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Micromammals from the 1995 Mammoth Excavation at West Runton, Norfolk, UK, morphometric data, biostratigraphy and taxonomic reappraisal.

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Abstract

In this paper, the small mammals recovered from sediments associated with the West Runton Elephant has been analysed and compared with sites in other parts of Europe. Major taxonomical problems are indicated and we suggest ways of utilising such morphological complexity to refine biostratigraphical and chronostratigraphic attributions.

The micromammal assemblage from the West Runton Elephant Site so far totals 16 species from the West Runton Forest Bed (WRFB). There are strong similarities with the arvicolid spectrum of basal layer H8 in the Koněprusy C 718 profile (Czech Republic), which accumulated under cooler conditions preceding the thermal maximum of an early Middle Pleistocene interglacial. Rare steppic indicators (e.g. *Cricetus*) at West Runton also imply a somewhat cooler and more continental climate than the present day, but overall the fauna is fully temperate in character. West Runton shares several stratigraphically significant small mammal taxa with Voigtstedt (Central Germany) and morphometric comparisons suggest that Voigtstedt may be slightly younger than West Runton. The presence of *Mimomys savini*, with a latest occurrence in the early part of Marine Isotope Stage (MIS) 15, together with the palaeomagnetic evidence suggests the WRFB may have been emplaced during the early part of MIS 17. However, given the complexity of the marine isotope curve during the early part of the Brunhes Chron and differences between global and

regional climatic evolution, it is difficult to assign the normally magnetized WRFB to a particular Marine Isotope Stage (MIS).

1. Introduction

East Anglia, with the West Runton Freshwater Bed (WRFB), in particular, is considered the ‘cradle’ for the development of small mammal palaeontology in the Quaternary. Many of the early developments in this field were made during the second half of the 19th and the first half of the 20th century by a distinguished group of palaeontologists that includes such famous names as Sir Charles Lyell (1797-1875), Sir Richard Owen (1804-1892), Edwin Tully Newton (1840-1930), Charles Immanuel Forsyth Major (1843-1923), and, in particular, Martin Alister Campbell Hinton (1883-1961). Their major achievement was to recognise that many of the small mammal taxa from the East Anglian ‘Crag’ and ‘Forest bed’ deposits were distinct from living species, despite their superficial morphological resemblances. This resulted in the description of 14 new micromammal species from the early Middle Pleistocene deposits at West Runton alone. The most familiar of these is the ancestral water vole *Mimomys savini* Hinton, 1910, an important member of an evolving lineage, which is central to arguments concerning the age of many Quaternary sites across Eurasia (Fejfar and Heinrich, 1980; Koenigswald and van Kolfschoten, 1996). Other species include *Sorex runtonensis* Hinton, 1911, *Sorex savini* Hinton, 1911, *Neomys newtoni* Hinton, 1911, *Sciurus whitei* Hinton, 1914, *Cricetus runtonensis* Newton, 1909, *Mimomys intermedius* Newton, 1882, *Mimomys majori*, Hinton 1910, *Microtus arvalinus* Hinton, 1923, *Microtus nivalinus* Forsyth Major, 1902, *Microtus nivaloides* Hinton, 1923, *Microtus ratticepoides* Hinton, 1923, *Microtus gregaloides* Hinton, 1923 and *Microtus arvaloides* Hinton, 1923. Opinions differ as to the validity of some of these, which has resulted in inconsistent usage in various parts of Europe and Russia. Such inconsistency hinders meaningful comparisons between sites and, in extreme situations, may lead to sites being assigned different ages on the basis of such supposed ‘faunal differences’.

Many of the holotypes and figured specimens from West Runton are housed in The Natural History Museum (London), together with a substantial collection of small mammal remains made by Alfred Collison Savin (1862-1948). Other important collections are curated at the Norwich Castle Museum, Norfolk, British Geological Survey Museum, Keyworth, University Museum of Zoology, Cambridge and the Harrison Zoological Museum, Sevenoaks. Most of these collections have a long curatorial history that has involved sorting into taxonomic groups and morphotypes. In these cases it is not possible to re-assemble an unbiased collection. A further problem with much of the museum material is that the exact stratigraphic provenance and method of recovery of many of the specimens is unknown. The stratigraphy at West Runton is complex and includes earlier temperate and cold stage deposits of Late Pliocene to early Middle Pleistocene age, as well as a later sequence of marine and freshwater sediments that overlie the WRFB (West, 1980). Most of these deposits are known to contain vertebrate remains (Stuart, 1975, 1981; Preece and Parfitt, 2000, 2008). These problems are unfortunate because the micromammalian fauna contained in the WRFB underpins much of our understanding of early Middle Pleistocene mammalian biostratigraphy.

The faunal information presented in this study derives from a new collection of micromammal remains recovered from sediments associated with a nearly complete skeleton of steppe mammoth (*Mammuthus trogontherii*), excavated from the WRFB in 1995 (Stuart and Lister, this volume). This rich collection, which provides an unbiased sample of the principal small mammal taxa found in the WRFB, is used for morphometric comparisons with collections from other parts of Europe, principally from sites in central and western Europe.

This paper is a collaboration between two small mammal specialists trained in different taxonomic traditions with the specific aim of addressing these problems. In this paper, we do not attempt a full taxonomic revision of these taxa, although a revision of the West Runton type material is in progress. Instead, we want to draw attention to the major problems and suggest ways of utilising such morphological complexity to refine biostratigraphical and chronostratigraphic attributions.

Secondary aims are to discuss of the palaeoecology of the small mammals together with aspects of assemblage taphonomy, the latter also provides information on the possible rate of deposition of the sediments containing the elephant.

2. Materials and Methods

2.1. Location, geological context and sampling methods

The West Runton elephant was discovered in 1990, and excavations in 1992 and 1995 recovered most of the skeleton. The West Runton Forest Bed (WRFB), the stratotype of the Cromerian Stage (West, 1980), is exposed at the base of coastal cliff sections, 3 km to the west of Cromer, Norfolk. The WRFB comprises a ca. 1.5 m thick deposit of marls and richly fossiliferous detritus muds that occupy a shallow channel cut into sands and gravels. These earlier sediments include fossil-rich marine ‘Crag’ of Late Pliocene age. The early Middle Pleistocene WRFB sediments were deposited by a small river, part of a much larger fluvial network that drained eastwards into the southern North Sea Basin (Gibbard and Boreham, this volume). Palynology and plant macrofossil evidence shows that the earliest marly sediments were deposited in a landscape dominated by herbaceous vegetation, fen and reedswamp (Cr Ib of West, 1980). This phase of inorganic sedimentation was succeeded by detritus muds containing pollen indicative of regional temperate forest (Cr IIa, Cr IIb of West, 1980). Pollen from the sediments containing the elephant skeleton indicates that only part of this succession (equivalent to Cr IIa of West, 1980) is represented at the elephant site (Peglar, this volume).

The new micromammal material comes from a column (squares 73 and 74), located within the main scatter of elephant bones. Here, samples were taken continuously at 5 cm intervals through the complete 1.35 m sequence of the organic detritus muds (equivalent to bed f of West, 1980). In the laboratory, 4,524 kg of matrix from the column was wet-sieved using a semi-automatic sieving machine (Ward, 1981), through a sieve with a mesh size of 0.5 mm. The resulting residues were then air-dried and picked for microvertebrates. The finer fractions were sorted under a binocular microscope, thus ensuring the complete recovery of all identifiable microvertebrate remains. In total more than 8,000 small mammal remains were recovered of which approximately 1,000 elements (mostly isolated teeth) were identified to species level. This is the largest well-stratified micromammal sample from the site, recovered using the most detailed sampling of the WRFB yet undertaken. The only other comparable study was that carried out by Stuart (1975) at locality 'AJS', approximately 30 m to the west of the elephant site, where three smaller sequential samples were collected and analysed for microvertebrates.

2.2. Measurements and abbreviations

In the following descriptions, lower case denotes lower teeth and upper case denotes upper teeth. All measurements are given in millimetres. Terminology of the occlusal surface of arvicolid molars (LRA – lingual re-entrant angle, BRA – buccal re-entrant angle, LSA – lingual salient angle, BSA – buccal salient angle) is after van der Meulen (1973) and terms used to describe enamel differentiation follow Martin (1987): 'negative' enamel differentiation (also known as '*Mimomys*' differentiation) refers to molars with thicker enamel on trailing and thinner enamel on leading edges of triangle prisms; 'positive' enamel differentiation (also known as '*Microtus*' differentiation) refers to molars with thinner enamel on trailing and thicker enamel on leading edges of triangle prisms. For morphometric comparisons of arvicolid m1s we use the following indices: A/L for the relative length of the anteroconid complex (ACC) (van der Meulen, 1973), and Hsd/L for the relative height of the buccal posterior tip of enamel-dentine junction line (linea sinuosa) (Hsd - hyposinuid. Rabeder, 1981; Maul et al., 1998a, b). For comparison of enamel thickness in *Mimomys* we use the enamel differentiation quotient (SDQ) with enamel thickness measurements following Heinrich (1978). Other measurements are defined when used.

3. Taxonomy

The following section discusses the taxonomy of the 1995-Mammoth Excavation micromammals and relevant ecological information. The remains indicate a total of 16 species, which are listed in Table 1. In this paper, the taxonomy used differs from that in recent discussions of the WRFB micromammals (e.g. Stuart, 1996; Preece and Parfitt, 2000). The previous taxonomies (Table 1, column 1 and 2) group successive fossil 'populations' into single-species lineages based on the identification of phyletic sequences. A disadvantage of this approach is that morphological and metrical differences between the fossil forms and their living descendents are downplayed because any differences cannot be categorized using a simple binomial classification. An alternative approach may identify multiple species in a phyletic sequence. One problem with this approach is that the differentiation of 'chronospecies' rests on arbitrary species boundaries in a phyletic sequence, which may exhibit a complex pattern of mosaic evolution. These differences of approach have important implications. For example, the species lists of Stuart and Parfitt (Stuart, 1996; Preece and Parfitt, 2000) have a modern 'flavour', whereas in the alternative taxonomy nearly all of the WRFB species are considered to be extinct (Table 1, column 3). While it is beyond the scope of this paper to resolve the taxonomic issues, we nevertheless provide detailed descriptions, which are illustrated where possible. The measurements presented also allow comparisons with other samples from key European assemblages.

[Table 1 here]

Mammalia Linnaeus, 1758
Lipotyphla Haeckel, 1866
Talpidae Gray, 1825
Talpinae Murray, 1866
Talpa Linnaeus, 1758
***Talpa* sp., *Talpa europaea* Linnaeus, 1758, *Talpa minor* Freudenberg, 1914**

Material: *Talpa* sp.: 3 antemolars, 2 M2, 1 M3, 6 lower molars, 1 m1, 2 radius fragments; *T. europaea*: 1 humerus fragment (Fig. 1a); *T. minor*: 1 radius (Fig. 1b).

Remarks: Identification of fossil mole species is based mainly on the size of postcranial bones. Although dental differences have also been described, the degree of intra- and interspecific variation in extant and fossil *Talpa* species is currently poorly known. In the 1995-Mammoth Excavation sample there are only two complete mole bones, a humerus (Fig. 1a) and radius (Fig. 1b), which can be determined as *Talpa europaea* and *Talpa minor* respectively. It has not been possible, on the basis of isolated teeth, to distinguish between *T. minor* and *T. europaea* in the West Runton collection, therefore these remains are assigned to *Talpa* sp. Table 2 gives measurements of the humerus and radius from the 1995 sample, together with those of a much larger sample of West Runton material in museum collections. These can be compared with material from other Pleistocene and Recent samples.

Formerly, fossil specimens of *T. europaea* size have been referred to as *T. praeglacialis* Kormos, 1930 or *T. fossilis* (Petényi, 1864). However, these may not be valid species, and their size falls within the range of variation observed in Recent populations of *T. europaea* (Maul, 2001 and references therein). Remains of Late Pliocene and Pleistocene *Talpa* smaller than those of the recent *T. europaea* are generally attributed to *T. minor*. The fossil species *T. gracilis* Kormos, 1930 is considered to be synonymous with *T. minor*. Today, several mole species are endemic to southern Europe, including two species (*T. stankovici* V. Martino & E. Martino, 1931 and *T. romana* Thomas, 1902) similar in size to *T. europaea*, as well as ‘dwarf’ moles of *T. minor* size (i.e. *T. caeca* Savi, 1822 and *T. occidentalis* Cabrera, 1907). These southern European species have not been identified in the fossil record from northern Europe. *Talpa europaea* does not provide any stratigraphic information, but the youngest records of *T. minor* in northwestern Europe is from the ‘Upper Sequence’ at Hoxne (Suffolk, Stuart et al. 1993), dating to a post-Hoxnian temperate episode within MIS 11 (Ashton et al., in prep.).

Moles are highly specialized burrowing insectivores, which avoid wet and sandy substrates, preferring soft fertile soils often in deciduous woodland or open meadows.

[Table 2 here]

[Figure 1 here]

Desmaninae Thomas, 1912

Desmana Gueldenstadt, 1777

***Desmana* sp.**

(= *Desmana moschata* (Linnaeus, 1758) auctt.)

Material: 3 antemolars, 1 upper incisor (Fig. 1c), 1 P4, 1 maxilla with M3, 1 M3, 2 upper molars, 1 mandible fragment without teeth, 1 humerus fragment, 1 calcaneus fragment.

Remarks: As in all talpids, the bones and teeth of water moles are easily recognizable because of their highly distinctive morphology. Schreuder (1940) and Stuart (1975, 1996) previously attributed the West Runton *Desmana* to the living Russian desman, *Desmana moschata* (Linnaeus, 1758). However, dimensions of the West Runton (Table 3) teeth are smaller than those of *D. moschata* but identical to those of *D. thermalis* given by Rümke (1985). This is the basis for the identification of *D. thermalis* at other early Middle Pleistocene sites, such as from Voigtstedt in Germany (Maul, 1990) or Přezletice in the Czech Republic (Fejfar, 1993). *Desmana thermalis* is a typical element of Late Pliocene to early Middle Pleistocene faunas in Europe (e.g. Tegelen in The Netherlands, Betfia 2 in Romania, Přezletice and Hundsheim in Austria and Voigtstedt), but *D. moschata* was also present in the same geographical region (e.g. in Germany at Hohensülzen (Storch et al., 1973) and Mosbach 2 (Schmidtgen, 1924)), at least from the late Early and early Middle Pleistocene onwards. The attribution to species on the basis of size alone may lead to spurious identifications. Recently, it has been shown that two size groups of *Desmana* occur after the Anglian Stage in England (Parfitt, 1998). A small form, with measurements within the range of the West Runton sample, occur in the early part of the Hoxnian (MIS 11) at Barnham, Suffolk (Parfitt, 1998), while a larger form, also attributed to *D. moschata*, occurs in younger deposits at Hoxne (Stuart et al., 1993). This suggests that there was considerable variation in the size of *D. moschata* during the latter part of the Middle Pleistocene, but the extent of size variation in earlier populations is currently unknown. The problem of identification is compounded by the sparse and fragmentary nature of the fossil material at most sites, together with the subtle morphological differences between *D. moschata* and *D. thermalis* described in the literature (Schreuder, 1940; Thenius, 1948; Heller, 1954). For these reasons the West Runton Desman is referred to *Desmana* sp. A detailed analysis of dental morphology in a larger sample may resolve the specific identity of the West Runton *Desmana* (cf. Schreuder, 1940).

Water moles are closely associated with water and feed mainly on small aquatic animals, such as fishes, frogs and invertebrates.

[Table 3 here]

Soricidae Gray, 1821

Soricinae Fischer von Waldheim, 1817

Sorex Linnaeus, 1758

Sorex cf. *minutus* Linnaeus, 1766

Material: 4 mandible fragments without teeth (Fig. 2A, B, b).

Remarks: Four shrew mandibles can be distinguished from *Sorex runtonensis* Hinton, 1911 on the basis of their small size (Table 4). The dimensions of the mandibles fall within the range of both *Sorex minutus* Linnaeus, 1766 and *S. minutissimus* Zimmermann, 1780. Sulkava (1990) has suggested that the position of the mental foramen distinguishes the mandible of *S. minutus* from that of *S. minutissimus*. According to Sulkava (ibid.) the foramen is situated below the protoconid of the m1 in *S. minutissimus*, whereas in *S. minutus* it is situated below the posterior margin of p4. However, observations on modern British *S. minutus* housed in The Natural History Museum (London) show that the foramen is in fact situated below the anterior part of the m1 or below the junction between p4 and m1. Similarly, Rzebik-Kowalska (2000) notes that in *S. minutus* the foramen is positioned below the anterior part of the m1, whereas in *S. minutissimus* the foramen is situated below the buccal re-entrant valley of the m1. This is the basis of the recent identification of *Sorex minutissimus* from the Forest-bed Formation at Norton Subcourse, Suffolk (Lewis et al., 2004). *Sorex minutus* was first recorded in the WRFB by Harrison and Clayden (1993), but previously unrecognised specimens of *S. minutus* have recently been found in museum collections. In the 1995 specimens, the foramen is situated below the anterior part of the m1 in three mandibles, but in the fourth specimen the anterior part of the mandible is damaged. We tentatively assign these specimens to *S.* cf. *minutus* pending a detailed comparison with reference material and small soricid mandibles from earlier WRFB collections.

The pigmy shrew is ecologically tolerant, living in open land as well as in humid forest, whereas the least shrew is distributed in continental parts of northern Europe.

Sorex runtonensis Hinton, 1911

Material: 2 lower incisors, 30 mandible fragments (Fig. 2C, c, D, d).

Remarks: Lower and early Middle Pleistocene ‘red-toothed’ shrews with the typical articular process of *Sorex* and intermediate in size between *S. araneus* Linnaeus, 1758 and *S. minutus* are commonly referred to as *S. runtonensis*. The phylogenetic relationship between *S. runtonensis* and modern *Sorex* species is controversial, with one school of thought suggesting that it is an ancestor of *S. tundrensis* Merriam, 1900 (Osipova et al., 2006), whereas others suggest that it may be an ancestor of *S. caecutiens* Millet, 1828 (Parfitt, 1998). Late Pleistocene records attributed to *S. runtonensis* imply that it became extinct during the Last Cold Stage (Harrison, 1996). There is a general increase in the size of *S. runtonensis* through the Pleistocene (Jánossy, 1969), which is illustrated by measurements of the mandible given in Table 5. This may have been unidirectional but there are too few specimens to confirm this assumption for many sites. Measurements of the height of the ascending ramus and m1-m3 length of the WRFB specimens are larger than those from Untermaßfeld (Germany), Les Valerots (France), Podumci (Croatia), Holstejn (Czech Republic) and smaller than those from Hundsheim, an observation consistent with the assumed stratigraphical position of West Runton (Table 4 and 5).

The ecology of *S. runtonensis* was probably similar to that of the living members of the *S. araneus* group, which are generally found in dense vegetation.

Sorex (*Drepanosorex*) Kretzoi, 1941

***Sorex* (*Drepanosorex*) *savini* Hinton, 1911**

Material: 1 upper incisor, 7 maxilla fragments, 9 lower incisors, 53 mandible fragments (Fig. 2e, F, G, g), 5 lower molars.

Remarks: *Sorex savini* is the most abundant shrew in the WRFB assemblage. Members of the subgenus *Drepanosorex* are larger than other contemporaneous *Sorex* species, and they are distinguished morphologically by having a fissident upper incisor and exoedaenodont cheek teeth. An additional character is the relative size of the P3 and P4. In *S. savini*, the P3 is large and relatively broad in relation to the P4 (cf. fig. 2e), whereas in other species of *Sorex* the P3 is relatively smaller in comparison to the P4 width.

Several species of *Drepanosorex* have been identified and these appear to represent an evolving lineage beginning with *S.* (*D.*) *praearaneus* Kormos, 1834 (type locality Villány 3, Hungary) - *S.* (*D.*) *margaritodon* Kormos, 1930 (type locality Betfia 2, Romania) - *S.* (*D.*) *savini* Hinton, 1911 (type locality West Runton) - *S.* (*D.*) *austriacus* Kormos, 1937 (type locality Hundsheim, Austria), which became extinct at the end of the early Middle Pleistocene. The taxonomic validity of *S.* (*D.*) *pachyodon* Pasa, 1948 is uncertain, but chronologically it lies between *S.* (*D.*) *praearaneus* from Tegelen and *S.* (*D.*) *margaritodon* from Betfia 2. The lineage shows a general size increase in successive populations (Table 5). The West Runton specimens are larger than those from Untermaßfeld and Betfia, but smaller than those from Hundsheim, which is in agreement with the stratigraphical position of West Runton (Table 4 and 5).

The unusual features of their dentition led Kormos (1935) to suggest that members of the subgenus *Drepanosorex* inhabited waterbodies. This interpretation is in complete accord with their relative abundance in aquatic depositional environments, such as at West Runton.

Neomys Kaup, 1829

***Neomys newtoni* Hinton, 1911**

Material: 1 lower incisor, 9 mandible fragments (Fig. 2H, h, I, i).

Remarks: The shape of the articular process (Fig. 2h, i) of the mandible distinguishes *Neomys* from *Sorex*. In the Neomyini, the articular facets are separated by a narrow interarticular bridge, which is also characteristic of the much larger shrew *Macroneomys* Fejfar, 1966 (Table 5). The taxonomy of Pleistocene *Neomys* is confused, the validity of the species described by Hinton (1911) on the basis of very scanty material from Britain is debatable, and the relationship of these forms to the extant species is unclear. According to the original description by Hinton (1911) *N. newtoni* is smaller than both extant European species of water shrew, *N. anomalus* Cabrera, 1907 and *N. fodiens* (Pennant, 1771). This observation is confirmed by measurements of the new material given in Table 4 and 5. The earliest record of *Neomys* is from Monte Peglia, Italy, dating to the late Early Pleistocene (van der Meulen, 1973). Records of Neomyini from the late Early and early Middle Pleistocene are sparse, consequently the relationship of *Neomys* to *Asoriculus* (the probable Late Pliocene ancestor of *Neomys*), the nature of size change and the status of *Neomys* species described for this period are currently unclear.

Based on the ecology of the living Neomyini, it is probable that *N. newtoni* was also a semiaquatic animal.

[Table 4 here]

[Table 5 here]

[Figure 2 here]

Rodentia Bowdich, 1821

Castoridae Gray, 1821

Castor Linnaeus, 1758

***Castor fiber* Linnaeus, 1758**

Material: 1 right M1 or M2 (Fig. 3A, a); 1 right p4 (Fig. 3B, b).

Remarks: The upper molar and the lower premolar are indistinguishable from those of *Castor fiber*. They belong to different individuals, since the p4 is much more worn than the M1/2. Table 6 gives measurements of these specimens. In general, the tooth morphology and size of *Castor* is relatively stable through the Pleistocene; however, the distance between the base of the crown and the base of the lateral enamel ‘infolds’ of the cheek teeth (striae in upper and striids in lower molars and premolars) change through time and can provide information on the relative age. This trend is best illustrated by the p4 (Kretzoi, 1977; Heinrich, 1989). Unfortunately, the p4 from West Runton is nearly completely worn and thus cannot be analysed.

Since beavers are strictly semi-aquatic animals they are useful palaeoenvironmental indicators. They inhabit large streams or lakes bordered by deciduous trees, the bark and branches of which form a significant part of their diet.

[Table 6 here]

[Figure 3 here]

Muridae Illiger, 1815

Cricetinae Murray, 1866

Cricetus Leske, 1779

***Cricetus runtonensis* Newton, 1909**

(= *Cricetus cricetus* (Linnaeus, 1758) auctt.)

Material: 1 right m1 (Fig. 3C, c).

Remarks: There is an extensive literature discussing the phylogeny of Pleistocene 'giant' hamsters (Schaub, 1930; Kurtén, 1960; Fahlbusch, 1976). However, there is currently no consensus over how many species are represented by this material, which is morphologically indistinguishable from the living *Cricetus cricetus*. An upper tooth row of *Cricetus* from West Runton was first described by Newton (1909) as *C. runtonensis*, but Stuart (1975) subsequently attributed this specimen to *C. cricetus*. Another large Pleistocene hamster maxilla was named *C. major* by Woldrich 1880, based on a specimen from the Late Pleistocene site of Vypustek, Moravia. Examination of the two type specimens and comparison with data from the literature reveal that both the upper and the lower molars of the Late Pleistocene *C. major* are distinctly larger than those of Middle Pleistocene *C. runtonensis* (Maul, 1999). This distinction is confirmed by size differences between other samples of late Early and early Middle Pleistocene age (e.g. Zalesiaki 1 and Kozi Grzbiet in Poland), which represent a smaller form, whereas *Cricetus* from late Middle Pleistocene localities (Petersbuch, Genkingen in Germany) is larger (Table 7). Currently, it is unclear whether both species belong to one lineage, with *C. runtonensis* being the ancestor of *C. major*. The m1 from the 1995-Mammoth Excavation is clearly larger than Recent *C. cricetus* and Early-early Middle Pleistocene *C. praeglacialis* Schaub, 1930, but similar in size to those of the *C. runtonensis* group. There are several sites (e.g. Koněprusy C718, Včeláre 1, Nagyhársányhegy 4 and Villány 6 and 8) where both *C. praeglacialis* and *C. runtonensis* have been recorded. This implies that the two taxa are indeed distinct species and that they are unlikely to represent geographic or chronological subspecies.

Hamsters are valuable environmental indicators because they are closely associated with steppe vegetation and dry meadow environments. Today they have a range that extends into western Europe, but only in areas with a continental climate.

[Table 7 here]

Arvicolinae Gray, 1821

Clethrionomyini (Kretzoi, 1969)

Clethrionomys Tilesius, 1850

***Clethrionomys hintonianus* Kretzoi, 1958**

(= *Clethrionomys glareolus* (Schreber, 1780) auctt.)

Material: 4 molars, 1 M2, 1 mandible with m1, 14 m1 (Fig. 4A, a, D, d, G, g), 2 m2.

Remarks: Molars of *Clethrionomys* are rooted and can be distinguished from those of *Mimomys savini* by their smaller size and differences in the shape of the anteroconid complex. The presence of crown cement and relatively thick molar enamel (Fig. 4A, D, G) distinguish these molars from those of *Pliomys*. It has been suggested that Pliocene and Pleistocene *Clethrionomys* represent a single lineage (*C. kretzoii* Kowalski, 1958 – *C. hintonianus* Kretzoi, 1958 – *C. acrorhiza* Kormos, 1933) leading to the extant bank vole *C. glareolus* (Rabeder, 1981), but the origin of the other Eurasian species (*C. rutilus* (Pallas, 1779) and *C. rufocanus* (Sundevall, 1846)) is currently obscure. The lineage is characterised by a progressive and marked increase in hypsodonty of the check teeth, an increase in the height of the linea sinuosa and changes in enamel pattern of the m1. Pleistocene *Clethrionomys* molars have a distinctly higher lineae sinuosae than Pliocene *C. kretzoii*, but lower lineae sinuosae than Recent *C. glareolus*. The status of *C. acrorhiza* from the Middle Pleistocene is uncertain; it has a higher linea sinuosa than *C. hintonianus*, but there are too few specimens to distinguish this species from *C. glareolus*. Additionally, Middle Pleistocene *C. hintonianus* can be distinguished from Recent and Late Pleistocene *C. glareolus* in having a m1 with a broad confluence between T4 and T5. In *C. glareolus* the connection between T4 and T5 is constricted by the provergent LRA3 (Rabeder, 1981). The West Runton specimens are characterised by Hsd/L values that fall within the range of *C. hintonianus* and they possess a broadly confluent T4-T5. The size of the West Runton specimens also falls within the range of *C. hintonianus* (Table 8).

Recent *Clethrionomys* species (*C. glareolus*, *C. rutilus* and *C. rufocanus*) are typical inhabitants of forest and it can be assumed that *C. hintonianus* also inhabited wooded habitats.

[Table 8 here]

Pliomyini Kretzoi, 1969

Pliomys Méhely, 1914

Pliomys episcopalis **Méhely, 1914**

Material: 11 molars, 3 m1 (Fig. 4B, b, E, e).

Remarks: Molars of *Pliomys* can be identified from a combination of characters, such as positive enamel differentiation, possession of roots and lack of crown cementum (Fig. 4B, E). The West Runton specimens are indistinguishable in size and morphology from *Pliomys episcopalis*. According to the Hsd/L value they are more advanced than Early Pleistocene *Pliomys episcopalis*, but similar to other early Middle Pleistocene samples (Table 9).

Ecologically, *P. episcopalis* is considered to be a forest inhabitant, since its relative abundance fluctuates in tandem with forest-adapted species in sequences such as Koněprusy C718 (Fejfar, 1961).

[Table 9 here]

Arvicolini Kretzoi, 1955

Mimomys Forsyth Major, 1902

Mimomys savini **Hinton, 1911**

Material: 259 molars, 104 upper incisors, 13 M1, 2 M2, 23 M3, 1 maxilla with M3, 1 maxilla without teeth, 5 palates, 121 lower incisors, 14 mandibles with m1, 9 mandibles without teeth, 133 m1 (Fig. 4C, c, F, f, H, h), 13 m2, 43 m3.

Remarks: Remains of *Mimomys savini* dominate the collections of small mammals from West Runton. The occlusal surface of *M. savini* molars resembles that of the recent water vole *Arvicola*, but the molars are rooted in adult individuals and the enamel differentiation is always negative (SDQ mean = 130, Table 10). The m1 has an 'enamel islet' in juveniles and a '*Mimomys* fold' is found in a small proportion of these teeth. Several authors have used the frequency of the 'enamel islet' and the '*Mimomys* fold' in different populations of *Mimomys* to place sites within a relative chronology (e.g. Cuenca-Bescós et al., 1999). One problem with this approach is that both features can disappear as the tooth wears down. Consequently the age structure of the fossil population (which could partly be a function of seasonal accumulation of the remains) may have an important influence on the relative frequency of these features. For example, a sample of *Mimomys* dominated by juvenile individuals may have a relatively high percentage on m1s with an 'enamel islet' and '*Mimomys* fold', whereas a sample of senile individuals from the same population would have a lower percentage of m1s exhibiting these features. The age structure of the population can nevertheless be derived from crown height measurements and the stage of root development, thus allowing differences in age structure between samples to be taken into account. We have therefore divided the 147 WRFB *Mimomys* m1s into groups, according to the stage of root development and relative crown height (crown height index = distal crown height on buccal side x 100/ tooth length). The frequency of the 'enamel islet' and *Mimomys*-fold' has quantified for each of the ontogenetic stages:

Stage 1 (4 complete and several broken specimens): Rootless m1s of the youngest individuals (crown height index <120) have an 'enamel islet' (a funnel-shaped structure) that opens towards the buccal side of the tooth at the chewing surface. This 'pre-islet' and a '*Mimomys*-fold' are present in all of the m1s assigned to Stage 1.

Stage 2 (4 complete and several broken specimens): In rootless m1s with a crown height index between 120 and 150, an 'enamel islet' is present in all cases (4 complete and several broken specimens), but a '*Mimomys*-fold' is present only in half of the specimens.

Stage 3 (11 specimens): Rootless m1s reach a maximum crown height index of 170. In m1s with a crown height index between 150 and 170 (e.g., Fig. 4C, c - the vestige of an islet (indicated by an arrow) can be seen under oblique light, but is hardly visible in this photograph), an 'enamel islet' or a '*Mimomys*-fold' are present in about half of the specimens. Both features are present in the same tooth in c. 25% of the specimens of this stage.

Stage 4 (c. 120 specimens): The 'enamel islet' is not present in rooted m1s, but occasionally the vestige of the islet is visible as an osteodentine trace (e.g., Fig. 4, F, H). The identification of the '*Mimomys*-fold' in Stage 4 molars is problematic. This arises because the position of the fold changes with wear. This can be seen in Fig. 4C-c, which shows that the fold moves towards a more anterior position lower down the crown. In this case a 'true' *Mimomys*-fold (i.e. a 'double' BSA3 or an enamel ridge located close to this angle) could transform into a 'false' *Mimomys*-fold (i.e. an enamel ridge located between the 3rd and 4th BSA). In the West Runton sample the latter character state is found in about 15% of the specimens of this stage.

Newton (1882), Forsyth Major (1902) and Hinton (1910) identified several species of *Mimomys* at West Runton, but these have subsequently been shown to represent variation within a single species (Kretzoi, 1965) for which the name *M. savini* has priority. Hinton (1926) first suggested that *M. savini* and *Arvicola* belong to the same lineage (*M. savini* - *Arvicola mosbachensis* (Schmidtgen, 1911) (often cited as *A. cantiana* (Hinton, 1910), *A. cantianus* (Koenigswald, 1970) or *A. terrestris cantiana* (Kolfschoten, 1990) - *A. terrestris* (Linnaeus, 1758)), and there would be some logic to include *M. savini* in the genus *Arvicola*. However, in order to avoid taxonomic and biostratigraphical confusion (e.g. the age of the stratigraphically important '*Mimomys*-*Arvicola* boundary'), in this paper we retain the name *M. savini* (see Maul, in press, for further discussion on this issue). Important features in the evolution of this lineage are changes in size of the m1 and in the distribution of molar enamel. A quotient (SDQ), originally proposed by Heinrich (1978), is widely used to quantify the relative thickness of molar enamel. These features have been recorded in samples from several regions across Europe (e.g. Germany (Heinrich, 1982), Italy (Maul et al. 1998), England (Parfitt in Preece et al., 2008) and in combination these features have been shown to have stratigraphical significance. However, it should be noted that some authors use different enamel thickness measurements to calculate the SDQ value. The ratio as originally defined by Heinrich (1978) used measurements on the m1 taken on all 7 salient angles ('SDQ7'). Later workers have modified this scheme and measured the other molars in addition to the m1 (van Kolfschoten, 1990), or have taken measurements on fewer triangles, using just three ('SDQ3'), especially Russian workers (e.g. Rekovets, 1990; Markova, 1998). Comparisons between samples are only possible if the same methodology is employed. Data obtained using each technique is distinguished by 'SDQ7' or 'SDQ3' respectively. SDQ7 values for West Runton (n = 49, min. = 114.57, mean = 139.59, max. = 163.14) and the German sites are given in Table 10. The mean SDQ3 of the West Runton sample is 134.81 (n = 49, min. = 104.40, max. = 171.40). Comparing the length and the SDQ7 of the West Runton sample with those of the Voigtstedt sample shows that there are small differences in values that suggest the West Runton *M. savini* population is more primitive than Voigtstedt. The WRFB population on the other hand is much more advanced than that from the late Early Pleistocene site of Untermaßfeld (Tab. 10).

The living water vole is a semi-aquatic rodent and it is probable that its ancestor *Mimomys savini* was also closely associated with aquatic habitats (Jánossy, 1962).

[Table 10 here]

[Figure 4 here]

Microtus Schrank, 1798

Microtus (*Microtus*) Schrank, 1798

***Microtus* '*arvalinus*' Hinton, 1923**

(= *Microtus* cf. *arvalis* (Pallas, 1778) auctt.)

Material: 69 m1 (Fig. 5a-b).

Remarks: Within the genus *Microtus* the various lineages (indicated by subgenera) differ in the shape of the anteroconid complex (ACC) and the connection between dentine fields in the m1. There is a general evolutionary tendency, found independently in all arvicolid lineages, for a relative increase of the length of the ACC in relation to the m1 length (A/L ratio of van der Meulen, 1973). Members of the subgenus *Microtus* are characterised by a closed dentine field between T4 and T5. Molars with this dental morphology and an anterior loop resembling that of the recent *M. arvalis* are common at West Runton (Fig. 5a-b). The name *Microtus arvalinus* is commonly used for the primitive members of this group, but according to Nadachowski (1990), the type of *Microtus nivaloides* Hinton, 1923 (figured by Forsyth Major, 1902, p. 106, Fig. 19) has the same arvaline morphology and therefore *nivaloides* is the valid name for reasons of priority. As a compromise, the name '*arvalinus'* has been retained (but in quotation marks) because this has become common usage. The discrimination between *Microtus arvalis* and its probable ancestor *Microtus* '*arvalinus*' is not clearly defined. Small A/L values (< 52) seem to be typical for *Microtus* '*arvalinus*' in comparison to modern samples of *M. arvalis* and *M. agrestis* (A/L > 54). The A/L value of the WRFB *Microtus* '*arvalinus*' sample is lower than the Voigtstedt sample (Table 12). The relationship of *Microtus* '*arvalinus*' to other species of *Microtus* with an arvaline first lower molar (e.g. *M. agrestis* (Linnaeus, 1761)*, M. arvalis* (Pallas, 1778) and *M. rossiaemeridionalis* Ognev, 1924) is uncertain, but *M.* '*arvalinus*' is widely believed to be ancestral to the living *M. arvalis*.

Additional

Microtus '*arvalinus*' was probably an open grassland animal, with an ecology similar to that of the *M. arvalis*.

Microtus (*Pallasiinus*) Kretzoi, 1964

***Microtus* (*Pallasiinus*) '*ratticepoides*' Hinton, 1923**

(= *Microtus oeconomus* (Pallas, 1776) auctt.)

Material: 7 m1 (Fig. 5c-d).

Remarks: The subgenus *Pallasiinus* is characterized by m1 with four closed triangles and a broad confluence between the T5 and the simple crescentic anterior cap. This molar morphology is characteristic of the living *M. oeconomus*, but it can also be found in Early Pleistocene vole assemblages (e.g. the *eoratticeps* morphotype from Deutsch Altenburg 2C1, Austria) within the morphological range of *Microtus* (*Allophaiomys*) *pliocaenicus*. In addition, specimens referred to *Allophaiomys* from Colle Curti (Italy) and Korotoyak (Russia) also have an oeoconomid morphology. However, not all of these finds are referred to the *Pallasiinus* group. The name *Microtus ratticepoides* is commonly used for the primitive members of the *Pallasiinus* group, but according to Nadachowski (1990), the type of *Microtus nivalinus* has the same oeoconomid morphology and should be used for reasons of priority. Here, the name *ratticepoides* has been retained (but in quotation marks) because this has become common usage. Attempts have been made to define the limits between these two taxa. Rekovets and Nadachowski (1995) used an A/L ratio of 50 to distinguish them; those with an A/L ratio below 50 were assigned to *M. ratticipoides* and those above 50 were attributed to *M. oeconomus*. However, there is much geographical variation in this ratio, such that modern populations in Poland and

Germany have A/L ratios below 50 but have nevertheless been assigned to *M. oeconomus*. Such inconsistencies highlight the difficulties in using this index to define the limit of *Microtus oeconomus* at A/L = >50. Morphologically, the West Runton lower first molars closely compare with Recent *M. oeconomus*, except that they are smaller and the ACC is relatively shorter. The A/L value of the West Runton sample is slightly less than that of the Voigtstedt sample (Table 12).

Microtus '*ratticepoides*', often listed as *M. oeconomus*, is well represented in early Middle Pleistocene faunas across northern Europe, particularly during cooler phases. It probably favoured continental conditions in accordance with its living descendant, and most likely inhabited poorly drained grassland.

Microtus (*Stenocranius*) Kastschenko, 1901

***Microtus* (*Stenocranius*) *gregaloides* (Hinton, 1923)**

Material: 41 m1 (Fig. 5e-f).

Remarks: *Microtus gregaloides* is probably ancestral to the narrow-skulled vole *M. gregalis* (Pallas. 1779), which it resembles in having a first lower molar with a reduced T6. However, *Microtus gregaloides* can be distinguished from *M. gregalis* in having a broad connection between the T4 and T5 (*Pitymys*-Rhombus). On this basis, Hinton (1923) used the name *Pitymys gregaloides* for these *Pitymys*-like molars from West Runton. The *Pitymys*-Rhombus has been used as the distinguishing feature of *Pitymys* and *Terricola*, but it appears to be plesiomorphic and probably all *Microtus* lineages passed through a phase with such a structure during their evolution. *Microtus gregaloides* differs from *M. gregalis* in having a shorter ACC (A/L: *M. gregaloides* = < c. 52, *M. gregalis* = > c. 52), a smooth BRA4, and a LRA4 greater than 90°. To date, m1s with '*gregalis*' morphotype have not recorded in the WRFB sample. *Microtus hintoni* Kretzoi, 1941 is also similar to *M. gregaloides* and seems to belong to the earliest *Microtus* taxa derived from the *Allophaiomys* group that characterize the Early Pleistocene (e.g. Maul and Markova, 2007). The ACC is similar to that of *M. gregaloides*, but shorter and more derived in the fourth lingual and third buccal re-entrant angle. Therefore *M. hintoni* is probably not a direct ancestor of *M. gregaloides*. Measurements and comparisons are given in Table 12. The WRFB sample is more derived than any late Early Pleistocene samples.

Microtus gregaloides was probably an inhabitant of grassland and it seems to have favoured continental climatic conditions during the early Middle Pleistocene.

Microtus (*Terricola*) Fatio, 1867

***Microtus* (*Terricola*) *arvalidens* Kretzoi, 1958**

(= *Microtus* (*Terricola*) sp. auctt.)

Material: 1 mandible with m1, 12 m1 (Fig 5g-h).

Remarks: Living members of *Microtus* that bear a '*Pitymys*-Rhombus' (broad connection between T4 and T5) are referred either to *Pitymys* or *Terricola* (Martin, 1987). Recent taxonomic revisions of living and fossil Eurasian voles with a *Pitymys*-like m1 morphology have subsumed these species within the subgenus *Terricola*.

Hinton (1923) named lower first molars with a '*Pitymys*-Rhombus' and an anterior cap morphology resembling the living *Microtus arvalis* from the WRFB *Pitymys arvaloides* Hinton, 1923. Subsequently, Kretzoi (1958) substituted the name *arvalidens* for *arvaloides* for reasons of homonymy. The morphology of the m1 in *Microtus arvalidens* is similar to the living common pine vole *M. subterraneus* (de Selys-Longchamps, 1836), but the ACC is shorter, indicated by the lower A/L values. *Microtus arvalidens* was probably the ancestor of *M. subterraneus*, but the discrimination between the two species is not clearly defined. The A/L value of the West Runton sample resembles that of other late Early Pleistocene samples (Table 12).

Microtus arvalidens appears to have favoured temperate conditions.

[Table 11 here]
[Table 12 here]

[Figure 5 here]

Murinae Illiger, 1815

Apodemus Kaup, 1829

Apodemus cf. *sylvaticus* (Linnaeus, 1758)

Material: 5 upper incisors, 1 M1 (Fig. 6a), 3 lower incisors, 1 mandible fragment with m1-m2 (Fig. 6d), 6 m1 (Fig. 6b-c).

Remarks: The molars match those of *Apodemus sylvaticus* in both morphology and size (Table 13). The measurements are smaller than both living *A. mystacinus* Danford et Alston, 1877 and *A. flavicollis* Melchior, 1834 and the extinct Pleistocene *A. alsomyoides* Schaub, 1938 and *A. dominans* Kretzoi, 1959. *A. atavus* Heller, 1936 can be excluded because it became extinct during the Pliocene and possesses additional accessory tubercles on m2 (Rietschel and Storch, 1974), which are lacking in our specimen. The West Runton molars can be distinguished morphologically from *A. microps* Kratochvil and Rosicky, 1952 and the Pleistocene *A. maastrichtiensis* van Kolfschoten, 1985, the mean values of which are both smaller than *A. sylvaticus*. Metrical analysis of the much larger samples of West Runton *Apodemus* teeth in museum collections suggests that only one species of *Apodemus* is represented in the WRFB. However, we tentatively assign the 1995 material to *A.* cf. *sylvaticus* because of the relatively small sample size and the metrical overlap of extreme values in the West Runton sample with *A. maastrichtiensis*.

Today, *A. sylvaticus* is found in a wide range of habitats, but it prefers open land along forest margins.

[Table 13 here]

[Figure 6 here]

4. Comparison between the micromammals from different levels of the 1995-Mammoth Excavation and with previous collections

The vertical distribution of the micromammals through the 1995 profile is summarised in Table 14. In Figure 7, the relative abundance of WRFB vole species is plotted, based on the percentage of the total first lower molars, but excluding the ubiquitous *Mimomys savini*. These show that there are no obvious stratigraphical changes in the distribution of the more common taxa, which are present virtually throughout the column. However, the number of identifiable bones from individual levels is often very low and several taxa are rare (e.g. *Castor fiber* is represented by two specimens and *Cricetus runtonensis* by one specimen only). Similarly, morphometric comparisons of m1 length and SDQ values of *Mimomys savini* show no significant differences between the upper and lower parts of the profile (Table 15). This suggests that the assemblage accumulated over a relatively short time interval and during a period of relative ecological stability, a conclusion supported by other lines of evidence from the site (Coope; Field and Pegler; Preece; Stuart and Lister, this volume). There are, however, indications that the sediments have been bioturbated, possibly through trampling by elephants and other large mammals. The mixing may have moved micromammal remains through the profile to some extent, but it did not incorporate earlier vertebrate material from the underlying 'Crag' sediments, although this might have happened with other fossil groups, as indicated by the occasional presence of *Cerastoderma* and other marine molluscs (D.H. Keen, personal communication).

[Table 14 here]

[Table 15 here]

The only other detailed study of the vertical distribution and assemblage composition of small vertebrates at West Runton was published by Stuart (1975), who wet-screened three bulk samples from a locality ('AJS') approximately 80 m to the west of the 1995 mammoth site. Stuart (1975, 1982) noted that although the concentration of terrestrial vertebrate material decreases sharply from bottom to top, the small mammal assemblages were almost identical. Indeed, the same common species are represented in both the 'AJS' and 1995-Mammoth Excavation samples and there are no significant differences between the two collections in terms of faunal representation (Table 16). The only species not found in the much smaller samples processed by Stuart are *Sorex* cf. *minutus*, *Castor fiber*, *Pliomys episcopalis* and *Cricetus runtonensis*, all of which are otherwise very rare at the site.

The micromammal remains of the 1995-Mammoth Excavation reflect nearly the complete species spectrum known from earlier collections (Table 16). However, there are several taxa, which were not found in the 1995 bulk samples. These include *Erinaceus* sp., *Macroneomys brachygnathus*, *Nyctalus noctula*, *Lepus* sp., *Sciurus whitei*, *Trogontherium cuvieri* and *Cricetulus migratorius*. The absence of these species in the 1995 samples is not altogether surprising, since these are also rare or very rare in the previous collections (see Stuart, 1975; Harrison and Bates, 1984; Harrison et al., 2006).

[Table 16 here]

5. Taphonomy and palaeoecology

The WRFB accumulated at the base of shallow fluvial channel. Sedimentological analysis indicates episodes of flowing water, but mostly sedimentation was by still or very slow-flowing water, possibly at the margins of the waterbody (Gibbard and Boreham, this volume). The micromammal remains are often fragmentary (isolated teeth dominate the assemblage), but otherwise rather well-preserved. The bones are unweathered, which indicates that they were buried soon after deposition. Importantly, none of the bones or teeth is water-rounded showing that the assemblage was not exposed to prolonged or high-energy fluvial transport. Nevertheless, post-depositional forces have affected some bones (e.g. crushing) and the dramatic drop in the number of specimens in the upper part of the column, which coincides with loss of molluscs (Sparks in West, 1980), most probably reflects weathering or decalcification (Hannam et al., 1996, Andrews this volume).

Some of the small mammal remains appear to have been accumulated by predators because specimens modified by digestion are present in the 1995 assemblage. This observation is supported by earlier taphonomic observations by Mayhew (1977), who identified diurnal birds of prey as an important source of small mammal material in his samples from the same deposit. Mayhew (ibid.) showed that digestive corrosion was present on a relatively high proportion of the arvicolid and murid teeth, which indicated that they had been partially digested before they were regurgitated by the avian predator. Furthermore, he suggested that the birds of prey were probably roosting in trees overhanging the site. This has implications for the palaeoecological reconstruction because the prey may have been captured in habitats several kilometres from the roost (Andrews, 1990). In addition to predators, other remains probably derive from animals that lived and died in the waterbody and fringing waterside habitats.

Concerning the habitats represented at West Runton, the small mammal fauna from the 1995 sample is dominated (5 out of 16 species, i.e. 31%) by species that are considered to be closely associated with water (e.g. *Desmana* sp., *Sorex savini*, *Neomys newtoni*, *Castor fiber* and *Mimomys savini*). Fossorial small mammals include voles, hamster and the two mole species (9 out of 16 species, i.e. 56%). Three species (18%) (*Sorex runtonensis*, *Clethrionomys hintonianus,* and *Pliomys episcopalis*) were probably forest inhabitants, whereas 6 species (36%) (*Cricetus runtonensis*, *Microtus* '*arvalinus*', *Microtus arvalidens*, *Microtus gregaloides*, *Microtus* '*ratticepoides*', *Apodemus* cf. *sylvaticus* can be considered as mainly open grassland indicators. The composition of the small mammals at WRFB therefore indicates a patchwork of different habitats dominated by open wetland environments, an interpretation in complete accord with evidence from other biological remains recovered in the same samples and with earlier interpretations of the small mammal assemblage from the site (Stuart, 1975).

The species composition of the West Runton micromammal assemblage can be compared with a broadly contemporary assemblage from Koněprusy C 718, Czech

Republic (Fejfar, 1961). The sequence of sediments filling a karstic feature at this site is important because it contains abundant small mammals that record successive parts of a climatic cycle, with continental conditions at the base (Fig. 7, layer H8) followed by a warm interglacial episode (layer H7-H) and a return to continental grassland (layer G-B) conditions at the top of the profile. An important component of the small mammal assemblage from the continental phases is the vole *Microtus gregaloides*. This species is also common at West Runton and at several other pre-Anglian sites in Britain, although importantly it is not found during the thermal maximum of the warm periods (e.g. Westbury-sub-Mendip Units 15/2, 5 and 11/4 - Andrews et al., 1999). Similarly, in the Koněprusy C 718 profile *M. gregaloides* is also absent in fully temperate/forested part of the succession. The total WRFB arvicolid assemblage (which does not show significant differences between the upper and lower layers, see above) is strikingly similar to the arvicolid spectrum from layer H8 at the base of the Koněprusy profile. This layer was deposited during a continental phase, and significantly has also yielded remains of *Mammuthus trogontherii* (Fejfar, 1961). From this evidence we can suggest that the WRFB at the elephant site also represents a comparable position within the climatic cycle. Although associated plant remains (pollen and plant macrofossils) indicate regional temperate woodland (reference), the complete lack of strong thermophiles a West Runton, such as Crocidurinae among micromammals, pond terrapin *Emys orbicularis* among reptiles (Böhme, this volume) beetles (Coope, this volume) and molluscs (Preece, this volume), together with the presence of continental and steppic small mammals (e.g. *Cricetulus migratorius*, *Cricetus*) implies a relatively more continental climate than today with slightly cooler mean annual temperature.

[Figure 7 here]

6. The age of the West Runton Freshwater Bed

Voles, lemmings and insectivores are the stratigraphically most important groups of micromammals in the European Pleistocene since they have diversified more than any other taxa over this relatively short geological time-span (e.g., Fejfar and Heinrich, 1983; Fejfar and Horáček, 1983). This rapid evolutionary radiation is exemplified by voles of the genus *Microtus* (Martin, 1993; Chaline et al., 1999; Jaarola et al., 2004). Today, *Microtus* is one of the most specious mammalian genera with at least 60 extant species distributed across the Holarctic region, all of which derive from ancestral *Allophaiomys* populations during the Early Pleistocene. Some arvicolids and other micromammalian taxa undertook long-range and rapid faunal migrations, and many have extensive geographical distributions, which expanded and contracted in response to changes in global climate. Together with a rapid species turnover and evolutionary change, these are features that make micromammals particularly valuable in the biostratigraphical subdivision of the Quaternary (Fejfar et al., 1998; Chaline et al., 1999). The basis of mammalian biostratigraphy is the comparison of faunal lists and morphological characteristics of taxa in different faunal assemblages (see Lister, 1992 for a discussion of the conceptual basis of Quaternary mammalian biostratgraphy). Problems arise because morphometric characters can vary across the range of a species leading to pronounced clinal gradients. These may shift in complex ways at different times, posing serious problems for conventional taxonomy (e.g. for *Arvicola* see Kolfschoten, 1993; for *Mammuthus* see Lister and

Sher, 2001). Differences in taxonomic philosophy amongst small mammal palaeontologists may be a further obstacle to understanding true phylogenetic relationships. In some cases these different traditions have led to a proliferation of names resulting in taxonomic confusion that has impeded a clear understanding of biostratigraphical correlations when using simple faunal lists alone. However, the complexity of evolutionary changes means that combinations of characters are likely to be temporally unique within a given geographical region, so providing critical biostratigraphical evidence for the age of particular deposits (Maul et al. 1998a, b). This approach is illustrated in Figure 8, where character morphoclines are plotted for several taxa, showing long-term trends, but also short-term fluctuations in morphometric characters.

[Figure 8 here]

The WRFB and the Cromerian Interglacial (sensu West, 1980) were originally believed to immediately pre-date the Anglian Glaciation because Anglian till overlies the interglacial sediments at West Runton (e.g. Turner, 1974). This parallels the situation in the German site Voigtstedt, which plays an important role in the search of faunal equivalents of the West Runton assemblage. The correlation of the WRFB (and the Cromerian Interglacial, sensu West, 1980) with Voigtstedt was first proposed by Stuart (1976), on the basis of faunal similarities between the two assemblages. Both sites were originally thought to represent the same interglacial that immediately preceded the Anglian/Elsterian Stage, which is now generally correlated with MIS 12 (e.g. Bowen, 1999). However, various lines of evidence suggest that the Cromerian as defined by West (1980) is a composite stage and that the WRFB is separated from the Anglian Stage by a succession of distinct temperate and cold episodes of varying duration and intensity (Preece and Parfitt, 2000; Lister and Stuart, 2001). Other British 'Cromerian' sites are possibly even older than West Runton (Parfitt et al, 2005), implying that the 'Cromerian' spans the interval between the Anglian/Elsterian Stage (478-423 kyr) and the Brunhes-Matuyama boundary (780 kyr). A key element in this subdivision is an important evolutionary transition in the water vole lineage, which is characterised by the replacement of *Mimomys*, with rooted molars, by *Arvicola* with continuously growing molars. Nowhere in Europe do small mammal assemblages with *Arvicola* occur beneath those with *Mimomys*. In this scheme, British 'Cromerian' sites can be broadly subdivided into two groups: an older group with *Mimomys* represented by Little Oakley (Lister et al., 1990) and Sugworth (Stuart, 1980) in addition to West Runton; and a younger group with *Arvicola* that includes Boxgrove (Roberts and Parfitt, 1999), Westbury-sub-Mendip (Bishop, 1982; Andrews et al. 1999), Ostend (Stuart and West, 1976), and the Sidestrand *Unio*-bed (Preece and Parfitt, 2000). Both stages are characterised by the occurrence of 'relict' taxa (e.g. *Sorex* (*Drepanosorex*), *Pliomys episcopalis*), some of which became extinct during MIS 12, and by evolutionary changes within several lineages. In Figure 8, morphometric data are plotted for several of the West Runton taxa compared with key European sites with independent dating evidence against the geomagnetic polarity record and with suggested correlations to the deep-sea oxygen isotope record.

The age of WRFB is constrained by palaeomagnetism, its relationship to the Anglian glacial deposits and biostratigraphy. A maximum age of the WRFB is established by palaeomagnetism. Recent studies have shown that the WRFB accumulated during a period of normal magnetic polarity (Maher and Hallam, 2005;

Maher, this volume), which, based on faunal composition, must post-date the Brunhes-Matuyama boundary. Referral to an earlier period of normal magnetisation (i.e. the Jaramillo normal Subchron) can be excluded on faunal grounds, because sites of this age have a primitive microtine fauna with '*Allophaiomys*'-like forms (e.g. Colle Curti, Italy (Abbazzi et al., 1998); Untermaßfeld, Germany (Maul, 2001); Le Vallonnet, France (Paunesco, 2002); Castagnone (Giraudi et al., 2003) and Korotoyak/Ostrogozhsk Suite, Russia (Markova, 2005), etc.).

In the deep-sea record, the transition from the reversed Matuyama Chron to the normally magnetized Brunhes Chron took place during early part of Marine Isotope Stage (MIS) 19, about 780,000 years ago (Zhou and Shackleton, 1999, Lisiecki and Raymo, 2005). This implies that the WRFB cannot be older than the later part of MIS 19. Furthermore, the palynology of the West Runton sequence suggests that the WRFB accumulated during a period of climatic amelioration from the end of a cold stage (correlated with the Beestonian by West, 1980) into the early temperate part of the Cromerian Interglacial (West, 1980). Other biological remains (e.g. molluscs, beetles, amphibian and reptiles) are consistent with deposition during the early part of an interglacial (Preece and Parfitt, 2000). This conclusion is now substantiated by the small mammal evidence (see above). Therefore, correlation of the WRFB with MIS 19 is highly unlikely. On palaeomagnetic, palaeobotanical and malacological grounds the deposits must therefore represent a later (post-MIS 19) interglacial.

A minimum age can be inferred from the presence at West Runton of the vole *Mimomys savini*. The transition from water voles with rooted molars (*Mimomys*) to unrooted molars (*Arvicola*) is recorded in Central Europe, where the earliest record of *Arvicola* is from Rhine sediments pre-dating the augite-hornblende boundary at Kärlich Gb (Koenigswald and van Kolfschoten, 1996). Somewhat younger is the nearby site of Miesenheim I, again with *Arvicola*, but from sediments that post-date the augite-hornblende boundary. Currently these sites lack reliable absolute age determinations, but the faunas represent two successive temperate stages that are demonstrably older than the Elsterian Stage (MIS 12). The Kärlich Gb small mammal fauna has been correlated with that from the Calcareous Member at Westbury Cave, Somerset, UK, on the basis of its small mammal fauna (Preece and Parfitt, 2000), which includes *Microtus gregaloides* and *Arvicola*. At Westbury the succession of small mammal faunas from the Calcareous Member records a complex sequence of climatic events, including both deciduous woodland faunas, implying fully temperate conditions, as well as intervening cold stage faunas with boreal and arctic species (Andrews et al. 1999). Boxgrove is correlated on the basis of its small mammals with Miesenheim I (Preece and Parfitt, 2000). Both sites have yielded abundant remains of *Arvicola*, together with *Microtus gregalis* (the descendent of *M. gregaloides*). The occurrence of *Microtus gregalis* at Boxgrove and Miesenheim suggests both sites post-date the Westbury sequence. At Boxgrove, marine and estuarine sediments are overlain by terrestrial deposits, which record a deteriorating climate that culminated in deposition of periglacial slope deposits, believed to date to the Anglian Stage (MIS 12). This evidence suggests that the transition from *Mimomys* to *Arvicola* in Western Europe took place before the end of the Cromerian Complex. Furthermore, the persistence of *Arvicola* throughout the Calcareous Member at Westbury and in later deposits at Boxgrove shows that the early (pre-MIS 12) part of the *Arvicola* Biozone must represent a long period of time with major climatic fluctuations, including at least four major temperate events (some of peak interglacial warmth), possibly spanning MIS 13 and part of 15.

Recent analysis of the small mammals from Isernia, Italy (Koenigswald and van Kolfschoten, 1996) and Mosbach 2, Germany (Maul et al., 2000) has identified a transitional stage in the evolution of *Arvicola* from *Mimomys*. At these sites, the adult water vole molars are unrooted, but several show closure of the crown base, which indicates that crown formation had ceased in some adult individuals (Koenigswald and van Kolfschoten, 1996, Fig. 3). This stage in the formation of roots is found in the molars of young individuals of *Mimomys* from West Runton, but in the Mosbach and Isernia assemblages closure of the crown base forms late in development and is found only in some older individuals. The Isernia and Mosbach 2 water voles have been assigned to *Arvicola* (Koenigswald and van Kolfschoten, 1996; Maul et al., 2000), but arguments could be advanced for their inclusion in *Mimomys* (Preece and Parfitt, 2008). Significantly, molars with closure of the crown base are not found in the very large *Arvicola* samples from Miesenheim I, Westbury Cave (Calcareous Member) or Boxgrove. At Isernia, high-precision ^{40}Ar/^{39}Ar dates of 610 +/- 10 ka and 606 +/- 2 ka have been obtained on volcanic tuffs that seal horizons containing the ‘transitional’ water vole population (Coltorti et al., 2005). Current evidence suggests that the *Mimomys-Arvicola* transition was broadly synchronous in England, Western and Central Europe and Italy. In Russia, transitional (or late *Mimomys*) populations are present in the Muchkapian Interglacial, which is correlated with MIS 15 (Markova, 2005). The Muchkapian water voles are also characterised by relatively high-crowned molars that form roots late in life. Although there are taxonomic uncertainties over the generic status of the early-MIS 15 water voles (see Preece and Parfitt, 2008), their molars are higher crowned than those from WRFB population implying that the WRFB may be older than MIS 15.

From the foregoing discussion, correlation of the WRFB with the early part of MIS 17 seems likely. The critical lines of evidence include new dates on the transitional water vole population from Isernia, together with the normal polarity of the WRFB and the climatic reconstruction indicating deposition during the early part of an interglacial.

7. Comparisons between the West Runton Freshwater Bed fauna and other European *Mimomys savini* faunas from the early Brunhes and late Matuyama Chrons

Several European micromammal faunas from normally magnetised fossiliferous layers have yielded *Mimomys savini* and advanced *Microtus* species, which therefore belong to the early Brunhes Chron.

One of these faunas is the extensive small mammal assemblage from a limnic horizon (‘Lehmschichten’) within fluvial sands from Voigtstedt (Central Germany). Like the WRFB, the Lehmschichten is also normally magnetised and therefore younger than the Brunhes-Matuyama boundary. Previous studies by Stuart (1981) and by Maul (1990) have compared the Voigtstedt small mammal fauna with that of the

WRFB. Both studies underline the close similarity of the two assemblages in terms of species composition and morphometric data, a conclusion supported by the more detailed comparison undertaken in this study. The taxonomy of the Voigtstedt micromammal fauna has been revised by Maul (1990 and unpublished), who has identified the following taxa: *Erinaceus* cf. *europaeus*, *Talpa* cf. *europaea*, *Talpa* cf. *minor*, *Desmana thermalis*, *Sorex* cf. *runtonensis*, *Sorex* (*Drepanosorex*) *savini*, *Neomys newtoni*, *Macroneomys brachygnathus*, *Lepus* sp., *Spermophilus dietrichi*, *Petauria helleri*, *Castor fiber*, *Trogontherium cuvieri*, *Cricetus* sp., *Cricetulus migratorius*, *Clethrionomys hintonianus*, *Mimomys savini*, *Microtus* '*arvalinus*', *Microtus* '*ratticepoides*' and *Apodemus flavicollis*, together with the palaeoecologically significant pond terrapin *Emys orbicularis*.

The new morphometric comparisons show only small differences between the West Runton and Voigtstedt micromammal taxa, but these differences are consistent in that they suggest the WRFB is slightly older than Voigtstedt.

Both the small mammal faunas from the WRFB and Voigtstedt display a mosaic of open grassland and forest habitats. However, several significant species were present at only one of the sites. These include *Microtus gregaloides* found at West Runton, but not at Voigtstedt. This extinct vole, considered to be the ancestral form of *Microtus gregalis*, probably inhabited grassland and may have preferred continental climatic conditions. West Runton has yielded several temperate species not found at Voigtstedt, such as *Microtus arvalidens*, *Sciurus whitei* and *Pliomys episcopalis*. On the other hand, Voigtstedt has 'temperate' species not found at West Runton, such as *Apodemus flavicollis* and *Petauria*, together with the steppic indicator *Spermophilus*. Differences in the taxonomic composition of the Voigtstedt and West Runton faunas may reflect geographical distance, environmental and regional climatic differences, or incomplete sampling of the small mammal faunas at these sites. Differences in palaeoecological conditions may be a significant factor, especially as Voigtstedt seems to be closer to the climatic optimum of the interglacial (Erd, 1965), whereas the WRFB was deposited during the early part of the interglacial. This conclusion is supported by the presence of a late form of *Mammuthus meridionalis* and *Emys orbicularis* and the lack of *M. gregaloides* at Voigtstedt. Significantly, the arvicolid spectrum of Voigtstedt compares closely to that of H1 of Koněprusy C 718 (cf. Figure 7). The vole percentages in Voigtstedt are: *M. arvalinus* 45%, *Clethrionomys* 15%, but with *M. ratticepoides* (lacking in Koněprusy C 718) accounting for 40 % of the total (at Koněprusy the remainder of the H1 assemblage is comprised of *M. arvalidens*, which accounts for 40% of the total). This comparison, together with the morphometric data and palaeoecological conclusions, provide additional support for the suggestion that Voigtstedt represents the optimum of interglacial, whereas the WRFB dates to an earlier stage within the same interglacial.

The *Mimomys* fauna from Přezletice also dates to the early Brunhes Chron. At this locality, the fossiliferous layer is normally magnetised and has yielded the following small mammal taxa: *Talpa minor, Talpa fossilis, Drepanosorex savini, Sorex subaraneus, Sorex minutus, Neomys newtoni, Desmana thermalis, Erinaceus praeglacialis, Trogontherium schmerlingi, Citellus primigenius, Apodemus* sp., *Cricetus cricetus, Allocricetus bursae, Lemmus* aff. *lemmus, Pliomys episcopalis, Clethrionomys* cf. *glareolus, Mimomys savini, Pitymys arvalidens, Microtus gregaloides, Microtus ratticepoides, Microtus nivaloides, Microtus arvalinus, Lepus* sp., together with rare large mammals, such as *Mammuthus trogontherii* (Fejfar, 1993). Morphometric values of the small mammal taxa are rather similar to those of the WRFB taxa, but A/L values are slightly lower for *M. ratticepoides* and *M. arvalidens* (Table 12).

The small mammal fauna from normally magnetised sediments at Kozi Grzbiet (Poland) is also similar to that from the WRFB. The site has yielded the following micromammals: *Sorex minutus*, *Sorex minutissimus*, *Sorex praealpinus*, *Sorex runtonensis*, *Sorex* (*Drepanosorex*) *savini*, *Sorex* (*Drepanosorex*) sp. 1, *Sorex subaraneus*, *Beremendia fissidens*, *Neomys newtoni*, *Macroneomys brachygnathus*, *Spermophilus polonicus*, *Petauria* sp., *Trogontherium cuvieri*, *Allocricetus bursae*, *Allocricetus ehiki*, *Cricetus runtonensis*, *Clethrionomys glareolus*, *Dicrostonyx simplicior*, *Lemmus* sp., *Sicista praeloriger*, *Muscardinus avellanarius*, *Glis* cf. *sackdillingensis*, *Eliomys* cf. *quercinus*, *Pliomys episcopalis*, *Pliomys lenki*, *Mimomys savini*, *Microtus* ex gr. *oeconomus*, *Microtus* ex gr. *agrestis*, *Microtus* (*Pitymys*) *arvalidens*, *Microtus* (*Stenocranius*) *gregaloides*, *Microtus nivaloides* and *Apodemus* cf. *flavicollis* (summarised in Nadachowski, 1990, Rzebik-Kowalska, 1994). The occurrence *Dicrostonyx* (an indicator of cold climate) in the lower part of the profile, together with temperate forms such as the glirids in the upper part of the profile suggests that deposition occurred during the transition from glacial to interglacial conditions during the early Brunhes.

In Southern Europe, the normally polarised fossiliferous layers of Rifreddo (Sant'Arcangelo Basin, Southern Italy) were also deposited during the early part of the Brunhes Chron. The deposits have yielded a temperate fauna with *Talpa* cf. *romana, Crocidura kornfeldi, Sorex* ex gr. *runtonensis-subaraneus, Macroneomys* cf. *brachygnathus, Allocricetus* cf. *bursae, Mimomys savini, Microtus* (*Terricola*) *arvalidens, Microtus* (*Iberomys*) *ex gr. huescarensis-brecciensis, Apodemus* cf. *sylvaticus* (Masini et al., 2005). Because of biogeographical reasons not all of the taxa are comparable with the West Runton fauna. The A/L value of *M.* (*T.*) *arvalidens* (Table 12) is very close to that of the WRFB sample.

Several sites with small mammal remains have sequences that record the Brunhes-Matuyama boundary. For example, at the Czech locality of Únětice (Koči and Šibrava, 1976), the Brunhes-Matuyama boundary is situated below the fossiliferous horizon. This horizon has yielded a sparse fauna including *Microtus* sp. (A/L – 50.3) and *Mimomys savini*. Both taxa occur in the WRFB, but the Únětice fauna is too poor for detailed comparisons.

At Mahlis (Germany), the Brunhes-Matuyama reversal has been recorded within the fossiliferous layer that has yielded a relatively diverse micromammal assemblage, which includes *Desmana* sp. cf. ex gr. *thermalis*, *Sorex* sp. (size of *S. runtonensis*-*S. subaraneus*), *Cricetus* sp., *Microtus* '*arvalinus*' and *Microtus* '*ratticepoides*' (Heinrich in Fuhrmann et al., 1977). All of these taxa are also present at West Runton. However, only 2 m1s of *Microtus* '*arvalinus*' are complete enough to provide A/L values (47.36 and 53.21).

Although it is possible find correlatives of the WRFB micromammals with other sites in Europe, it is currently difficult to distinguish these faunas from those of late Matuyama age (780 – 990 kyr). In part, this is because of the small size of the late Matuyama micromammal assemblages and paucity available morphometric data.

The inverse magnetised fossiliferous layers of Dorn-Dürkheim 3 contain *Mimomys savini* and *Microtus hintoni* and therefore referred to the late Matuyama (Franzen et al., 2000). The material is too scanty for a morphometric comparison with other faunas.

At Atapuerca (Spain) an apparently uninterrupted succession of cave sediments records negative polarity in layers TD3-6. At this locality, the Brunhes-Matuyama boundary is present in the overlying layer TD 7 (Cuenca-Bescós, et al. 1995, 1998, 1999). This sequence is believed to date from MIS 21 to the early part of MIS 19 or older (Cuenca-Bescós et al., 1998). The microfauna from TD3-6 includes several taxa that are also present in the WRFB, such as *Mimomys savini* and *Microtus* (*T.*) *arvalidens* and *Microtus* (*S.*) *gregaloides*. *Mimomys savini* exhibits a relatively high percentage (14%) of lower first molars with an enamel islet (a primitive feature) compared with only 7% in the WRFB assemblage (Cuenca-Bescós et al., 1999). However, Cuenca-Bescós et al., (1999) do not score the relative frequency of these features for the different ontogenetic stages in their samples and consequently the significance of the differences in the frequency of the enamel islet between assemblages is unclear. *Microtus* (*T.*) *arvalidens* samples from different levels in the TD3-6 sequence have A/L ratios that are similar or larger than values from West Runton (in TD3 mean = 55 (n = 4), TD 4 mean = 52 (4), TD 5 mean = 52 (9), TD 6 mean = 53.2 (12)), whereas for *M.* (*S.*) *gregaloides* the A/L value is smaller in comparison to WRFB (in TD 3 mean = 51 (n = 12), TD 4 mean = 52 (19), TD 5 mean = 49 (59), TD6 mean = 51 (2), data from Cuenca-Bescós et al., 1995, 1999). The similarities in faunal composition and in the evolutionary level of *Microtus* (*T.*) *arvalidens* seen at sites of obviously different ages in different regions demonstrates the difficulty in separating faunas dating to the latter part of the *Mimomys* Biozone.

The faunas listed above can be grouped on the basis of absolute dating, stratigraphical superimposition and palaeomagnetism. Where independent dating methods cannot be applied, faunas can be assigned on the basis of their faunal content and the A/L values of *Microtus*. Four groups can be recognised from the interval spanning the Jaramillo Subchron to the MIS 12 cold stage:

Group 1:

Sites of broadly Jaramillo age pre-date the differentiation of *Microtus* species with a closed T4-T5 dentine field in the lower first molar (as in 'true' *Microtus* species, such as *M.* '*arvalinus*' and in *M.* '*ratticepoides*'). This interval is characterised by *Microtus* morphotypes with a confluence between triangles of the anteroconid complex (T4-T5-T6). Such morphotypes are characteristic of primitive *Microtus* species, commonly assigned to the subgenus *Allophaiomys*. *Allophaiomys* is a primitive evolutionary level ('metaregion' sensu Martin and Tesakov, 1998) occurring in all lineages, which ultimately gave rise to more progressive *Microtus* species after the Jaramillo. Thus, the so-called 'advanced *Allophaiomys*' forms recorded during this subchron are probably representatives of different *Microtus* lineages. Those from Colle Curti, Italy (Abbazzi et al., 1998) and Korotoyak/Ostrogozhsk Suite, Russia (Markova, 2005) seem to have some affinities to the *Pallasiinus* group (see above). The finds from Untermaßfeld, Germany (Maul, 2001), Le Vallonnet, France (Paunesco, 2002) and Castagnone (Giraudi et al., 2003) are less primitive and closer in morphology to the other lineages of the subgenera *Microtus*, *Stenocranius* or

Terricola. Although A/L values of *Microtus* populations from the Jaramillo show considerable variation, the mean value is always less than 49. The earliest occurrence of 'true' *Microtus* may be from the type-site of the Bavel interglacial in The Netherlands (van Kolfschoten, 1990); however, the stratigraphical provenance of this material has been questioned by van Kolfschoten and Markova (2005).

Group 2:

During the period between the termination of the Jaramillo Subchron and the onset of the Brunhes Chron 'advanced *Allophaiomys*' forms disappear and 'true *Microtus*' become dominant (van Kolfschoten and Markova, 2005). In these faunas A/L values of *Microtus* display a greater range of variation (relating to the diversification of different lineages), within the limits illustrated in Fig. 8. Other faunas with published A/L values are Sackdillingen and Hohensülzen (Germany), Somssich-hegy 2, Nagyharsányhegy 4, Villány 6, Villány 8/lower part (Hungary) and Huéscar (Spain) (for further references see in Maul, 2001).

Group 3:

This group includes faunas of early Brunhes age, which contain *Mimomys savini.* Mean A/L values of *Microtus* from early Brunhes sites (West Runton, Voigtstedt, Přezletice, Kozi Grzbiet, Mahlis, Únětice) are given in Figure 8. Further faunas of this period may include Süßenborn, Husarenhof 4, Weißenburg 7 (Germany), Tarkö/layer 16, Kövesvárad, Osztramos 12 in Hungary, Koněprusy C 718, Koněprusy Jk 1-3 (Czech Republic) and Včeláre 1 and Gombasek (Slovakia). Somssich-hegy 2 (Hungary) and Betfia 7/loess deposit (Romania) might belong to either group 2 or 3 (for further references see in Maul, 2001).

Group 4:

These faunas post-date the *Arvicola-Mimomys* transition. The presence of *Arvicola* distinguishes this Group 4 from Group 3, but in terms of faunal composition there are many species in common and only minor morphometric differences between taxa present in both groups (Fig. 8). Sites in Group 4 include Boxgrove, Westbury-sub-Mendip, Mauer and Mosbach 2, Hundsheim, Tarkö (layers 1-15). All these faunas contain *Pliomys episcopalis*, which probably became extinct during the Anglian/Elsterian Glaciation (MIS 12) (Koenigswald and Heinrich, 1999).

8. Conclusion

Historically, the micromammal fauna from the type Cromerian West Runton Freshwater Bed has provided an important 'fixed-point' in the biostratigraphy of the European early Middle Pleistocene. Unfortunately, the stratigraphical provenance of specimens collected in the late 19th and early 20th centuries is frequently uncertain and these collections are believed to be biased as a result of the collecting techniques employed. Extensive sampling of the WRFB during the '1995-Mammoth Excavation' has yielded a large unbiased assemblage, which provides the basis for detailed morphometric comparisons. Analysis of this assemblage largely supports previous taphonomic and environmental interpretations, but the detailed sampling employed shows that faunal composition is homogenous through the section. In addition, there are no significant differences in either the faunal content or morphometry between assemblages from the upper and lower parts of the section. These observations are consistent with rapid deposition of the WRFB.

On the basis of faunal composition and morphometric data, the WRFB micromammal fauna shows the greatest similarities with the faunas from Voigtstedt and Přezletice. The WRFB micromammals accumulated during the pre-optimum interval of an interglacial, which, based on the species content and evolutionary stage of *Mimomys*, probably occurred during the early part of MIS 17. Although it is tempting to equate the WRFB with an odd numbered Marine Isotope stages, long terrestrial sequences show a greater complexity of climatic fluctuations during the early Middle Pleistocene. For example, the pollen record from early Pleistocene lacustrine sediments at Tenaghi Philippon (Greece), records as many as 15 distinct peaks in arboreal pollen, which are separated by cold periods characterised by high frequencies of non-arboreal pollen (Tzedakis et al. 2006). Whether this complexity is also reflected in the northern part of Europe is currently uncertain, however, sub-stage variability has been invoked by Preece and Parfitt (2000) to account for the number of faunally distinct temperate stages in the British 'Cromerian Complex'.

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Figure captions

Figure 1. Talpidae from the 1995-Mammoth Excavation at West Runton. (a) *Talpa europaea*, right humerus fragment (WR95/74-80-30); (b) *Talpa minor*, right radius (WR95/74-77-27); (c) *Desmana* sp., left upper incisor (WR95/74-40-26). (a-c) lateral view.

Figure 2. Soricidae from the 1995-Mammoth Excavation at West Runton. *Sorex* cf. *minutus*, mandibles (A – WR95/74-80-25, B, b – WR95/74-40-21); *Sorex runtonensis*, mandibles (C, c – WR95/74-39-21 , D, d – WR95/73-79-103); *Sorex savini*, P3-P4 (e – WR95/73-68-121, F – WR95/73-46-161, G, g – WR95/74-037-21); *Neomys newtoni*, mandibles (H, h – WR95/74-76-25 , I, i – WR95/73-25-33). (A-I) mandible, buccal view, (b-d, g-i) condylar view, (e) occlusal view. All specimens are left, except (F, G, g), which have been inverted.

Figure 3. *Castor fiber* and *Cricetus runtonensis* from the 1995-Mammoth Excavation at West Runton. *Castor fiber* right M1 or M2 (A, a – WR95/74-75-301), right p4 (B, b – WR95/73-046-201); *Cricetus runtonensis* right m1 (C, c – WR95/74-105-11). (A-C) occlusal view, (a) lingual view, (b, c) buccal view.

Figure 4. Rooted arvicolids from the 1995-Mammoth Excavation at West Runton. *Clethrionomys hintonianus*, m1 (A, a – WR95/73-28-54, D, d - WR95/74-032-014, G, g - WR95/73-079-063); *Pliomys episcopalis*, m1 (B, b - WR95/73-044-063, E, e - WR95/74073-014); *Mimomys savini*, m1 (C, c - WR95/73-047-005, F, f - WR95/73-047-004 H, h - WR95/73-044-004). (A-H) occlusal view, (a-h) buccal view. Specimens D, d, H, h are left, A-C, a-c, E-G, e-g have been inverted.

Figure 5. *Microtus* from the 1995-Mammoth Excavation at West Runton. *Microtus* '*arvalinus*', m1 (a – WR95/74-77-11, b – WR95/74-74-16); *Microtus* '*ratticepoides*', m1 (c – WR95/73-99-41, d – WR95/74-37-13); *Microtus gregaloides*, m1 (e – WR95/73-72-53, f – WR95/74-40-11); *Microtus arvalidens*, m1(g – WR95/74-75-11, h – WR95/74-74-13). All specimens in occlusal view. Specimens a, b, d, f, h are left, c, e, g, have been inverted.

Figure 6. *Apodemus* from the 1995-Mammoth Excavation at West Runton. *Apodemus* cf. *sylvaticus*, M1 (a – WR95/74-32-26); m1 (b – WR95/74-33-23, c – WR95/74-32-25); m1 and m2 (d – WR95/74-30-11). All specimens in occlusal view. All specimens are left, except c, which has been inverted.

Figure 7. Comparison of percentage representation of vole species (excluding *Mimomys savini*) through the profile at West Runton with Koněprusy C 718, Czech Republic.

Figure 8. Grouping of micromammal faunas of the late Early and early Middle Pleistocene based on faunal content and morphometric data. Abbreviations: Ata TD3-6 – Atapuerca Trinchera Dolina (TD) 3-6; Box – Boxgrove; Cast – Castagnone; CollCu – Colle Curti; Hohs – Hohensülzen; Is – Isernia; Korot – Korotoyak/Ostragozhsk suite; Mah – Mahlis; Mosb – Mosbach 2; Na-4 – Nagyharsányhegy 4; Prz – Přezletice; Rif – Rifreddo; Sckd – Sackdillingen; Unt – Untermaßfeld; Vil6 – Villány 6; Vil8/low – Villány 8/lower part; Voi – Voigtstedt;

WR – West Runton; WsM – Westbury-sub-Mendip. Note, rectangles delimiting sites indicate uncertainty regarding the age of the deposits.

Table captions

Table 1. List of micromammalian taxa recovered from the 1995-Mammoth Excavation at West Runton, and alternative names used in recent publications. † = Extinct.

Table 2. Measurements (in mm) of the humerus and radius in samples of various *Talpa* species. Abbreviations: E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene.

Table 3. Measurements (in mm) of P4 and M3 in samples of *Desmana thermalis* and *D. moschata*. Abbreviations: E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLI – Late Pliocene.

Table 4. Mandible measurements (in mm) of soricids from West Runton.

Table 5. Mandible measurements (in mm) of soricids from various localities. Abbreviations: (T) is type specimen or specimen from the type locality, E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLI = Late Pliocene.

Table 6. Dental measurements (in mm) of *Castor fiber* from various localities. Abbreviations: M-PLEI = Middle Pleistocene.

Table 7. Lower first molar measurements (in mm) of *Cricetus* samples from various localities. Abbreviations: E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLEI – Late Pleistocene.

Table 8. Measurements (in mm) of the m1 of *Clethrionomys* from various localities. Abbreviations: (T) denotes type specimen or specimen from the type locality, E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLI = Late Pliocene.

Table 9. Measurements (in mm) of the m1 of *Pliomys* from various localities. Abbreviations: (T) denotes type specimen or specimen from the type locality, E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLI = Late Pliocene.

Table 10. Measurements (in mm) of the m1 of *Mimomys savini* and *Arvicola* from various localities. Abbreviations: E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLEI = Late Pleistocene.

Table 11. Measurements (in mm) of the m1 of *Microtus* species from West Runton. A/L index after van der Meulen (1973).

Table 12. Measurements (in mm) of the m1 of *Microtus* species from various localities. A/L-, B/W-, C/W- indices after van der Meulen (1973). Abbreviations: E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLEI = Late Pleistocene.

Table 13. Measurements (in mm) of the M1 and m1 of murid species from various localities. Abbreviations: (T) denotes type specimen or specimen from the type locality, E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLI = Late Pliocene.

Table 14. Distribution of the micromammal remains in successive levels of the sample column from square 73 and 74 (1995-Mammoth Excavation).

Table 15. Length (in mm) measurements and SDQ7 values of *Mimomys savini* m1s from the upper (3.70-4.35 m O.D.) and lower (3.00-3.70 m O.D.) levels of the profile.

Table 16. Small mammal taxa from the 1995-Mammoth Excavation compared to that of previous collections from the WRFB (Stuart, 1975; Preece and Parfitt, 2000, taxonomically modified).

Table 1

List of micromammalian taxa recovered from the 1995-Mammoth Excavation at West Runton, and alternative names used in recent publications. † = Extinct.

Stuart, 1996	Preece and Parfitt, 2000	This paper
Talpa europaea	*Talpa europea*	*Talpa europaea*
Talpa minor †	*Talpa minor* †	*Talpa minor* †
Desmana moschata	*Desmana moschata*	*Desmana* sp.
Sorex minutus	*Sorex minutus*	*Sorex* cf. *minutus*
Sorex runtonensis †	*Sorex runtonensis* †	*Sorex runtonensis* †
Sorex savini †	*Sorex savini* †	*Sorex savini* †
Neomys newtoni †	*Neomys* sp.	*Neomys newtoni* †
Castor fiber	*Castor fiber*	*Castor fiber*
Cricetus cricetus	*Cricetus cricetus*	*Cricetus runtonensis* †
Clethrionomys glareolus	*Clethrionomys glareolus*	*Clethrionomys hintonianus* †
Pliomys episcopalis †	*Pliomys episcopalis* †	*Pliomys episcopalis* †
Mimomys savini †	*Mimomys savini* †	*Mimomys savini* †
Microtus cf. *arvalis*	*Microtus* cf. *arvalis*	*Microtus* ‘*arvalinus*’ †
Microtus oeconomus	*Microtus oeconomus*	*Microtus* ‘*ratticepoides*’ †
Pitymys gregaloides †	*Microtus gregaloides* †	*Microtus gregaloides* †
Pitymys arvalidens †	*M.* (*Terricola*) sp.	*Microtus arvalidens* †
Apodemus sylvaticus	*Apodemus sylvaticus*	*Apodemus* cf. *sylvaticus*

Table

Table 2

Measurements (in mm) of the humerus and radius in samples of various *Talpa* species. Abbreviations: E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene.

stratigraphic age	taxonomic referral (according to cited author)	locality	reference	humerus							
				distal epiphysis width				diaphysis width			
				n	min	mean	max	n	min	mean	max
Recent	*Talpa europaea*	Europe	Niethammer, 1990	63	6.70		9.90	63	3.30		4.70
late M-PLEI	*Talpa europaea*	Petersbuch	Koenigswald, 1970	90	7.40	8.32	9.30	90	3.50	3.85	4.25
early M-PLEI	*Talpa europaea*	Boxgrove	Parfitt, 1999	29	7.30	8.28	9.20	38	3.59	3.87	4.30
early M-PLEI	*Talpa europaea*	Voigtstedt	Stuart, 1981, Maul, 1990	2	7.80	7.81	7.82	2	3.66	3.68	3.70
early M-PLEI	***Talpa europaea***	***West Runton***	**this paper**	**1**		**8.17**		**1**		**3.71**	
early M-PLEI	*Talpa europaea*	West Runton	Stuart, 1981	2	8.80	8.90	9.00	3	3.64	3.73	3.78
late E-PLEI	*Talpa fossilis*	Hohensülzen	Malec in Storch et al., 1973	2	9.00	9.10	9.20	2	4.30	4.35	4.40
late E-PLEI	*Talpa europaea*	Untermaßfeld	Maul, 2001	2	8.43	8.78	9.14	3	4.14	4.43	4.64
			all *T. europaea* mentioned above		**6.70**		**9.90**		**3.30**		**4.70**
late M-PLEI	*Talpa minor*	Petersbuch	Koenigswald, 1970	46	5.40	5.96	6.50	46	2.70	2.96	3.35
early M-PLEI	*Talpa minor*	Boxgrove	Parfitt, 1999	29	5.88	6.73	7.85	40	2.73	3.18	3.52
early M-PLEI	*Talpa minor*	Voigtstedt	Stuart, 1981, Maul, 1990	13	6.21	6.58	7.00	18	3.06	3.19	3.43
early M-PLEI	*Talpa minor*	Husarenhof 4	Koenigswald, 1973	2	6.25	6.82	7.40	2	3.04	3.28	3.45
early M-PLEI	*Talpa minor*	West Runton	Stuart, 1981	36	6.60	7.27	7.80				
late E-PLEI	*Talpa minor*	Hohensülzen	Malec in Storch et al., 1973	4	6.60	6.75	6.90	5	3.30	3.36	3.50
			all *T. minor* mentioned above		**5.40**		**7.85**		**2.70**		**3.52**

				radius			
				length			
				n	min	mean	max
early M-PLEI	*Talpa praeglacialis*	Erpfingen	Heller, 1958	5	11.90	12.36	13.00
late E-PLEI	*Talpa fossilis*	Hohensülzen	Malec in Storch et al., 1973	2	12.40	12.85	13.30
late E-PLEI	*Talpa praeglacialis*	Sackdillingen	Heller, 1930	1		13.00	
late E-PLEI	*Talpa europaea*	Untermaßfeld	Maul, 2001	1		13.00	
			all *T. europaea* mentioned above		**11.90**		**13.30**
early M-PLEI	*Talpa minor*	Hundsheim	Rabeder, 1972	17	10.00	10.49	11.60
early M-PLEI	*Talpa minor*	Erpfingen	Heller, 1958	30	9.39	9.90	11.40
early M-PLEI	*Talpa minor*	Voigtstedt	Maul, 1990	1		10.55	
early M-PLEI	*Talpa minor*	Kővesvárad	Jánossy, 1963	2	10.00	10.25	10.50
early M-PLEI	***Talpa minor***	**West Runton**	**this paper**	**1**		**10.80**	
late E-PLEI	*Talpa minor*	Hohensülzen	Malec in Storch et al., 1973	2	10.90	11.00	11.10
late E-PLEI	*Talpa fossilis*	Monte Peglia	van der Meulen, 1973	5	10.85	11.05	11.50
			all *T. minor* mentioned above		**9.39**		**11.60**

Table 3

Measurements (in mm) of P4 and M3 in samples of *Desmana thermalis* and *D. moschata* . Abbreviations: E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLI – Late Pliocene.

stratigraphic age	taxonomic referral (according to cited author)	locality	reference	P4								M3							
				length				width				length				width			
				n	min	mean	max	n	min	mean	max	n	min	mean	max	n	min	mean	max
Recent	*Desmana moschata*	Ukraine	Rümke, 1985	13	3.12	3.36	3.53	13	2.79	2.91	3.05	14	2.31	2.42	2.63	14	3.37	3.58	3.85
early M_PLEI	***Desmana* sp.**	**West Runton**	**this paper**	**1**		**3.07**		**1**		**2.37**		**2**	**2.19**	**2.28**	**2.36**	**2**	**2.91**	**2.94**	**2.98**
E-PLEI	*Desmana thermalis*	Betfia 2	Rümke, 1985	2	3.04	3.07	3.10	2	2.48	2.61	2.75	1		2.00		1		2.90	
late L-PLI	*Desmana thermalis*	Tegelen	Rümke, 1985	12	2.68	2.95	3.27	12	2.25	2.37	2.50	10	1.68	1.89	2.12	10	2.45	2.70	2.91

Table

Table 5
Mandible measurements (in mm) of soricids from various localities. Abbreviations: (T) is type specimen or specimen from the type locality, E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLI = Late Pliocene.

stratigraphic age	taxonomic referral (according to cited author)	locality	reference	ascending ramus				m1-m3							
				height				coronar length				alveolar length			
				n	min	mean	max	n	min	mean	max	n	min	mean	max
Recent	*Sorex araneus*	Central Europe	Heinrich, 1983	593	4.20	4.63	5.05	1205	3.50	3.79	4.10				
Recent	*Sorex minutus*	Central Europe	Hutterer, 1990	20	2.80	3.32	4.10								
Recent	*Sorex minutus*	Central Europe	Heinrich, 1983	8	3.03	3.15	3.25	8	3.00	3.07	3.19				
Recent	*Sorex minutissimus*	Finland	Sulkava, 1990	14	2.80	3.03	3.20								
early M-PLEI	*Sorex minutus*	Boxgrove	Parfitt, 1999	2	2.90		3.00								
early M-PLEI	*Sorex minutus*	Westbury	Bishop, 1982	2	2.80		3.10	2	2.60		3.10				
early M-PLEI	*Sorex minutissimus*	Kozi Grzbiet	Rzebik-Kowalska, 1991	2	2.73	2.77	2.81	6	2.75	2.84	2.91				
early M-PLEI	***Sorex* cf. *minutus***	**West Runton**	**this paper**	**1**		**3.18**						**3**	**2.48**	**2.67**	**2.79**
early M-PLEI	*Sorex runtonensis*	Boxgrove	Parfitt, 1999	30	3.82	4.01	4.20								
early M-PLEI	*Sorex runtonensis*	Westbury-sub-Mendi	Bishop, 1982	14	3.89	4.06	4.31	14	3.45	3.59	3.86				
early M-PLEI	*Sorex* cf. *helleri*	Hundsheim	Rabeder, 1972	9	3.90	4.08	4.20	9	3.40	3.58	3.80				
early M-PLEI	*Sorex subaraneus*	Tarkő/layer 1-15	Jánossy, 1969	21	3.70	4.06	4.60	21	3.20	3.63	4.10				
early M-PLEI	*Sorex* aff. *runtonensis*	Kővesvárad	Jánossy, 1963	3	3.92		3.97	2	3.45	3.51	3.57				
early M-PLEI	***Sorex runtonensis***	**West Runton**	**this paper**	**5**	**3.47**	**3.86**	**4.24**	**4**	**3.24**	**3.54**	**3.69**	**18**	**2.96**	**3.29**	**3.59**
early M-PLEI	*Sorex runtonensis* (T)	West Runton	Jánossy, 1969	21	3.40	3.96	4.20	22	3.30	3.55	3.80				
early M-PLEI	*Sorex runtonensis* (T)	West Runton	Hinton, 1911	1		3.74		1		3.41					
early M-PLEI	*Sorex runtonensis*	Villány 8	Jánossy, 1969	24	3.70	3.90	4.10	24	3.30	3.48	3.70				
early M-PLEI	*Sorex* sp.	Mahlis	Heinrich in Fuhrmann et al., 1977	1		4.00						1		3.80	
late E-PLEI	*Sorex runtonensis*	Hohensülzen	Malec in Storch et al., 1973					2	4.00	4.05	4.10				
late E-PLEI	*Sorex* cf. *runtonensis*	Sackdillingen	Brunner, 1934		3.87		4.02		3.60		3.70				
late E-PLEI	*Sorex runtonensis*	Podumci 1	Malez, Rabeder, 1984	6	3.82	3.87	4.05	8	3.31	3.52	3.60				
late E-PLEI	*Sorex runtonensis*	Untermaßfeld	Maul, 2001	1		4.00		3	3.23	3.38	3.45				
late E-PLEI	*Sorex runtonensis*	Les Valerots	Jeannet in Giacobini et al., 1980	1		3.90		1		3.60					
late E-PLEI	*Sorex runtonensis*	Holštejn	Musil, 1966						3.50		3.60				
late E-PLEI	*Sorex runtonensis*	Monte Peglia	van der Meulen, 1973	18	3.59	3.76	4.07	1		3.52					
late L-PLI	*Sorex* aff. *runtonensis*	Schernfeld	Dehm, 1962	42	3.30		3.70	1		3.25					
early M-PLEI	*Sorex savini*	Boxgrove	Parfitt, 1999	15	5.32	5.66	6.00								
early M-PLEI	*Drepanosorex austriacus* (T)	Hundsheim	Rabeder, 1972	14	5.70	5.95	6.40	16	4.20	4.42	4.60				
early M-PLEI	*Sorex savini*	Sudmer-Berg 2	Koenigswald, 1972	1		ca.5,80		1		ca.4,40					
early M-PLEI	*Sorex savini*	Mosbach	Bahlo, Malec, 1969	1		5.65		1		4.40					
early M-PLEI	*Sorex savini*	Westbury-sub-Mendi	Bishop, 1982	4	5.40	5.47	5.70	4	4.10	4.22	4.30				
early M-PLEI	*Sorex savini*	Tarkő/layer 1-15	Jánossy, 1969	3	5.60	5.70	5.80								
early M-PLEI	*Sorex savini*	Voigtstedt	Maul, 2001	1		5.57						2	4.00	4.07	4.14
early M-PLEI	*Sorex savini*	Husarenhof 4	Koenigswald, 1973	2	5.25	5.45	5.65	1		4.10					
early M-PLEI	*Sorex savini*	Přezletice	Maul, 2001	8	5.20	5.34	5.60	1		4.10					
early M-PLEI	***Sorex savini***	**West Runton**	**this paper**	**4**	**5.35**	**5.70**	**5.85**	**9**	**4.00**	**4.18**	**4.40**	**26**	**3.52**	**3.77**	**4.18**
early M-PLEI	*Sorex savini* (T)	West Runton	Jánossy, 1969	24	5.30		5.90	1		4.07					
early M-PLEI	*Sorex savini* (T)	West Runton	Hinton, 1911	1		5.61		1		4.07					
late E-PLEI	*Drepanosorex savini*	Hohensülzen	Malec in Storch et al., 1973	2		5.40									
late E-PLEI	*Sorex* cf. *savini*	Sackdillingen	Brunner, 1934	2	5.30	5.35	5.40	3	3.90	3.93	4.00				
late E-PLEI	*Sorex margaritodon-savini*	Untermaßfeld	Maul, 2001	2		5.25		2	4.09	4.13	4.18				
late E-PLEI	*Sorex margaritodon* (T)	Betfia 2	Maul, 2001	3	4.95	5.21	5.54	3	3.48	3.74	3.90				
early E-PLEI	*Sorex margaritodon*	Osztramos 8	Jánossy, 1972	6	4.80		5.10	1		4.00					
early E-PLEI	*Sorex pachyodon* (T)	Soave/Cava Sud	Pasa, 1947		4.30		4.60		3.60		3.90				
late L-PLI	*Sorex praearaneus*	Tegelen	Reumer, 1984	10	4.13	4.36	4.53	2	3.51	3.67	3.82				
Recent	*Neomys anomalus*	Central Germany	Heinrich, 1983	30	4.00	4.23	4.45	30	4.00	4.33	4.50				
Recent	*Neomys fodiens*	Central Germany	Heinrich, 1983	30	4.70	5.04	5.44	30	4.42	4.68	4.92				
early M-PLEI	*Neomys* sp.	Boxgrove	Parfitt, 1999	4	4.15	4.21	4.30								
early M-PLEI	*Neomys* cf. *newtoni*	Westbury	Bishop, 1982	3	4.10	4.20	4.30	1		4.35					
early M-PLEI	***Neomys newtoni***	**West Runton**	**this paper**	**7**	**3.75**	**4.03**	**4.47**					**5**	**3.14**	**3.45**	**3.86**
early M-PLEI	*Neomys newtoni* (T)	West Runton	Hinton, 1911			3.75									
late E-PLEI	*Neomys* cf. *newtoni*	Monte Peglia	van der Meulen, 1973	2	4.41		4.62			3.93					
early M-PLEI	*Macroneomys brachygnathus* (	Koněprusy C 718	Fejfar, 1966	3	6.50	6.64	6.83	1		5.00					

Table 4
Mandible measurements (in mm) of soricids from West Runton

		ascending ramus height	m1-m3 coronar length	m1-m3 alveolar length	articular process height	upper facet width	lower facet width	lower incisor buccal length
Sorex cf. *minutus*	n	1		3	1	1	1	
Sorex cf. *minutus*	min			2.48				
Sorex cf. *minutus*	mean	3.18		2.67	1.28	0.49	0.80	
Sorex cf. *minutus*	max			2.79				
Sorex cf. *minutus*	sd			0.16				
Sorex runtonensis	n	5	4	18	6	6	6	2
Sorex runtonensis	min	3.47	3.24	2.96	1.43	0.49	0.93	3.56
Sorex runtonensis	mean	3.86	3.54	3.29	1.61	0.72	1.14	3.58
Sorex runtonensis	max	4.24	3.69	3.59	1.89	0.93	1.55	3.61
Sorex runtonensis	sd	0.33	0.20	0.20	0.18	0.16	0.21	0.04
Sorex savini	n	4	9	26	9	9	9	7
Sorex savini	min	5.35	4.00	3.52	2.16	0.95	1.50	3.71
Sorex savini	mean	5.70	4.18	3.77	2.58	1.28	1.58	4.17
Sorex savini	max	5.85	4.40	4.18	2.74	1.48	1.72	4.43
Sorex savini	sd	0.23	0.14	0.17	0.19	0.17	0.07	0.25
Neomys newtoni	n	7		5	8	8	7	
Neomys newtoni	min	3.75		3.14	1.52	0.54	0.84	
Neomys newtoni	mean	4.03		3.45	1.96	0.84	1.25	
Neomys newtoni	max	4.47		3.86	2.19	0.95	1.58	

Table 6

Dental measurements (in mm) of *Castor fiber* from various localities. Abbreviations: M-PLEI = Middle Pleistocene.

stratigraphic age	taxonomic referral (according to cited author)	locality	reference	M1							
				occlusal length				occlusal width			
				n	min	mean	max	n	min	mean	max
Recent	*Castor fiber*	Germany	Reichenau, 1912	11	5.50	6.67	7.80	11	6.00	7.47	10.00
early M-PLEI	***Castor fiber***	**West Runton**	**this paper**	**1**		**6.49**		**1**		**9.93**	

				M2							
				occlusal length				occlusal width			
				n	min	mean	max	n	min	mean	max
Recent	*Castor fiber*	Germany	Reichenau, 1912	11	5.80	6.49	7.20	11	6.00	6.93	8.30

				p4							
				occlusal length				occlusal width			
				n	min	mean	max	n	min	mean	max
Recent	Castor fiber	Germany	Reichenau, 1912	10	5.60	8.14	10.20	10	6.60	7.67	9.20
late M-PLEI	*Castor fiber*	Ehringsdorf	Heinrich, 1991	10	8.00	9.32	10.40	10	6.80	7.88	9.20
late M-PLEI	*Castor fiber*	Bilzingsleben	Heinrich, 1991	47	7.80	9.30	11.00	49	6.60	7.57	9.00
early M-PLEI	*Castor fiber*	Süßenborn	Heinrich, 1991	5	8.30	9.04	10.00	6	7.30	7.80	8.00
early M-PLEI	***Castor fiber***	**West Runton**	**this paper**	**1**		**9.27**		**1**		**6.39**	

Table 7
Lower first molar measurements (in mm) of *Cricetus* samples from various localities. Abbreviations: E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLEI – Late Pleistocene.

stratigraphic age	taxonomic referral (according to cited author)	locality	reference	m1							
				length				width distal			
				n	min	mean	max	n	min	mean	max
Recent	*Cricetus cricetus*	Germany	Storch et al., 1973	59	2.85	2.97	3.12	59	1.70	1.80	1.95
Recent	*Cricetus cricetus*	Poland	Pradel, 1985	86	2.78	3.03	3.35	86	1.65	1.80	2.01
late L-PLEI	*Cricetus cricetus*	Poland	Pradel, 1988			3.20				1.83	
			all *C. cricetus* mentioned above		**2.78**		**3.35**		**1.65**		**2.01**
late M-PLEI	*Cricetus cricetus major*	Genkingen 2	Ziegler, 1995	1		3.87					
late M-PLEI	*Cricetus major*	Petersbuch	Fahlbusch, 1976	18	3.55	3.73	3.97	18	1.98	2.17	2.37
			all *C. major* mentioned above		**3.55**		**3.97**		**1.72**		**2.37**
early M-PLEI	*C. cricetus runtonensis*	Uppony/Schicht 10	Maul, 2001	2	3.01	3.40	3.79	2	1.72	2.02	2.32
early M-PLEI	***Cricetus runtonensis***	**West Runton**	**this paper**	**1**		**3.46**		**1**		**2.01**	
early M-PLEI	*Cricetus runtonensis*	Kozi Grzbiet	Pradel, 1988	31	3.01	3.35	3.74	28	1.80	1.94	2.10
late E-PLEI	*Cricetus* cf. *runtonensis*	Untermaßfeld	Maul 2001					1		1.93	
late E-PLEI	*Cricetus runtonensis*	Zalesiaki 1	Pradel, 1988	3	2.98	3.36	3.64	3	1.82	1.92	2.04
late E-PLEI	*Cricetus major*	Holštejn	Musil, 1966	7	3.00		3.60	7	1.90		2.30
early E-PLEI	*Cricetus runtonensis*	Kadzielnia	Fahlbusch, 1969	1		3.40		1		2.03	
			all *C. runtonensis* mentioned above		**2.98**		**3.79**		**1.72**		**2.32**
early M-PLEI	*Cricetus cricetus praeglacialis*	Villány 8	Chaline, 1972	3	2.70	2.86	3.04	3	1.58	1.67	1.74
E-PLEI	*Cricetus cricetus praeglacialis*	Betfia 2 (Type specimen)	Hir, 1997			3.25				1.80	
E-PLEI	*Cricetus cricetus praeglacialis*	Betfia 2 (Type locality)	Hir, 1997			3.12				1.80	
			all *C. praeglacialis* mentioned above		**2.70**		**3.25**		**1.58**		**1.80**

Table 8

Measurements (in mm) of the m1 of *Clethrionomys* from various localities. Abbreviations: (T) denotes type specimen or specimen from the type locality, E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLI = Late Pliocene.

stratigraphic age	taxonomic referral (according to cited author)	locality	reference	m1								
				length					hyposinuid/buccal length (Hsd/L)			
				n	min	mean	max	sd	n	min	mean	max
Recent	*Clethrionomys rutilus*	Finland	Maul, 2001	50	1.77	2.06	2.30					
Recent	*Clethrionomys rufocanus*	Finland	Maul, 2001	50	1.95	2.45	3.01					
Recent	*Clethrionomys glareolus*	Eastern Germany	Maul, 2001	19	2.39	2.64	2.79		19	116.67	134.07	146.67
late M-PLEI	*Clethrionomys glareolus*	Petersbuch	Maul et al., 1998a	10	1.85	1.97	2.08		10	119.23	131.33	142.31
early M-PLEI	*Clethrionomys glareolus*	Boxgrove	Parfitt, 1999	130	1.65	2.05	2.31					
early M-PLEI	*Clethrionomys glareolus*	Westbury-sub-Mendip	Bishop, 1982	1		2.40						
early M-PLEI	*Clethrionomys acrorhiza*	Hundsheim	Rabeder, 1981						1		131.03	
early M-PLEI	*Clethrionomys acrorhiza* (T)	Brasov	Kormos, 1933	2		2.25						
early M-PLEI	*Clethrionomys* cf. *hintonianus*	Voigtstedt	Maul, 1990	2	2.08	2.11	2.13					
early M-PLEI	***Clethrionomys hintonianus***	**West Runton**	**this paper**	**15**	**1.89**	**2.11**	**2.36**	**0.14**	**2**	**109.60**	**110.33**	**111.07**
late E-PLEI	*Clethrionomys hintonianus*	Neuleiningen 5, 15	Maul et al., 1998a	15	1.91	2.09	2.30		8	102.94	110.50	125.00
E-PLEI	*Clethrionomys hintonianus*	Deutsch Altenburg 2C1	Rabeder, 1981	62	2.07	2.21	2.39		28	100.00	115.84	119.25
late L-PLI	*Clethrionomys kretzoii*	Schernfeld	Carls, Rabeder, 1988	40	1.89	2.13	2.30		40	100.00	102.35	106.09
late L-PLI	*Clethrionomys kretzoii*	Neuleiningen 4, 11	Maul et al., 1998a	16	1.91	2.23	2.49		10	71.67	87.31	100.00

Table 9

Measurements (in mm) of the m1 of *Pliomys* from various localities. Abbreviations: (T) denotes type specimen or specimen from the type locality, E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLI = Late Pliocene.

stratigraphic age	taxonomic referral (according to cited author)	locality	reference	m1								
				length					hyposinuid/buccal length (Hsd/L)			
				n	min	mean	max	sd	n	min	mean	max
early M-PLEI	*Pliomys episcopalis*	Boxgrove	Parfitt, 1999	12	2.18	2.32	2.41					
early M-PLEI	*Pliomys episcopalis*	Westbury-sub-Mendip	Bishop, 1982	1		2.65						
early M-PLEI	*Pliomys episcopalis*	Kozi Grzbiet	Nadachowski, 1985	25	2.12	2.46	2.84					
early M-PLEI	***Pliomys episcopalis***	**West Runton**	**this paper**	**3**	**1.79**	**2.06**	**2.32**	**0.37**	**1**		**138.16**	
late E-PLEI	*Pliomys episcopalis*	Hohensülzen	Storch et al., 1973	8	2.30	2.40	2.50					
late E-PLEI	*Pliomys episcopalis*	Somssich-hegy 2	Maul, 2001	10	1.92	2.34	2.58					
late E-PLEI	*Pliomys episcopalis*	Untermaßfeld	Maul, 2001	3	2.60	2.65	2.68					
late E-PLEI	*Pliomys episcopalis*	Neuleiningen 15	Maul et al., 1998a	4	2.38	2.55	2.64		1		130.56	
late E-PLEI	*Pliomys episcopalis*	Monte Peglia	van der Meulen, 1973	4	2.39	2.44	2.54					
E-PLEI	*Pliomys episcopalis*	Deutsch Altenburg 2C1	Rabeder, 1981	37	2.35	2.64	2.81		21	115.32	112.12	114.59
E-PLEI	*Pliomys simplicior*	Deutsch Altenburg 2C1	Rabeder, 1981	34	2.21	2.49	2.67		20	97.74	99.60	110.11
late L-PLI	*Pliomys schernfeldensis* (T)	Schernfeld	Carls, Rabeder, 1988	40	2.35	2.55	2.85		40	39.15	49.41	60.07

Table 10

Measurements (in mm) of the m1 of *Mimomys savini* and *Arvicola* from various localities. Abbreviations: E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLEI = Late Pleistocene.

stratigraphic age	taxonomic referral (according to cited author)	locality	reference	lower m1													
				length					SDQ7					SDQ3			
				n	min	mean	max	sd	n	min	mean	max	sd	n	min	mean	max
Recent	*Arvicola terrestris*	Central Germany	Frahnert, 1991	30	3.45	3.78	4.20		30	70.00	85.00	100.00					
late L-PLEI	*Arvicola terrestris*	Krockstein	Heinrich, 1982	40	3.65	4.04	4.60		40	72.20	89.08	102.93					
late L-PLEI	*Arvicola terrestris*	Burgtonna 2	Heinrich, 1990	41	3.40	3.76	4.42		64	76.00	98.44	115.00					
late L-PLEI	*Arvicola mosbachensis*	Taubach	Heinrich, 1990	11	3.48	3.95	4.20		9	97.19	105.15	115.52					
late M-PLEI	*Arvicola mosbachensis*	Ehringsdorf/Lower Travertine	Heinrich, 1990	8	3.52	3.70	3.86		7	102.57	112.30	126.38					
late M-PLEI	*Arvicola mosbachensis*	Petersbuch 1	Maul et al., 2000	10	3.48	3.65	4.00		11	107.87	126.16	146.40					
early M-PLEI	*Arvicola terrestris canitana*	Boxgrove	Parfitt, in Preece et al., 2007	80	2.84	3.40	3.92		13	122.40	139.60	163.50					
early M-PLEI	*Arvicola cantiana*	Westbury-sub-Mendip	Parfitt, in Preece et al., 2007	30	3.14	3.36	3.63		30	116.90	135.60	170.40					
early M-PLEI	*Arvicola mosbachensis*	Mosbach 2	Maul et al., 2000	44	3.06	3.25	3.50		45	117.60	133.34	159.27					
early M-PLEI	*Arvicola mosbachensis*	Miesenheim 1	Van Kolfschoten, 1990	18	3.21	3.50	3.71		29	126.00	152.03	180.00					
early M-PLEI	*Mimomys savini*	Voigtstedt	Maul, 1990	115	3.00	3.38	3.80		20	107.14	133.66	159.64					
early M-PLEI	***Mimomys savini***	**West Runton**	**this paper**	**49**	**2.89**	**3.33**	**3.72**	**0.17**	**48**	**114.57**	**139.59**	**163.14**	**11.08**	**49**	**104.40**	**134.81**	**171.4**
late E-PLEI	*Mimomys savini*	Untermaßfeld	Maul, 1990	8	3.15	3.29	3.50		11	129.59	151.00	179.18					
late E-PLEI	*Mimomys savini*	Neuleiningen 5	Maul et al, 1998	10	3.06	3.16	3.37		10	125.36	140.24	163.93					

Table 11

Measurements (in mm) of the m1 of *Microtus* species from West Runton. A/L-, B/W-, C/W- indices after v

		L	A/L	B/W	C/W	B2/W2	C2/W2
M. (M.) arvalinus	n	47	47	47	47	47	47
M. (M.) arvalinus	min	2.18	44.61	1.74	1.40	33.00	7.84
M. (M.) arvalinus	mean	2.58	50.47	4.55	3.40	53.97	31.08
M. (M.) arvalinus	max	2.96	54.64	16.40	6.59	87.00	72.45
M. (M.) arvalinus	sd	0.18	2.31	2.80	1.22	11.79	12.30
M. (P.) ratticepoides	n	6	6	6	6		
M. (P.) ratticepoides	min	2.17	44.81	19.73	2.60		
M. (P.) ratticepoides	mean	2.34	46.86	29.30	4.22		
M. (P.) ratticepoides	max	2.57	48.58	46.85	5.38		
M. (P.) ratticepoides	sd	0.14	1.36	9.89	1.07		
M. (S.) gregaloides	n	35	35	35	35		
M. (S.) gregaloides	min	2.19	48.50	1.65	16.23		
M. (S.) gregaloides	mean	2.40	52.56	3.93	24.15		
M. (S.) gregaloides	max	2.77	56.60	7.08	35.32		
M. (S.) gregaloides	sd	0.15	1.92	1.25	4.98		
M. (T.) arvalidens	n	14	14	14	14	14	14
M. (T.) arvalidens	min	2.31	49.56	2.19	9.12	28.74	31.15
M. (T.) arvalidens	mean	2.49	52.94	4.62	19.73	39.68	43.21
M. (T.) arvalidens	max	2.68	55.94	7.70	29.26	59.36	74.17
M. (T.) arvalidens	sd	0.11	1.98	1.78	4.78	8.88	12.21

Table 12
Measurements (in mm) of the m1 of *Microtus* species from various localities. Abbreviations: E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-I

stratigraphic age	taxonomic referral (according to cited author)	locality	reference	m1 length n	min	mean	max	A/L n	min	mean	max
Recent	*Microtus agrestis*	Poland	Nadachowski, 1982	30	2.83	3.05	3.32	30	50.00	54.00	61.00
Recent	*Microtus arvalis*	Poland	Nadachowski, 1982	30	2.48	2.67	2.84	30	50.00	54.00	57.00
early M-PLEI	*Microtus agrestis*	Boxgrove	Parfitt, 1999	24	2.30	2.70	2.95	11	47.00	51.00	56.00
early M-PLEI	*Microtus arvalis*	Boxgrove	Parfitt, 1999	24	1.99	2.40	2.71	9	48.00	51.00	55.00
early M-PLEI	*Microtus* cf. *arvalis*	Westbury-sub-Mendip	Bishop collection	13	2.64	2.85	3.14	13	46.00	50.46	53.00
early M-PLEI	*Microtus arvalinus*	Voigtstedt	Maul, 2001	10	2.16	2.50	2.78	10	48.50	51.13	54.84
early M-PLEI	***M. (M.) arvalinus***	**West Runton**	**this paper**	**47**	**2.18**	**2.58**	**2.96**	**47**	**44.61**	**50.47**	**54.64**
early M-PLEI	*Microtus arvalinus*	Prezletice	this paper	35	2.23	2.69	3.11	35	44.37	50.70	55.09
late E-PLEI	*Microtus arvalinus*	Hohensülzen	this paper	8	2.40	2.60	2.84	8	46.15	48.14	50.79
Recent	*Microtus oeconomus*	Poland	Nadachowski, 1982	30	2.74	2.98	3.37	30	43.00	48.00	52.00
early M-PLEI	*Microtus oeconomus*	Boxgrove	Parfitt, 1999	8	2.29	2.48	2.67	3	47.00	48.00	50.00
early M-PLEI	*Microtus* cf. *oeconomus*	Westbury-sub-Mendip	Bishop collection	10	2.27	2.45	2.62	10	39.80	46.34	49.95
early M-PLEI	*Microtus ratticepoides*	Voigtstedt	Maul et al., 1998a	9	2.32	2.50	2.78	9	44.33	46.95	47.92
early M-PLEI	***M. (P.) ratticepoides***	**West Runton**	**this paper**	**6**	**2.17**	**2.34**	**2.57**	**6**	**44.81**	**46.86**	**48.58**
early M-PLEI	*M. (P.) ratticepoides*	Prezletice	this paper	4	2.41	2.67	2.77	4	44.89	45.72	46.59
late L-PLEI	*Microtus gregalis*	Poland	Nadachowski, 1982	20	2.48	2.67	2.84	20	52.00	55.00	59.00
early M-PLEI	*Microtus gregalis*	Boxgrove	Parfitt, 1999	8	2.18	2.35	2.57	8	49.00	50.00	52.00
early M-PLEI	*Pitymys gregaloides*	Westbury-sub-Mendip	Bishop collection	13	2.34	2.49	2.64	13	47.00	51.10	54.00
early M-PLEI	***M. (S.) gregaloides***	**West Runton**	**this paper**	**35**	**2.19**	**2.4**	**2.77**	**35**	**48.50**	**52.56**	**56.60**
late E-PLEI	*Pitymys gregaloides*	Hohensülzen	this paper	6	2.50	2.58	2.78	4	49.29	49.82	50.00
late E-PLEI	*Pitymys gregaloides*	Atapuerca/TD5	Cuenca Bescos, 1995	59	2.40	2.60	2.90	59	46.00	49.00	52.00
Recent	*Pitymys subterraneus*	Poland	Nadachowski, 1982	20	2.49	2.62	2.72	32	50.00	53.00	55.00
early M-PLEI	*M.* (*T*.) cf. *subterraneus*	Boxgrove	Parfitt, 1999	32	2.11	2.40	2.61	31	46.00	53.00	58.00
early M-PLEI	*Pitymys arvaloides*	Westbury-sub-Mendip	Bishop collection	2	2.48		2.61	2	53.00		55.00
early M-PLEI	***M. (T.) arvalidens***	**West Runton**	**this paper**	**14**	**2.31**	**2.49**	**2.68**	**14**	**49.56**	**52.94**	**55.94**
early M-PLEI	*M. (T.) arvalidens*	Prezletice	this paper	3	2.33	2.51	2.68	3	48.86	50.33	51.82
early M-PLEI	*M. (T.) arvalidens*	Rifreddo	Masini et al. 2005	12	2.31	2.58	2.75	12	50.00	51.70	54.55
late E-PLEI	*Pitymys arvalidens*	Somssich-hegy 2	this paper	9	2.60	2.80	2.90	9	48.00	52.00	54.00
late E-PLEI	*Terricola arvalidens*	Atapuerca/TD5	Cuenca Bescos, 1995	9	2.11	2.32	2.68	28	47.27	51.81	55.56

Table 13

Measurements (in mm) of the M1 and m1 of murid species from various localities. Abbreviations: (T) denotes type specimen or specimen from the type locality, E-PLEI = Early Pleistocene, M-PLEI = Middle Pleistocene, L-PLI = Late Pliocene.

stratigraphic age	taxonomic referral (according to cited author)	locality	reference	M1								m1									
				length				distal width				length					distal width				
				n	min	mean	max	n	min	mean	max	n	min	x	max	sd	n	min	x	max	sd
Recent	*Apodemus mystacinus*	Greece	Niethammer, 1978b	27	2.38	2.40	2.52					27	2.30	2.36	2.45						
Recent	*Apodemus flavicollis*	Central Germany	Maul, 2001	21	1.88	2.07	2.25	21	1.19	1.30	1.38	21	1.75	1.88	2.00		21	1.13	1.17	1.25	
Recent	*Apodemus sylvaticus*	Central Germany	Maul, 2001	28	1.69	1.88	2.00	28	1.13	1.18	1.25	10	1.59	1.68	1.82		10	0.91	1.02	1.09	
Recent	*Apodemus microps*	Moravia	Heinrich in Benecke et al., 1990	13	1.60		1.80					13	1.50		1.81						
late M-PLEI	*Apod. maastrichtiensis* (T)	Maastricht-Belvedere 4	van Kolfschoten, 1985	7	1.51	1.67	1.82	7	1.02	1.06	1.09	11	1.37	1.50	1.60		11	0.84	0.91	0.95	
early M-PLEI	*Apod. maastrichtiensis*	Boxgrove	Parfitt, 1999	4	1.62	1.71	1.82	4	1.01	1.06	1.11	4	1.56	1.61	1.66		4	0.89	0.91	0.93	
early M-PLEI	*Apodemus sylvaticus*	Boxgrove	Parfitt, 1999	36	1.76	1.84	1.97	36	1.12	1.19	1.29	45	1.61	1.72	1.81		45	0.95	1.03	1.08	
early M-PLEI	*Apodemus flavicollis*	Voigtstedt	Maul, 2001	1		2.11		1		1.28		3	1.80	1.88	2.00		3	1.05	1.10	1.20	
early M-PLEI	***Apodemus* cf. *sylvaticus***	**West Runton**	**this paper**	**1**		**1.83**		**1**		**1.13**		**6**	**1.55**	**1.63**	**1.73**	**0.06**	**6**	**0.94**	**1.00**	**1.08**	**0.06**
late E-PLEI	*Apodemus sylvaticus*	Hohensülzen	Storch et al.1973	23	1.70	1.80	2.00	23	1.10	1.17	1.30	24	1.50	1.71	1.80		24	0.90	1.02	1.10	
late E-PLEI	*Apodemus* cf. *sylvaticus*	Podumci	Malez, Rabeder, 1984	4	1.66	1.86	2.02	4	1.12	1.21	1.29	17	1.56	1.78	1.98		17	0.97	1.08	1.15	
late E-PLEI	*Apodemus* cf. *sylvaticus*	Untermaßfeld	Maul, 2001	3	1.80	1.81	1.82	3	1.11	1.17	1.22	6	1.61	1.73	1.86		6	0.94	0.98	1.05	
late E-PLEI	*Apodemus* cf. *dominans*	Monte Peglia	van der Meulen, 1973	11	2.05	2.14	2.28	11	1.33	1.37	1.45	13	1.87	1.97	2.14		14	1.07	1.16	1.23	
E-PLEI	*Apodemus flavicollis*	Pirro Nord 1	de Giuli, Torre, 1984	7	2.01	2.05	2.10	7	1.30	1.34	1.39	17	1.82	1.88	1.98		17	1.07	1.14	1.20	
late L-PLI	*Apodemus* aff. *alsomyoides*	Schernfeld	Dehm, 1962	1		2.17	1.00			1.30		1		2.05			1		1.15		
late L-PLI	*Apodemus atavus*	Willershausen	Rietschel, Storch, 1974	1		1.80		1		1.20		2	1.70	1.75	1.80		2	1.00	1.05	1.10	

Table 14
Distribution of the micromammal remains in successive levels of the sample column from square 73 and 74 (1995-Mammoth Excavation).

metres O.D.	sample no	sample weight (kg)	number of identifiable specimens	*Talpa* sp.	*Talpa europaea*	*Talpa minor*	*Desmana* sp.	*Sorex* cf. *minutus*	*Sorex runtonensis*	*Sorex savini*	*Neomys newtoni*	*Castor fiber*	*Cricetus runtonensis*	*Clethrionomys hintonianus*	*Pliomys episcopalis*	*Mimomys savini*	*Microtus 'arvalinus'*	*Microtus 'ratticepoides'*	*Microtus gregaloides*	*Microtus arvalidens*	*Apodemus* cf. *sylvaticus*
4.35-4.30	73/14	10.05																			
4.30-4.25	74/08	42.30	30																		
4.25-4.20	74/09	32.75	30																		
4.20-4.15	74/10, 73/21	189.10	33	1						1						1					
4.15-4.10	74/11	77.55	75							1						1	1				
4.10-4.05	74/29	131.45	113								1					11			1		
4.05-4.00	73/24, 74/30, 74/30b	218.20	198							2					1	28	1		1	1	1
4.00-3.95	73/25, 74/31	216.70	179				1		2	1	1			1		28	1		2		
3.95-3.90	73/26, 74/32	215.20	577	4					3	2				1		24	3		2		4
3.90-3.85	73/27, 74/33	235.20	305						4	4				2		29	5			1	1
3.85-3.80	73/28, 74/37	254.90	347						3	5	1			1		49	3	1	1	1	3
3.80-3.75	74/38	107.10	278	1						3						3	2				
3.75-3.70	74/39, 73/44	227.30	542	2					4	8					1	75	5		3	1	1
3.70-3.65	74/40, 73/45, 73/45b	221.85	587				2	2	1	6	1				1	54	7	1	2		1
3.65-3.60	73/46, 74/73	113.45	705	1						5	1	1			6	43	7		2		
3.60-3.55	73/47, 74/74	204.25	668				2	1	1	4				4	2	65	8		3	2	
3.55-3.50	74/75	91.75	304						1	2		1				4				2	
3.50-3.45	73/68, 74/76	213.05	428	1			2		3	4	1			3		54	5	1	7	1	
3.45-3.40	74/77	75.95	313	2		1	2			3				1		7	1		2		
3.40-3.35	74/78	95.45	345						2	1						2	2				1
3.35-3.30	73/72, 74/80	195.00	502	2	1		2	1	3	4	1			1		47	3	1	7	1	
3.30-3.25	73/79, 74/102	203.80	358						3	4	1			7		44	2	1	2	1	
3.25-3.20	74/103	54.25	197								2					3	2			1	
3.20-3.15	73/95, 74/104	163.75	362							3				1	2	64	3		1		3
3.15-3.10	73/97, 74/105	163.75	326				1		1	5			1			27	1	1	1		1
3.10-3.05	73/98, 74/106	163.20	444						1	3					1	50	5		4	1	
3.05-3.00	73/99, 74/107	166.15	171	1						4						28	2	1			
	sum	4083.45	8418	15	1	1	12	4	32	75	10	2	1	22	14	741	69	7	41	13	16

Table 15

Length (in mm) measurements and SDQ7 values of *Mimomys savini* m1s from the upper (3.70-4.35 m O.D.) and lower (3.00-3.70 m O.D.) levels of the profile.

	m1 length					SDQ7				
	n	min	mean	max	sd	n	min	mean	max	sd
upper levels	24	2.89	3.31	3.72	0.18	23	114.57	139.22	156.61	11.52
lower levels	26	2.98	3.34	3.66	0.17	26	114.57	138.94	163.14	11.01

Table 16
Small mammal taxa from the 1995-Mammoth Excavation compared to that of previous collections from the WRFB (Stuart, 1975; Preece and Parfitt, 2000, taxonomically modified).

West Runton previous collections	Locality ‘AJS’ (Stuart, 1975)	1995-Mammoth Excavation
Erinaceus sp.		
Desmana sp.	+	+
Talpa minor	+	+
Talpa europaea	+	+
Sorex minutus		cf.
Sorex runtonensis	+	+
Sorex savini	+	+
Neomys newtoni	+	+
Macroneomys brachygnathus		
Nyctalus noctula		
Lepus sp.		
Sciurus whitei		
Castor fiber		+
Trogontherium cuvieri		
Cricetulus migratorius		
Cricetus runtonensis		+
Clethrionomys hintonianus	+	+
Pliomys episcopalis		+
Mimomys savini	+	+
Microtus ‘arvalinus’	+	+
Microtus ‘ratticepoides’	+	+
Microtus gregaloides	+	+
Microtus arvalidens	+	+
Apodemus sylvaticus	+	cf.

Figure01

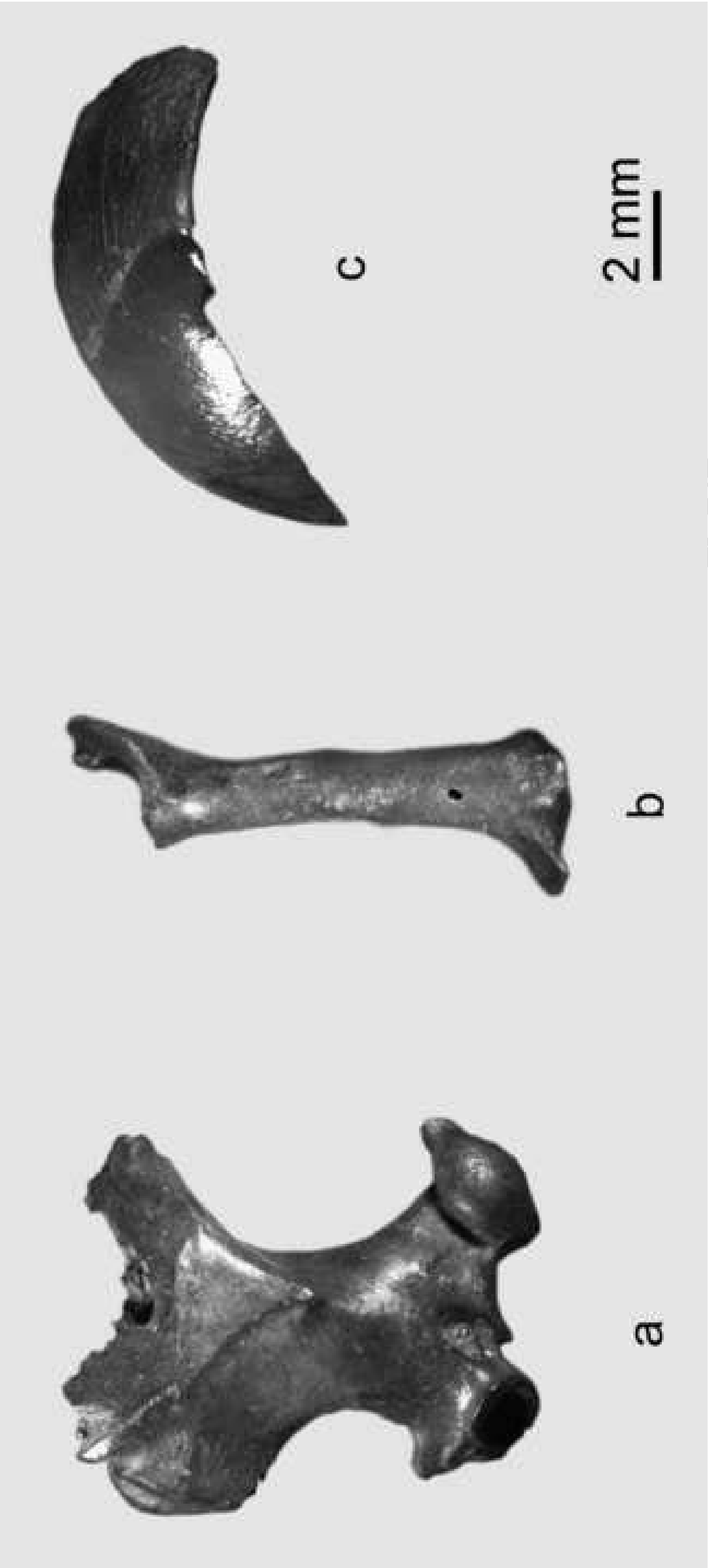


Figure02

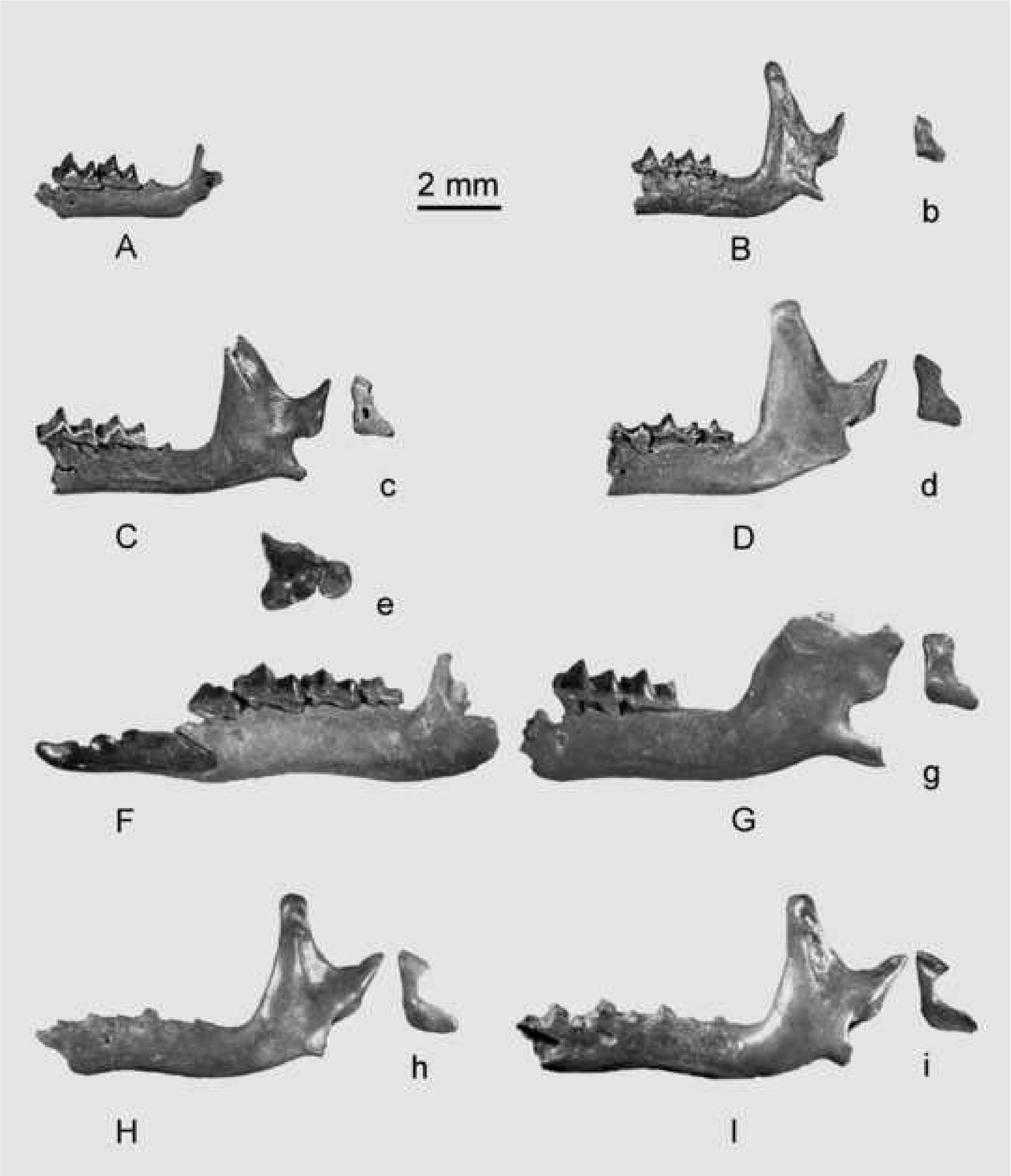
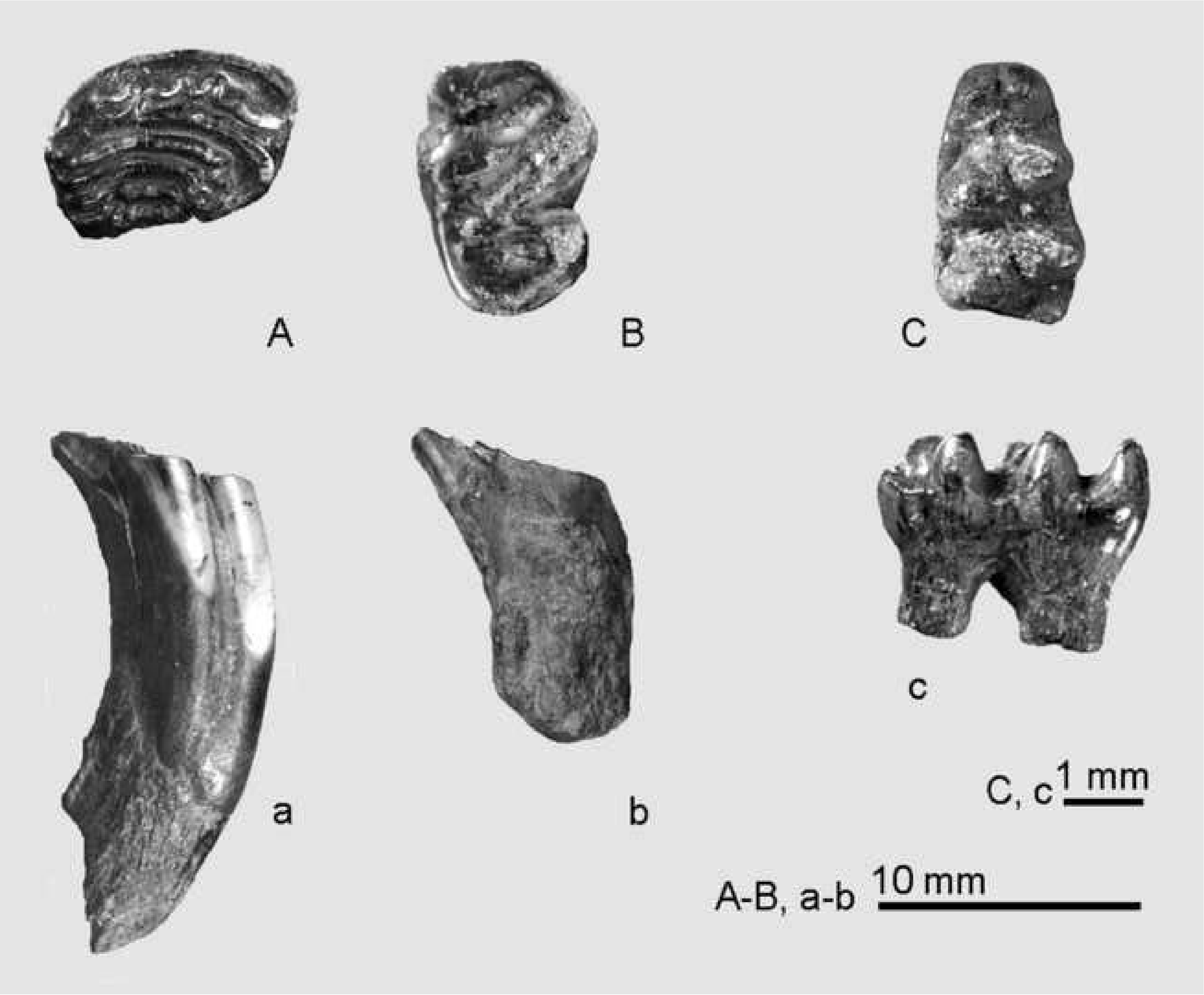


Figure03



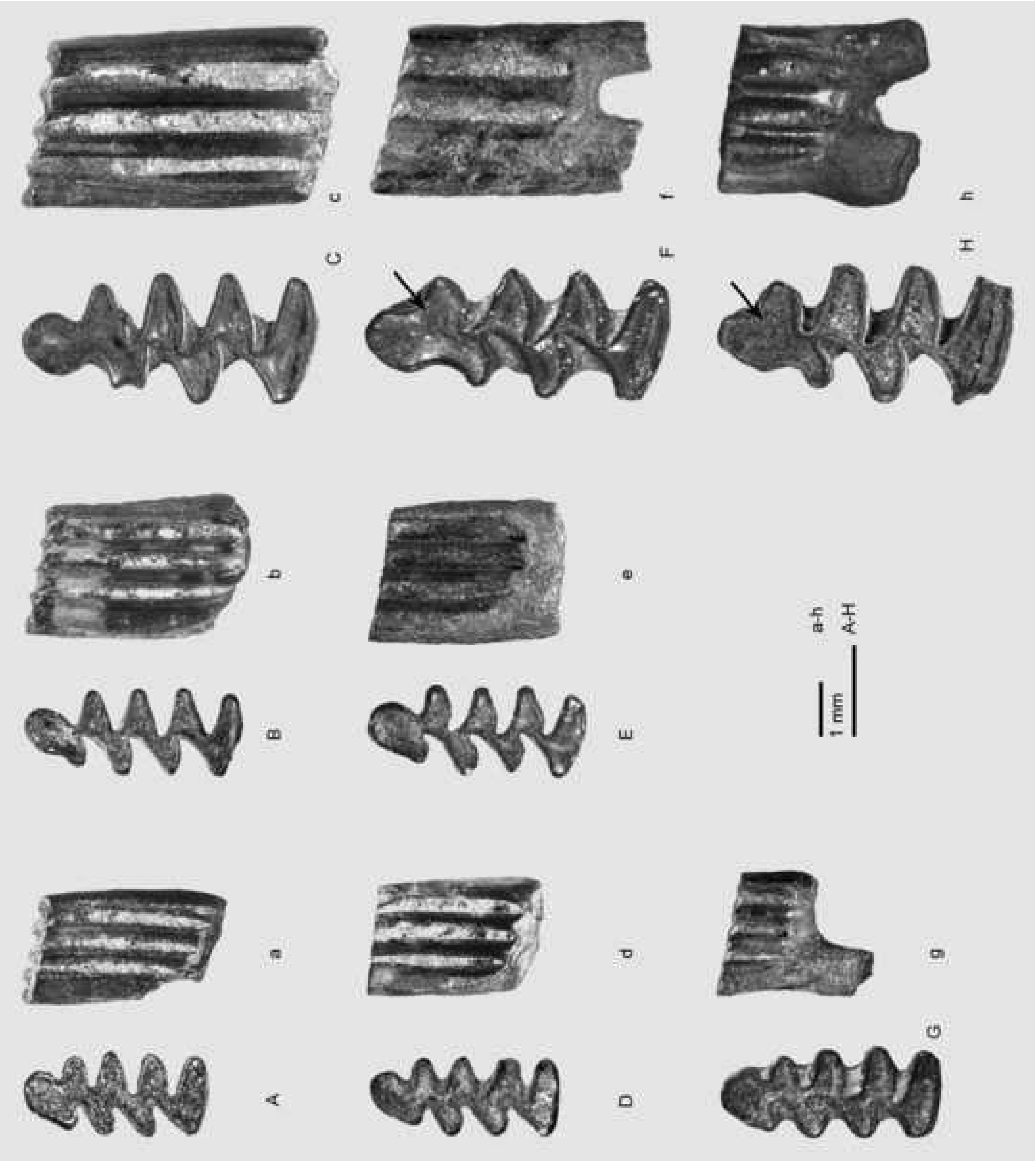
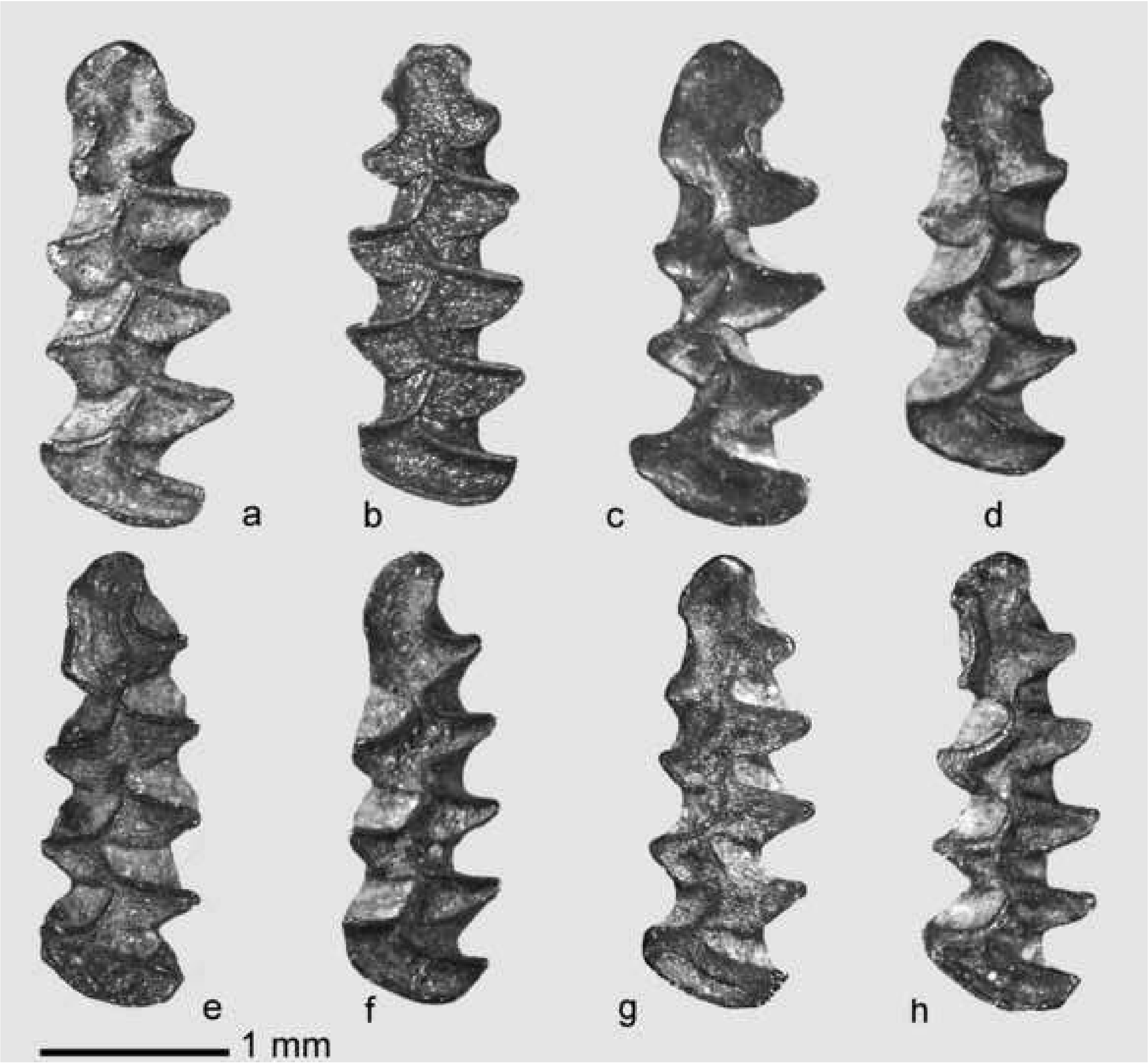


Figure04

Figure05



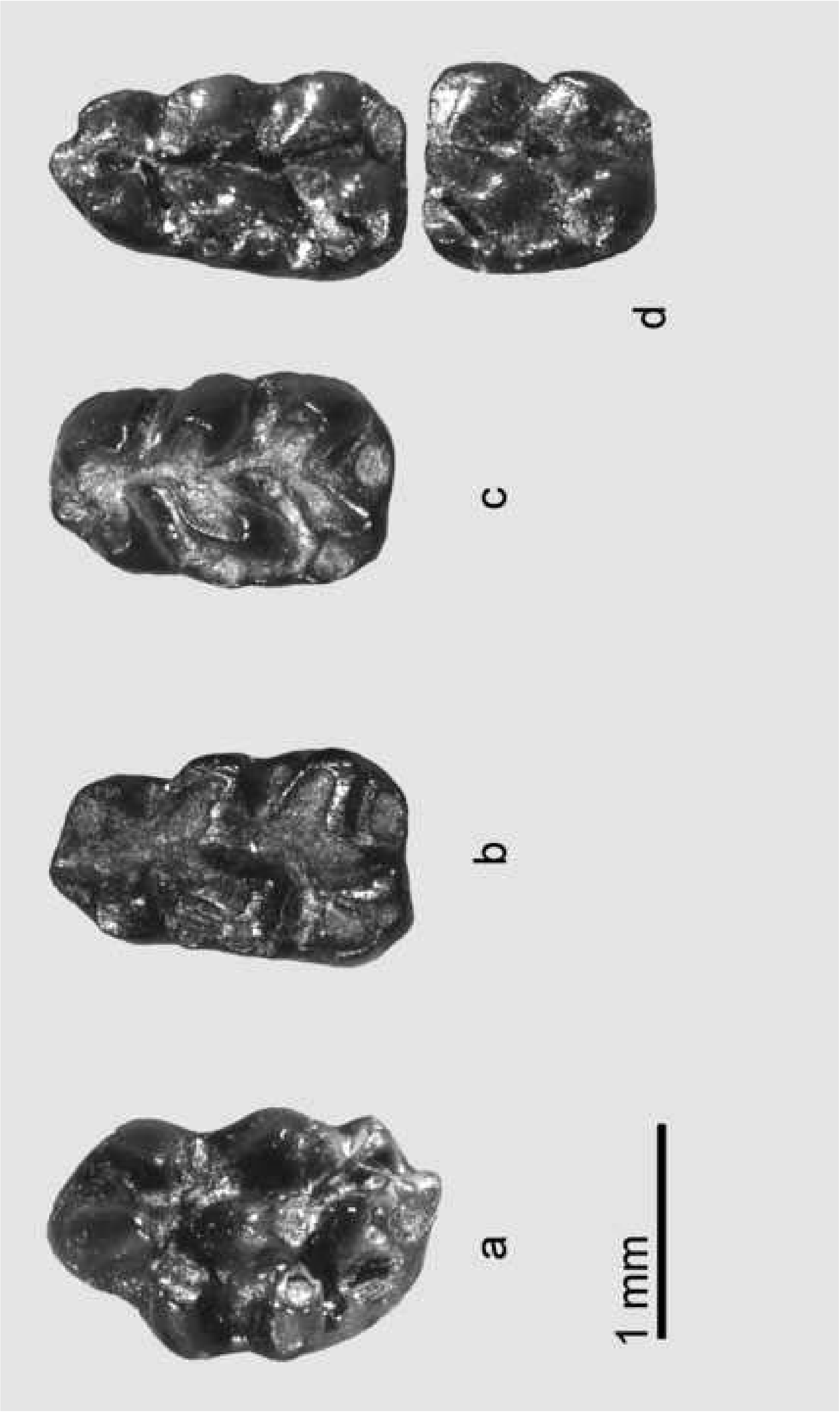


Figure06

Figure07

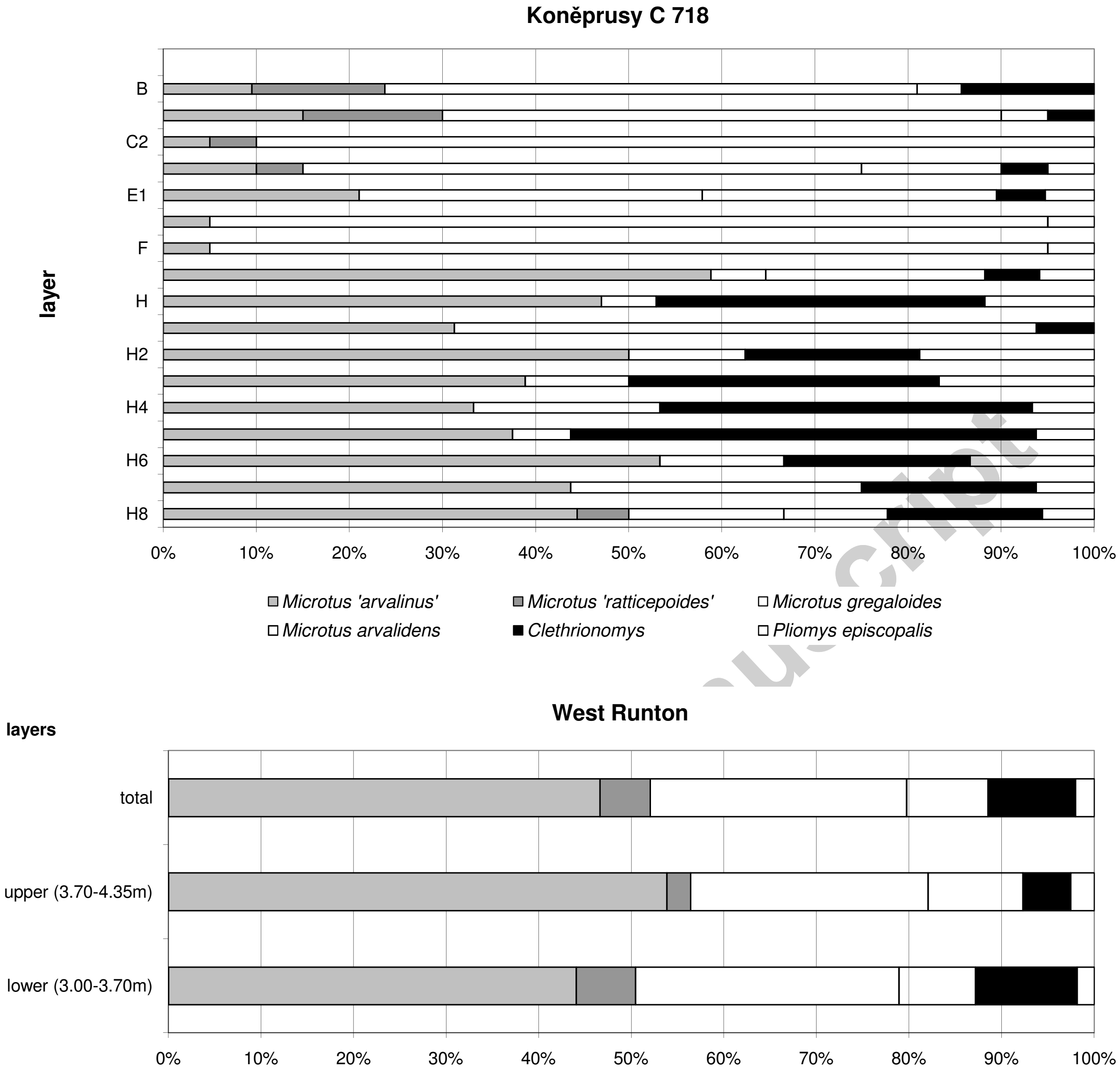
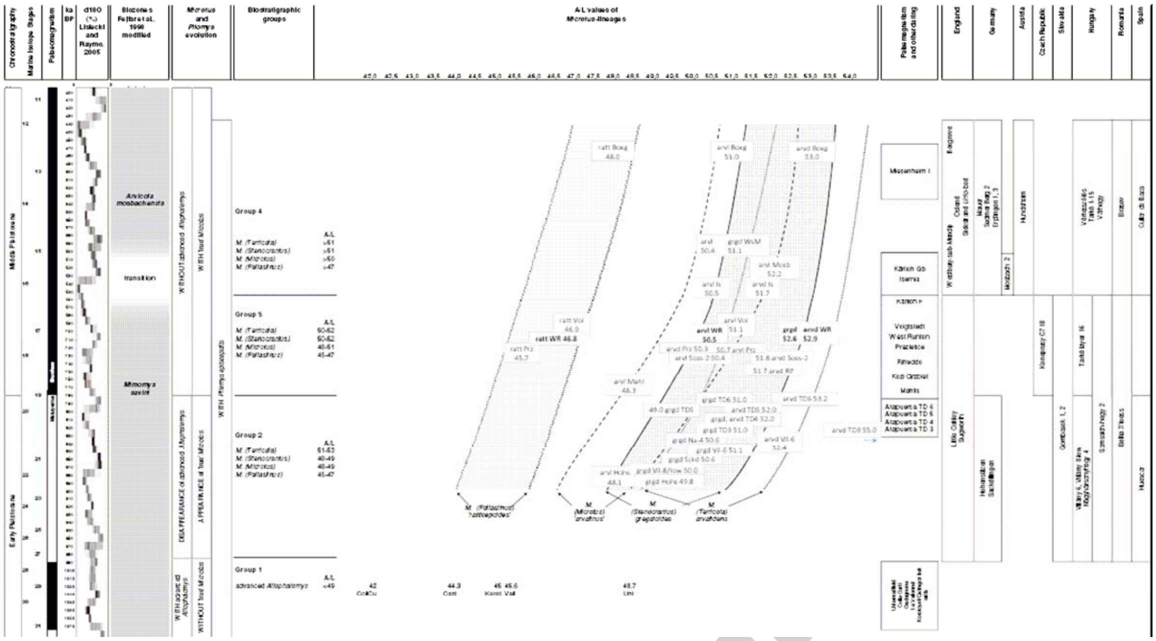

Koněprusy C 718
layer
B
C2
E1
F
H
H2
H4
H6
H8
0%
10%
20%
30%
40%
50%
60%
70%
80%
90%
100%
▨ Microtus 'arvalinus'
▨ Microtus 'ratticepoides'
☐ Microtus gregaloides
☐ Microtus arvalidens
■ Clethrionomys
☐ Pliomys episcopalis
West Runton
layers
total
upper (3.70-4.35m)
lower (3.00-3.70m)
0%
10%
20%
30%
40%
50%
60%
70%
80%
90%
100%

Fig. 8


Chronostratigraphy
Marine Isotope Stages
Paleomagnetism
ka BP
d18O (‰) Lisiecki and Raymo, 2005
Biozones Fejfar et al., 1998 modified
Microtus and Pliomys evolution
Biostratigraphic groups
A/L values of Microtus-lineages
42,0 42,5 43,0 43,5 44,0 44,5 45,0 45,5 46,0 46,5 47,0 47,5 48,0 48,5 49,0 49,5 50,0 50,5 51,0 51,5 52,0 52,5 53,0 53,5 54,0
Palaeomagnetism and other dating
England
Germany
Austria
Czech Republic
Slovakia
Hungary
Romania
Spain
Middle Pleistocene
Early Pleistocene
Brunhes
Matuyama
Arvicola mosbachensis
transition
Mimomys savini
WITHOUT advanced Allophaiomys
WITH 'real' Microtis
WITH Pliomys episcopalis
DISAPPEARANCE of advanced Allophaiomys
APPEARANCE of 'real' Microtis
WITH advanced Allophaiomys
WITHOUT 'real' Microtis
Group 4
A/L
M. (Terricola) >51
M. (Stenocranius) >51
M. (Microtus) >50
M. (Pallasiinus) >47
Group 3
A/L
M. (Terricola) 50-52
M. (Stenocranius) 50-52
M. (Microtus) 48-51
M. (Pallasiinus) 45-47
Group 2
A/L
M. (Terricola) 51-53
M. (Stenocranius) 48-49
M. (Microtus) 48-49
M. (Pallasiinus) 45-47
Group 1
A/L
advanced Allophaiomys <49
42 Col/Cu
44.3 Cast
45 Karst
45.6 Vall
48.7 Lmi
ratt Boeg 48.0
arvl Boeg 51.0
arvd Boeg 53.0
arvl 50.4
grgd WsM 51.1
arvl Mosb 52.2
arvl Is 50.5
arvd Is 51.7
ratt Voi 46.0
ratt WR 46.8
ratt Prz 45.7
arvl Voi 51.1
arvl WR 50.5
grgd 52.6
arvd WR 52.9
arvd Prz 50.3
50.7 arvl Prz
arvl Sûss-2 50.4
51.8 arvd Sûss-2
51.7 arvd Rif
arvl Mahl 48.3
grgd TD6 51.0
arvd TD6 53.2
49.0 grgd TD5
arvd TD5 52.0
grgd, arvd TD4 52.0
grgd TD3 51.0
arvd TD3 55.0
grgd Na-4 50.6
arvd VI-6 52.4
grgd VI-6 51.1
grgd Sckd 50.6
arvl Hohs 48.1
grgd VI-8/low 50.0
grgd Hohs 49.8
M. (Pallasiinus) 'ratticepoides'
M. (Microtus) 'arvalinus'
M. (Stenocranius) gregaloides
M. (Terricola) arvalidens
Miesenheim I
Kärlich Gb Isernia
Kärlich F
Voigtstedt
West Runton
Prezletice
Rifreddo
Kozi Grzbiet
Mahlis
Atapuerca TD 6
Atapuerca TD 5
Atapuerca TD 4
Atapuerca TD 3
Untermassfeld
Colle Curti
Castagnone
La Vallonnet
Kozi Grzbiet
Westbury-sub-Mendip
Boxgrove
Ostend
Sidestrand Unio-bed
Little Oakley
Sugworth
Mauer
Süssenborn 2
Erpfingen 1, 3
Mosbach 2
Hohensülzen
Sackdilingen
Hundsheim
Koneprusy C718
Gombasek 1, 2
Vértesszőlős
Tarkő 1-15
Villány
Tarkő layer 16
Villány 6, Villány Somlyó
Nagyharsányhegy 4
Somssichhegy 2
Betfia 7
Betfia IX
Bezov
Cullar de Baza
Huescar