacki* size). However, at Pakefield the situation is complicated by the additional presence of still smaller, unidentified dental remains, some with features recalling *Leptobos*, another recallling *Bubalus*; and of a larger species, probably *Bos primigenius*. If the presence of *B. primigenius* were confirmed, it would be the oldest record of aurochs in the British Isles.

6. Discussion

The present study demonstrates that new material will be required to further elucidate the taxonomic position of rhinoceroses and large bovids from the early Middle Pleistocene of Britain, and their relationships with coeval populations from continental Europe. The taxonomic conclusions of this paper, based on the four main sites of Pakefield, West Runton, Westbury and Boxgrove, are summarised in Table 3. Despite the small samples available for some taxa at certain localities, the following general observations can be drawn:

a. In addition to the common *Stephanorhinus hundsheimensis*, there are hints of undescribed *Stephanorhinus* taxa at Pakefield and West Runton. One, ‘species A’, is shared between the two sites, while the other, ‘species B’, is found only at West Runton. While the former might suggest a similar geological age for the sites, the latter implies that they are not precisely coeval.
b. At Boxgrove, in addition to *S. hundsheimensis*, a rhino similar to *S. megarhinus* (a form generally associated with the Pliocene) occurs. This record, if corroborated, supports the contention that the species survived well beyond its supposed Pliocene–Early Pleistocene range.
c. At Westbury, a small bison referable to *B. schoetensacki* (that also occurs at the other three sites) is present in both the Pink (earlier, temperate) and Yellow (later, colder) Breccias. In the Yellow Breccia, it is accompanied by a larger bison which may be *B. priscus*. This co-occurrence suggests an immigration of *B. priscus* from outside, rather than autochthonous European origin of *priscus* from *schoetensacki.*
d. As many as four bovid species may be represented at Pakefield, with dominant *B.* cf. *schoetensacki*, the probable earliest occurrence in Britain of *Bos primigenius*, and possibly two smaller species of unclear identification.

Taken as a whole, the mammal faunas from Pakefield and West Runton on one hand, and from Westbury and Boxgrove on the other, have features indicating an older age for the two sites of the Forest-bed Formation (Parfitt, 1999; Schreve et al. 1999; Maul and Parfitt, in press). The two Families considered here do not, at the present state of knowledge, contribute clear biostratigraphic evidence on this point. However, as suggested by molluscs and some of the mammals (Preece and Parfitt, 2000, 2008; Stuart and Lister, 2001), there are also age differences within each of these two groups, and this is supported by the reassesment of the Rhinocerotidae and Bovidae.

Table 3
Summary of rhinoceroses and large bovids identified in this study, plus data from Little Oakley from Lister et al. (1990). PB, Pink Breccia, YB, Yellow Breccia.

Species	Little Oakley	Pakefield	West Runton	Westbury	Boxgrove
Stephanorhinus hundsheimensis		x	x	x	x
Stephanorhinus sp. A aff. *S. etruscus/ hundsheimensis*		x	x		
Stephanorhinus sp. B aff. *S. etruscus/ hundsheimensis*			x		
Stephanorhinus cf. *megarhinus*					x
Bison cf. *schoetensacki*	?	x	x	x (PB & YB)	x?
Bison cf. *priscus*				x (YB)	
Small bovid indet.		x (two types)			
Large bovid, cf. *Bos primigenius*		x			

In the taxa examined here, the Pakefield assemblage shows a remarkable diversity of forms, with an unusual rhino and possibly three unusual bovids in addition to the species found at other sites. Parfitt et al. (2005) suggested, from the presence of *Mimomys pusillus* at Pakefield, that the latter site pre-dated West Runton. On the other hand, the probable earliest British appearance of *Palaeoloxodon* (straight-tusked elephant) at Pakefield but not at West Runton, was suggested as possible evidence of younger age (Stuart and Lister, 2001). A very similar situation pertains to the record of *Bos primigenius* at Pakefield, if its absence from West Runton is not due to inadequate sampling or a cooler climate (Parfitt et al., 2005). Together, these data corroborate the difference between the two sites, but leave their relative age an open question.

Similarly, the voles from Boxgrove point to a somewhat later date than the whole of the Westbury sequence (Preece and Parfitt, 2000). The evidence from other mammal families (e.g. size differences in red deer: Lister et al., in press) corroborates a difference in age between the interglacials at the two sites. The apparent occurrence of *Bison priscus* in the upper levels at Westbury (the Yellow Breccia), not found in the available material from Boxgrove, could be seen to favour a younger age if regarded as a first appearance datum, but might merely reflect the more open environment of the Yelllow Breccia. The occurrence of *Stephanorhinus* cf. *megarhinus* at Boxgrove is also unique among the sites considered here, and indeed in the entire British Pleistocene.

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Appendix. Supplementary information

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.quaint.2010.05.010.

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