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New material of the shrew *Macroneomys* FEJFAR, 1966 (Mammalia, Soricomorpha, Soricidae) from the British early Middle Pleistocene, with comments on its palaeobiology and European range

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Abstract. A lower incisor and two lower premolars of *Macroneomys*, from the early Middle Pleistocene archaeological site at Pakefield (Suffolk, UK), add to the relatively small number of finds of this enigmatic shrew known from the Pleistocene of Europe. Molluscs and vertebrates associated with the Pakefield *Macroneomys* suggest deposition in a large, fast-flowing river, bordered by open herbaceous vegetation and regional deciduous woodland. *Macroneomys* from Sugworth (near Oxford) and West Runton (Norfolk) is also associated with fluvial environments. This suggests that the species may have had an ecological preference for aquatic habitats. The thick enamel and bulbous morphology of the lower premolars from Pakefield may indicate a specialization for crushing, consistent with a diet of 'hard' or abrasive foods that may have included large molluscs and small vertebrates.

Key words: *Macroneomys*, Pakefield, Cromer Forest-bed Formation, early Middle Pleistocene, palaeoecology.

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I. INTRODUCTION

Macroneomys is a large neomyine shrew first described some forty-five years ago from deposits of early Middle Pleistocene age at Koněprusy (cave C 718) in the Czech Republic (FEJFAR 1966). To date only a single species (*M. brachygnathus* FEJFAR, 1966) is known from Europe, represented by fragmentary and scanty remains at 13 localities, ranging from Spain in the west to Poland in the east (Fig. 1). It was widespread in central Europe during

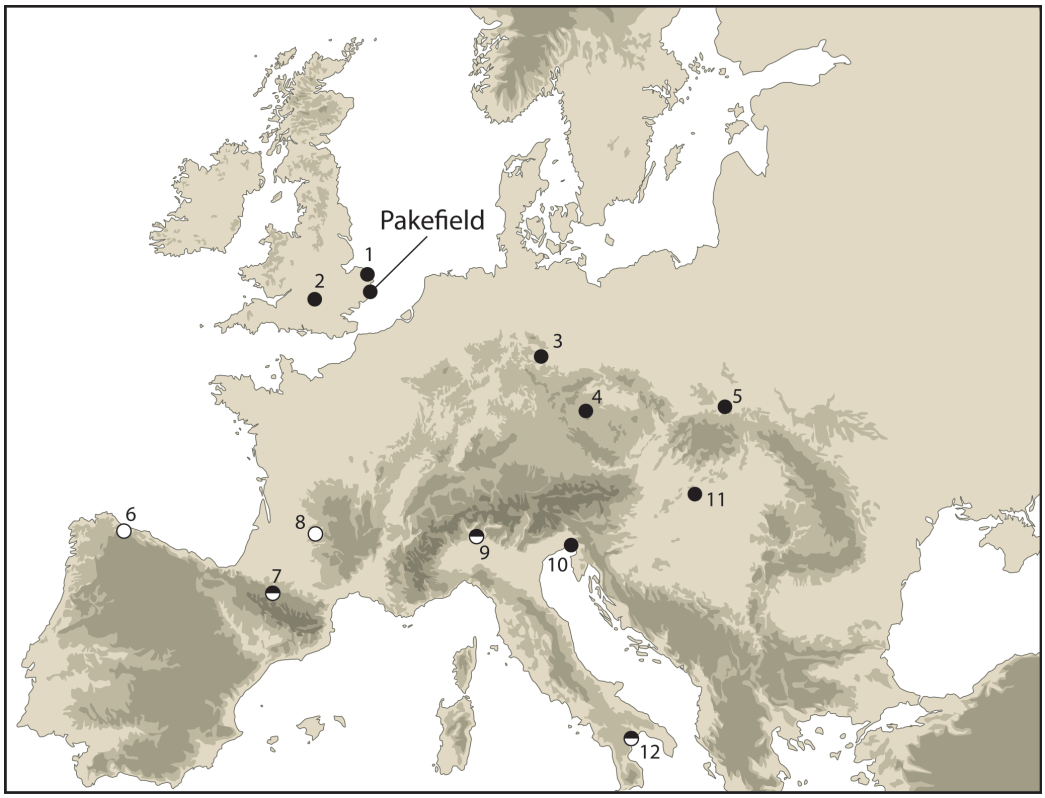

Fig. 1. Map showing the distribution of *Macroneomys*, based on MAUL and RZEBIK-KOWALSKA (1998), with additions (this paper, BONA et al. 2008, FANFANI 1998, MASINI et al. 2005). The species is now known from 13 localities; it also may be present at as many as five localities in northeastern Italy (Boscochiesanuova, Fornaci di Cornedo, San Giovanni di Duino, San Vito di Leguzzano, Zoppega II), where BONA et al. (2008) has suggested that remains of a large neomyine shrew were perhaps mistakenly ascribed to the insular Mediterranean endemic shrew *Nesiotites*. Symbols: ● – Late Biharian; ◓ – early Toringian; ○ – late Toringian. Sites: 1 – West Runton; 2 – Sugworth; 3 – Voigtstedt; 4 – Koněprusy C718; 5 – Kozi Grzbiet; 6 – Somiedo; 7 – Montoussé 3; 8 – Abimes de la Fage; 9 – Fontana Marella Cave; 10 – Vosogliano; 11 – Kövesvárad; 12 – Rifreddo.

the early Middle Pleistocene, but during the late Middle Pleistocene, its range appears to have contracted to upland areas in southwestern France and northeastern Spain (Fig. 1, PARFITT, PINTO and HARRISON, unpublished data). In Britain, *Macroneomys* has recently been recognized at the Cromerian type locality of West Runton and at Sugworth, based on isolated mandibular teeth that were originally referred to *Beremendia fissidens* (HARRISON et al. 2006). In this paper, we describe three teeth of *Macroneomys* recovered during recent archaeological excavations at Pakefield, Suffolk, UK (PARFITT et al. 2005). This record is important because the site has yielded exceptionally rich fossil assemblages (PARFITT et al. 2005, Supplementary Information) which, together with isotopic, pedological and sedimentological information (CANDY et al. 2006), provide new insights into the ecology and environmental preferences of this enigmatic shrew.

II. THE LOCALITY: STRATIGRAPHY AND AGE

At Pakefield, near Lowestoft (Suffolk), early Middle Pleistocene interglacial sediments forming part of the southern exposure of the Cromer Forest-bed Formation have been mapped over a distance of ~1 km in cliff sections and on the beach (WEST 1980). The cliffs at Pakefield were first explored palaeontologically during the second half of the nineteenth century and gained prominence following the discovery of Lower Palaeolithic stone tools in 2000, making it one of the oldest archaeological sites in northern Europe (PARFITT et al. 2005, 2008; ROEBROEKS 2005). The geological succession at Pakefield has been described by BLAKE (1877, 1884, 1890), WEST (1980) and LEE et al. (2006). The interglacial succession includes overbank deposits and palaeosols ('Rootlet Bed' CANDY et al. 2006) overlain by shelly ferruginous sands and gravels ('*Unio*-bed') and a laminated organic-rich silty mud, which occupy a large river channel (LEE et al. 2006). The channel sediments are extremely fossiliferous and have yielded abundant vertebrate remains, beetles, ostracods and plant macrofossils as well as a good pollen record (WEST 1980). Although broadly 'Cromerian' in character, the vertebrate and molluscan faunas are unique and do not precisely match any other site in Britain or on the continent (STUART & LISTER 2001). Significant mammalian species include the ancestral water vole *Mimomys savini* indicating an age early in the 'Cromerian Complex', together with other taxa (*Palaeoloxodon antiquus*, *Hippopotamus* sp. that are absent from the Cromerian stratotype at West Runton. Although West Runton and Pakefield are of slightly different ages (probably representing different interglacials), it has not been possible to resolve their relative stratigraphical positions (BREDA et al. 2010;, LISTER et al. 2010; PENKMAN et al. 2010; PARFITT et al. 2005).

III. DESCRIPTION OF MATERIAL

Three isolated macroneomyid specimens (Pak.(AHOB).21: left lower incisor (i), Pak.(AHOB).22: left p4, Pak.(AHOB).23: left p4; Fig. 2) have been recovered from the '*Unio*-bed' samples.

The crown of the lower incisor (Fig. 2 a-b) is almost complete, but the posterior margin and root are missing. There is a single low cuspule on the cutting edge, which is connected to a cingulum that extends towards the broken posterior margin of the crown. Wear is restricted to the tip, which is blunt and robust. The external face is convex and finely wrinkled. The internal surface is flattened with a narrow ledge that runs along the posterior border, from the crown-root junction to the tip (Fig. 2 b). The incisor is similar in length to that of *Neomys fodiens*, but much thicker.

The two p4s (Fig. 2 c-f) are complete, apart from the minor damage to the crown base and absent roots. Both teeth are moderately worn, but conform well to the illustration of the p4 of *Macroneomys* cf. *brachygnathus* illustrated by JAMMOT (1975, Fig. 1) from La Fage, France. The p4 is large, two-cusped and enormously inflated. The cusps are connected by a ridge that extends towards the posterior-lingual corner of the crown and encloses the postero-lingual basin. The enamel is thick and wrinkled, but no trace of original pigmentation can be discerned. The root structure is not preserved.

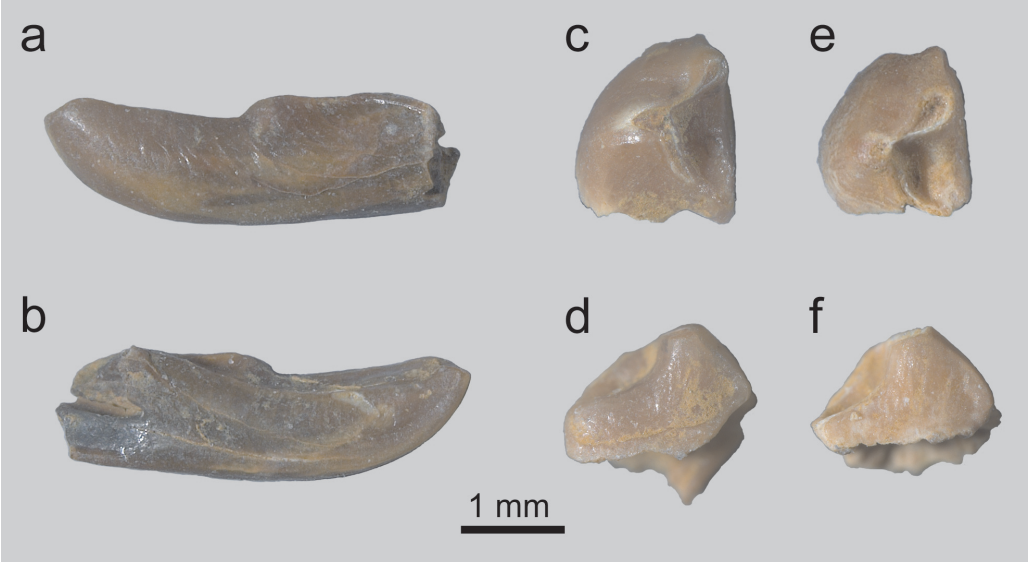

Fig. 2 a-f. *Macroneomys* teeth from Pakefield: a-b – left lower incisor (Pak.(AHOB).21) in labial (a) and lingual (b) view; c-d – left p4 (Pak.(AHOB).22) in occlusal (c) and lingual (d) view; e-f – left p4 (Pak.(AHOB).23) in occlusal (e) and lingual (f) view.

IV. ASSOCIATED INSECTIVORES

Associated insectivore remains from Pakefield are very scarce, consisting mostly of isolated (often fragmentary) teeth and mandibles. An incomplete humerus and part of a mandibular ramus are the only remains of mole, provisionally attributed to *Talpa minor*. The single largest taxon represented in the Pakefield insectivore sample is a small soricid, represented by four mandible fragments, an upper incisor, p4 and two lower molars, which are indistinguishable from early Middle Pleistocene *Sorex runtonensis* from West Runton. The taxonomic affinity of this species is uncertain; it may be conspecific with Late Pleistocene *S. kennardi*, as suggested by HARRISON (1996), but other authors (OSIPOVA et al. 2006; PARFITT 1998) have suggested affinities with the living Arctic shrew *S. arcticus* or Laxmann's shrew *S. caecutiens*. Larger soricids are rare, but include *Sorex* (*Drepansorex*) sp., identified from an upper antemolar, as well as four cheek teeth that match *Neomys*.

V. PALAEOECOLOGY OF *MACRONEOMYS*

The three British records of *Macroneomys* are significant because their geological context and association with an exceptionally diverse range of biological remains help to refine our knowledge of *Macroneomys* ecology and environmental preferences (see MAUL & RZEBIK-KOWALSKA 1998).

At Pakefield, temperate conditions are indicated by the associated mammalian fauna and by beetles and plant macrofossils from the laminated organic mud that directly over-

lies the *Macroneomys* horizon (*Unio*-bed). These assemblages indicate an early Middle Pleistocene age and include several thermophiles that require warmer summers than presently experienced in southern England (CANDY et al. 2010; COOPE 2006). The sandy gravel of the '*Unio*-bed' contains freshwater interglacial molluscs, which indicate a large, fast-flowing river. Although the '*Unio*-bed' was deposited close to the mouth of the river, there is no indication of estuarine or tidal influence.

A similar aquatic environment was available for *Macroneomys* at Sugworth, where a series of sand and gravel-filled channels of the Proto-Thames system cut into Kimmeridge Clay bedrock. These early Middle Pleistocene fluvial deposits have yielded four teeth of *Macroneomys* published by HARRISON, PARFITT and STUART (2006), as well as a lower third molar recovered from recently processed samples (PARFITT, unpublished data). The *Macroneomys* teeth all come from the same channel, which was infilled with fossiliferous organic-rich sediments, thought to have formed as a point bar on the inside of a meander. Associated pollen spectra indicate deposition during the late temperate substage of an interglacial (GIBBARD & PETTIT 1978). The molluscs from this site hint at a continental climate (PREECE 1989; GILBERTSON 1980), but strong evidence that summers were warmer than those of the present are provided by the beetles and plants macrofossils (OSBORNE 1980; CANDY et al. 2010). Coleopteran-based temperature reconstructions based on the *Mutual Climatic Range* method are almost identical to those from Pakefield, suggesting mean temperature of the warmest month between 17°C and 22°C and mean temperature of the coldest month between –6°C and +4°C (CANDY et al. 2010).

The two *Macroneomys* molars from West Runton were also recovered from sandy fluvial sediments (bed g of WEST 1980). The molluscs from this deposit (which overlies the early temperate substage (Cr. II) organic detritus muds) provide strong evidence of active stream conditions in a temperate climate.

VI. SUMMARY AND CONCLUSIONS

The rare, large shrew *Macroneomys* is now known from three localities in southern England. Previously undescribed material from Pakefield includes a lower incisor and two p4s, from a minimum of two individuals. Pakefield, Sugworth and West Runton are notable because they provide a clear insight into the nature of the depositional environment and climatic conditions. Comparing palaeoenvironmental evidence from Pakefield, West Runton and Sugworth suggests that *Macroneomys* inhabited rivers or streams with flowing water and floodplains that supported a diverse interglacial vegetational mosaic of open grassland and reed-beds, with shaded scrub and woodland nearby. Coleopteran-based temperature reconstructions from Sugworth and Pakefield suggest that *Macroneomys* was present in southern England during periods of exceptional warmth and a more continental climate (COOPE 2006; PREECE 1989). At West Runton, the *Macroneomys*-bearing horizon (bed g) overlies the main WRFB (early temperate substage), but it has not yielded plant or beetle remains. The available evidence suggests that the West Runton deposits may have formed during a different interglacial to those at Sugworth and Pakefield (PREECE & PARFITT 2000; STUART & LISTER 2001; BREDA et al. 2010; LISTER et al. 2010; MAUL & PARFITT 2010).

Inferring aspects of *Macroneomys* biology from its skeletal remains is problematic as the upper dentition has not been described in detail and its skull and post-crania are unrec-

ognised. Dentally, *Macroneomys* is the most derived of the neomyine shrews. Its combination of extremely bulbous and thick-enamelled teeth suggest a specialization for hard food items, with molluscs perhaps being the bulk of the diet.

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