PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Vertebrate Fauna from the Interglacial Deposits at Sugworth, Near Oxford

A. J. Stuart

Phil. Trans. R. Soc. Lond. B 1980 **289**, 87-97
doi: 10.1098/rstb.1980.0028

THE VERTEBRATE FAUNA FROM THE INTERGLACIAL DEPOSITS AT SUGWORTH, NEAR OXFORD

By A. J. STUART
Museum of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.

(*Communicated by F. W. Shotton, F.R.S. – Received* 16 *May* 1979)

CONTENTS

The fossil vertebrate material from Sugworth comprises freshwater fishes, Amphibia, a snake and fourteen mammalian taxa, including *Sorex* cf. *savini*, *Beremendia* cf. *fissidens* (the first British record), *Mimomys savini*, *Pliomys episcopalis* and *Dicerorhinus etruscus*. Several taxa are not recorded from later than the Cromerian interglacial and the presence of *Mimomys savini* indicates a pre-Zone Cr IV age, in agreement with a pollen Zone Cr IIIb age, based on palaeobotanical evidence.

The terrestrial vertebrate material was for the most part probably disarticulated and broken by the activities of predators and by transport in the river.

The fauna is consistent with the palaeobotanical evidence for regional temperate forest, but shows some differences in taxa from that of West Runton (Zone Cr II), and woodland rodents are relatively much more abundant in the younger deposits, probably due in part to local habitat differences.

Sugworth provides the only adequate vertebrate fauna of Zone Cr IIIb age so far known from Britain.

1. Collection of material

Samples of sediment were taken from the horizons with seams of sands, gravels and detritus muds, rich in shells, since experience has shown that most small mammal remains occur in this type of lithology. Because of the considerable amount of time and labour necessary to process the sediment for fossil vertebrate material it was impracticable to take systematically spaced samples through the entire deposit.

Sixteen samples, each weighing approximately 20 kg, were collected and taken back to the laboratory for processing. One sample, W, was collected from immediately above the Kimmeridge Clay on the west side. The remainder were collected from five horizons, A to E (A being the lowest), ranging from 1 to 3.5 m above the arbitrary base level, in the northern half of the east side section (see Shotton *et al.* 1980, figure 4). These samples, each confined to about 0.5 m thickness, form a fairly continuous sequence through about 2.5 m of the deposit.

The samples were wet-sieved, retaining everything larger than 1 mm in diameter, and the concentrate dried and sorted. Some of the smallest mammalian material, in particular many shrew cheek teeth and third molars of *Apodemus*, were undoubtedly lost through the sieve. This loss is not, however, very serious, and it is not practicable to use a smaller sieve size, because of the problems involved in sorting the much larger quantities of concentrate obtained.

The horizons from which vertebrate remains were collected are given in table 1.

TABLE 1. FAUNAL LIST AND STRATIGRAPHICAL OCCURRENCE OF TAXA

<table>
<tr><th></th><th colspan="6">sample horizons and numbers of samples</th></tr>
<tr><th></th><th>W
(1)</th><th>A
(1)</th><th>B
(3)</th><th>C
(6)</th><th>D
(3)</th><th>E
(2)</th></tr>
<tr><td>Pisces</td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>*Esox lucius* L., pike</td><td>−</td><td>−</td><td>+</td><td>+</td><td>+</td><td>+</td></tr>
<tr><td>Cyprinid fishes (at least 2 species)</td><td>+</td><td>+</td><td>+</td><td>+</td><td>+</td><td>−</td></tr>
<tr><td>Amphibia</td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>*Rana* sp., frog and/or *Bufo* sp., toad</td><td>−</td><td>−</td><td>+</td><td>+</td><td>+</td><td>+</td></tr>
<tr><td>Reptilia</td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>cf. *Natrix natrix* (L.), grass snake</td><td>−</td><td>−</td><td>−</td><td>−</td><td>+</td><td>−</td></tr>
<tr><td>Mammalia</td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Insectivora</td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>*Sorex* cf. *minutus* L., pigmy shrew</td><td>−</td><td>−</td><td>+</td><td>−</td><td>+</td><td>−</td></tr>
<tr><td>*Sorex* cf. *savini* Hinton, extinct shrew</td><td>−</td><td>−</td><td>−</td><td>−</td><td>+</td><td>−</td></tr>
<tr><td>*Beremendia* cf. *fissidens* (Petenyi), extinct shrew</td><td>−</td><td>−</td><td>+</td><td>−</td><td>−</td><td>−</td></tr>
<tr><td>*Talpa minor* Freudenberg, extinct mole</td><td>−</td><td>−</td><td>+</td><td>−</td><td>−</td><td>−</td></tr>
<tr><td>Rodentia</td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>*Mimomys savini* Hinton, extinct water vole</td><td>+</td><td>−</td><td>+</td><td>+</td><td>+</td><td>−</td></tr>
<tr><td>*Clethrionomys glareolus* (Schreber), bank vole</td><td>−</td><td>+</td><td>+</td><td>+</td><td>+</td><td>−</td></tr>
<tr><td>*Pliomys episcopalis* Mehely, extinct vole</td><td>−</td><td>+</td><td>+</td><td>+</td><td>+</td><td>−</td></tr>
<tr><td>*Microtus* cf. *arvalis* (Pallas), common vole</td><td>−</td><td>−</td><td>+</td><td>+</td><td>+</td><td>−</td></tr>
<tr><td>*Apodemus sylvaticus* (L.), wood mouse</td><td>−</td><td>+</td><td>+</td><td>+</td><td>+</td><td>−</td></tr>
<tr><td>Perissodactyla</td><td colspan="6"></td></tr>
<tr><td>*Dicerorhinus etruscus* (Falconer), extinct rhinoceros</td><td colspan="6">from gravels, south end of east side section (H. A. Osmaston)</td></tr>
<tr><td>Artiodactyla</td><td colspan="6"></td></tr>
<tr><td>*Cervus elaphus* L., red deer</td><td colspan="6">tooth from gravels, south end of east side section (H. A. Osmaston)</td></tr>
<tr><td>cf. *Cervus elaphus* L.</td><td colspan="6">phalanx from middle east side section, 2.3 m above arbitrary base level (A. Goudie)</td></tr>
<tr><td>*Megaceros* sp., giant deer</td><td colspan="6">from gravels at south end of east side section (H. A. Osmaston)</td></tr>
<tr><td>Cervidae indet</td><td colspan="6">antler fragment, tibia from east side section</td></tr>
<tr><td>*Bison* sp., bison or *Bos* sp., aurochs</td><td colspan="6">from east side section (A. J. S.)</td></tr>
</table>

2. TAXONOMY

For faunal list see table 1.

Esox lucius L., pike

Material: 22 teeth.

Cyprinid fishes

Material: 53 isolated pharyngeal teeth.

Rana *sp. and/or* Bufo *sp., frog and/or toad*

Material: 7 humeri; 7 ulna-radii; 5 pelvics; 2 urostyles.

cf. Natrix natrix (*L.*), *grass snake*

Material: 2 fragmentary vertebrae.

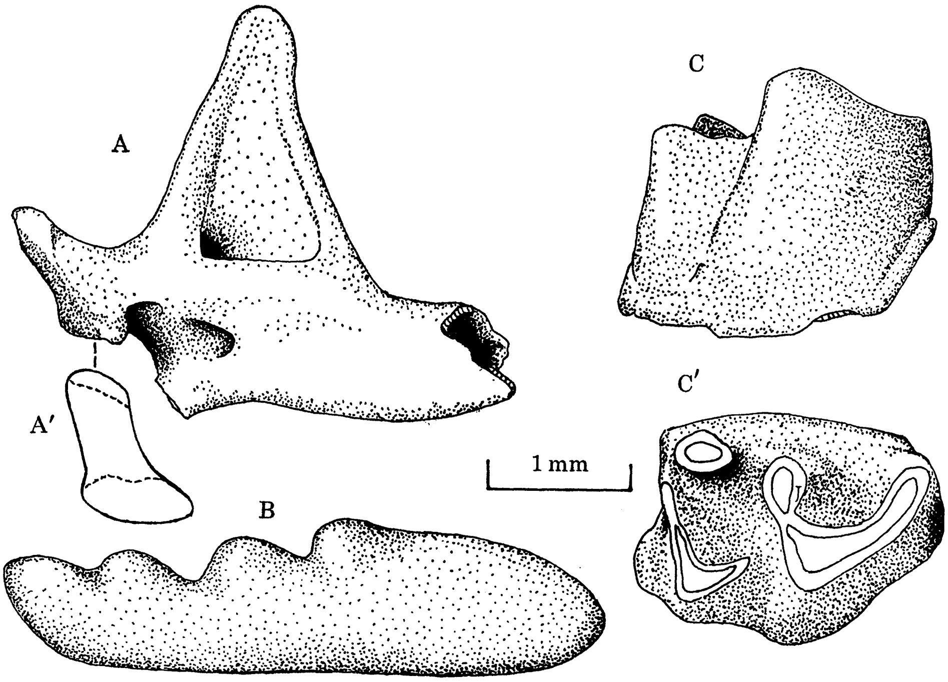

FIGURE 1. Fossil shrew material: A, *Sorex* cf. *minutus*, posterior portion of left mandible; A′, posterior view of condyle, same specimen; B, *Sorex* cf. *savini* I$_1$, buccal view; C, *Beremendia* cf. *fissidens*, right mandibular molar, buccal view; C′, crown view, same specimen.

Sorex *cf.* minutus *L., pigmy shrew*

Material: posterior part of mandible: 2 mandible fragments lacking teeth; humerus.

Measurement: coronoid height of mandible, 2.90 mm.

This material represents a shrew smaller than both the living *Sorex araneus* L. and the smallest fossil shrew from Cromerian of West Runton, *Sorex runtonensis* Hinton (Hinton 1911). The posterior mandible fragment (figure 1 A) is identical in size and shape with that of the living *Sorex minutus*.

Sorex *cf.* savini *Hinton, extinct shrew*

Material: 2 I$_1$.

The incisors (figure 1B) are identical with those of *S. savini* from the Cromerian of West Runton (Hinton 1911).

Beremendia *cf.* fissidens (*Petenyi*), *extinct shrew*

Material: 3 M$_1$ or M$_2$.

Measurements: mandibular molars length 2.14, width 1.60; length 2.24, width 1.76; length 2.24, width 1.74 mm.

The molars are far larger than those of any fossil or living shrew previously known from Britain (figure 1C). The large size, presence of black pigmentation extending nearly to the base of the crown, and the entire buccal cingulum (Repenning 1967), suggest that the specimens should be referred to *B. fissidens*, but the specific identification must be tentative on the basis of such sparse material.

Talpa minor *Freudenberg, extinct mole*

Material: M_2 fragment; mandible fragment with P_1; M_3.

Measurements: M_3 length 1.84, width (trigonid) 0.92 mm.

Two species of mole *Talpa minor* and *Talpa europaea* were present in England during the Cromerian (Stuart, in preparation). They differ in size, *Talpa europaea* being larger, and each species also shows considerable sexual dimorphism in size, as do modern moles, of which the

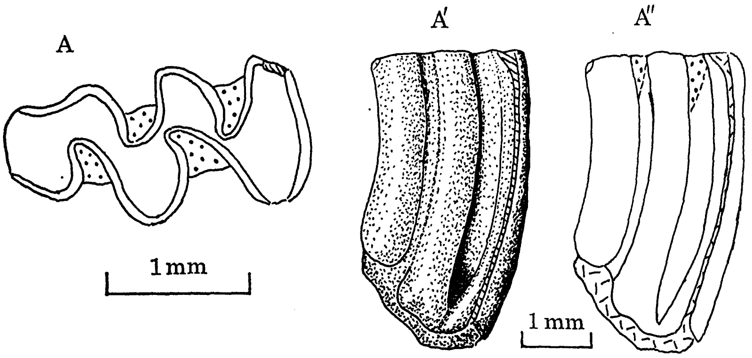

Figure 2. *Mimomys savini* right M^3: A, crown view; A′, lingual view; A″, diagrammatic lingual view, same specimen (N.B. smaller scale).

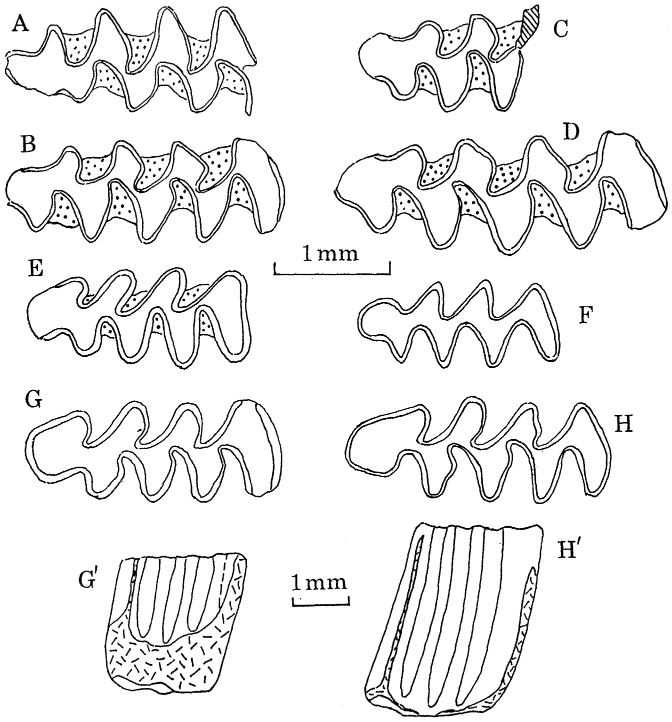

Figure 3. Fossil small vole M_1's, crown views. A–D, *Microtus* cf. *arvalis*: A, left M_1; B–D, right M_1's, all lacking roots. E, F, *Clethrionomys glareolus*: E, right M_1 with roots (adult); F, right M_1 without roots and cement (young). G, H, *Pliomys episcopalis*, right M_1's with roots but lacking cement; G′, H′, buccal views, same specimens (N.B. smaller scale).

males are larger than the females. The sparse material from Sugworth represents very small individuals, which are probably females of *Talpa minor*.

Mimomys savini (*Hinton*), *extinct water vole*

Material: 2 I^1; 2 I_1; M^1; M^2; M^3; M_1 fragment; M_2; M_3; mandible fragment; 2 humeri; 1 femur.

Measurements: M^3 length 2.28, width (anterior loop) 1.16 mm.

The molars are large, hypsodont, rooted, except for one from a young individual, and with thicker enamel on the convex side of the angles (figure 2A). They closely resemble those of *Mimomys savini* from the type Cromerian, Zone II, deposits at West Runton, Norfolk (Hinton 1926; Stuart 1975). The absence of an enamel islet in M^3 and persistence of the posterior lingual valley throughout the crown (figure 2B) confirm that the vole is *Mimomys savini* rather than *Mimomys pliocaenicus*.

Clethrionomys glareolus (*Schreber*), *bank vole*

Material: 4 M^1; 4 M^2; 6 M^3; 7 M_1; 6 M_2; 2 M_3.

Measurements: M_1 length 2.02, width 0.96; length 1.94, width 0.92; length 2.02, width 0.90; length 2.14, width 0.94 mm.

In all but a few from very young individuals, the fossil molars referred to this species are rooted and the enamel is generally undifferentiated, although there is a tendency for that on the convex sides of the angles to be a little thicker (figure 3E, F). Other useful distinguishing characters are the sparseness of cement, especially in young teeth, the roundness of the angles and confluency of the dentine areas on the crown.

Pliomys episcopalis *Mehely*, *extinct vole*

Material: 3 M^1; 3 M_1; M_3.

Measurements: M_1 length 2.40, width 0.98; length 2.34, width 1.00 mm.

The molars referred to this species are distinguished from those of other voles by the combination of lack of cement in the valleys, presence of roots in adults, and thicker enamel on the concave sides of the angles (figure 3G, H). The M_1 compare closely with those of *Pliomys episcopalis* from various early Middle Pleistocene sites on the Continent (see, for example, Koenigswald 1972, figs 4, 5).

Microtus *cf.* arvalis (*Pallas*), *common vole*

Material: 2 M^1; 3 M^2; 5 M^3; 6 M_1; 6 M_2; 3 M_3.

Measurements: M_1 length 2.56, width 1.00; length 2.96, width 1.02.

The molars of *Microtus* remain unrooted in adults and have thicker enamel on the concave sides of the angles. The shape of the anterior loop on M_1 (figure 3A–D) is similar to the majority of those from the Cromerian of West Runton (Stuart 1975) and to living *Microtus arvalis* and *Microtus agrestis*. Since none of the M^2 recovered show the extra angle diagnostic of *Microtus agrestis*, the Sugworth material is tentatively assigned to *Microtus arvalis*.

Indeterminate small vole

Material: 15 I^1; 11 I_1; 1 palate fragment; 5 mandible fragments.

Apodemus sylvaticus (*L.*), *wood mouse*

Material: 9 I^1; 10 I_1; 12 M^1; 6 M^2; 7 M_1; 4 M_2 (1 in mandible fragment).

Measurements: M_1 length 1.82, width 1.04; length 1.86, width 1.18; length 1.80, width 1.00; length 1.72, width 1.02; length 1.78, width 1.16.

In both size and dental characters, the Sugworth material is identical with modern *Apodemus sylvaticus* (L.) (figure 4). The closely related living species *Apodemus flavicollis* (Melchior) is almost indistinguishable osteologically except by its greater size.

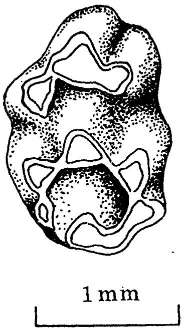

Figure 4. *Apodemus sylvaticus*, crown view of right M^1.

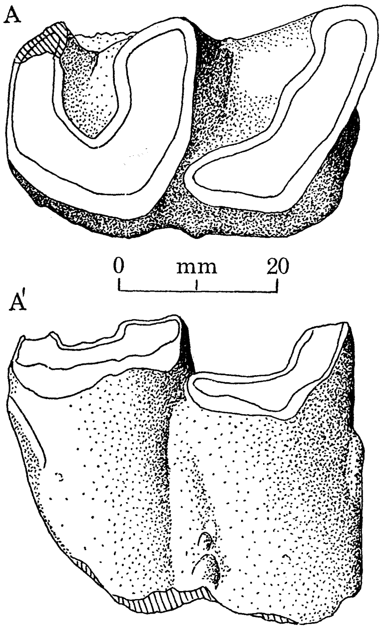

Figure 5. *Dicerorhinus etruscus*, left mandibular molar: A, crown view; A′, buccal view, same specimen.

Dicerorhinus etruscus (*Falconer*), *extinct rhinoceros*

Material: left mandibular molar, probably M_3.

Measurements: length (crown base, lingual side) 47.5, width (crown base) 32.0 mm.

The roots of the tooth are broken off, probably as a result of damage during transport in the river. The specimen compares very closely with rhinoceros material from the Cromer Forest Bed Series, including the type Cromerian of West Runton (Newton 1882) and differs from *Dicerorhinus hemitoechus* (Falconer) and *Dicerorhinus kirchbergensis* (Jäger), recorded from the Hoxnian stage (Sutcliffe 1964), in its relative brachyodonty, more pronounced cingulum and, especially, the small size (figure 5).

Cervus elaphus *L.*, *red deer*

Material: right M_3 (figure 6A); also probably referable to this species: proximal phalanx.

Measurements: M_3 length 29.5, width 14.0 mm (crown base).

Megaceros *sp.*, *giant deer* (*extinct*)

Material: left M_1 or M_2 (figure 6B).

Measurements: length 28.0, width 19.0 mm (crown base).

Cervidae indet

Material: Proximal portion of right tibia, broken-off antler tine.

Measurements of tibia: proximal antero-posterior length 56.5, proximal width (at right angles to previous measurement) 56.0 mm.

The specimen agrees in size with modern *Dama dama*, fallow deer.

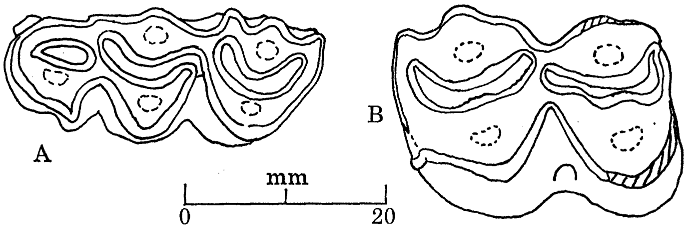

Figure 6. A, *Cervus elaphus*, crown view right M_3; B, *Megaceros* sp., crown view of left M_1 or M_2.

Bison *sp. or* Bos *sp., bison or aurochs*

Material: proximal phalanx.

Indeterminate large mammals

Material: rib; caudal vertebra, bone fragments.

3. Taphonomy

With the exception of one *Apodemus sylvaticus* mandible with M_2 in place, the Sugworth fossil mammal material comprises isolated bones and teeth, many of which are fragmentary. The more resistant parts of the skeleton, e.g., teeth, caudal vertebrae and the anterior portions of rodent mandibles, make up most of the remains. As at West Runton (Stuart 1975) and many other sites, teeth are proportionately much better represented than elements of the postcranial skeleton.

The amphibian and fish remains are similarly fragmentary and, in contrast to the material from the West Runton Upper Freshwater Bed, delicate elements such as fish scales have not been preserved. The poorer state of preservation of the Sugworth material, in comparison with that of West Runton, is probably related to the generally coarser sediment, in turn reflecting the higher energy of the depositional environment.

Of the samples examined, much the highest concentration of both mammalian and fish remains occurs in those from horizon B (table 2). Relatively few remains were obtained from the other horizons and one sample from horizon E contained virtually no identifiable material.

Table 2. Mean numbers of skeletal elements per sample (youngest first)

horizon (number of samples in parentheses)	rodent molars	rodent incisors	mammal limb bones	mammal vertebrae	*Rana/Bufo* bones	fish teeth	fish vertebrae	reworked Jurassic teeth
E (2)	0	0	0	0.5	0.5	0.5	0	0
D (3)	4.0	0.7	1.7	0	1.3	3.0	2.0	1.0
C (6)	1.5	1.3	0.2	0.5	0.4	1.7	1.3	1.5
B (3)	23.0	12.7	4.0	3.7	5.0	18.0	10.3	3.0
A (1)	4.0	0	0	0	0	1.0	1.0	1.0
W (1)	1.0	0	0	0	0	0	1.0	6.0

The rough correlation of numbers of mammal and fish remains in the samples suggests that the varying abundance of vertebrate material at particular horizons results from variations in sedimentation rates and/or concentration of bones and teeth by current action. This contrasts with the situation at West Runton (Stuart 1975), where numbers of fish remains were maintained where there was a sharp decrease in abundance of mammalian material, suggesting that the input of terrestrial material to the depositional site was varying.

Mayhew (1977) has emphasized the role of predatory birds as accumulators of fossil small-mammal remains in Pleistocene fluviatile sediments. He was able to closely match characteristically corroded teeth and bones (about 30% of the total sample) from fluviatile deposits of Cromerian age at West Runton with specimens from the regurgitated pellets of modern kestrels (*Falco tinnunculus* L.) and buzzards (*Buteo buteo* (L.)). This corrosion, the result of the powerful digestive juices of these diurnal avian predators, is not seen in material recovered from modern owl pellets, which is virtually unaltered. On the basis of this evidence, Mayhew suggested that a major part of the fossil small-mammal material from West Runton and from other fluviatile deposits was transported to the depositional site by both diurnal and nocturnal (owls) avian predators.

Mellet (1974) suggested that most or all fossil small-vertebrate accumulations were deposited, in the faecal droppings of mammalian and other predators, in or near the depositional site. Corrosion of bones and teeth is also seen in modern material from this source.

A small proportion (roughly 20%) of the Sugworth small-mammal remains shows signs of corrosion, e.g., erosion of the base and crown ends of the external angles of vole molars, that can be closely matched with examples, described by Mayhew, from the pellets of diurnal predatory birds. It is therefore very probable that, as at West Runton, much of the Sugworth fossil material was also accumulated by avian, and perhaps by mammalian, predators.

Mayhew envisaged the West Runton and other similar fossil assemblages as resulting largely from pellets dropped directly into the water by birds roosting on trees overhanging the river. It is, perhaps, more probable that most of the material from bird pellets, carnivore droppings and the remains of both large and small mammals that died close to the depositional site, were all washed in from the ground surface as the river eroded across its floodplain.

Much work needs to be done on the taphonomy of vertebrate remains in comparable modern situations before we shall be near to understanding the complex origins of such fossil assemblages.

In addition to material of Pleistocene age, a number of vertebrate specimens were recovered that have evidently been reworked from the Kimmeridge Clay. These are invariably very rolled and not likely to be confused with the Pleistocene remains. They comprise shark teeth, reptile teeth, one tooth possibly of a multituberculate, and a number of bone fragments. Not surprisingly, the highest concentration of reworked material was found in the sample (horizon W) from immediately above the Kimmeridge Clay.

4. PALAEOECOLOGY

The Sugworth fossil vertebrate material is a very imperfect sample of the original fauna, in that no medium-sized, and few large, mammals are represented. This is an unfortunate consequence of the very temporary nature of the exposure. Many deposits of comparable fossil content, e.g., the West Runton Upper Freshwater Bed (Stuart 1975), have yielded much more complete faunas because collecting was possible over a period of many years. Sufficient small-vertebrate remains were however obtained from Sugworth for some meaningful comparisons to be made with other sites.

The Sugworth material comprises: freshwater fishes, including more than one species of Cyprinidae; frogs and/or toads; a snake; a number of small mammals belonging to the orders Insectivora and Rodentia; and relatively rare large mammals, and is therefore broadly similar to the vertebrate assemblages from most sites with fluviatile deposits. Again, at most such sites bird remains are extremely rare, and their absence from Sugworth is unremarkable.

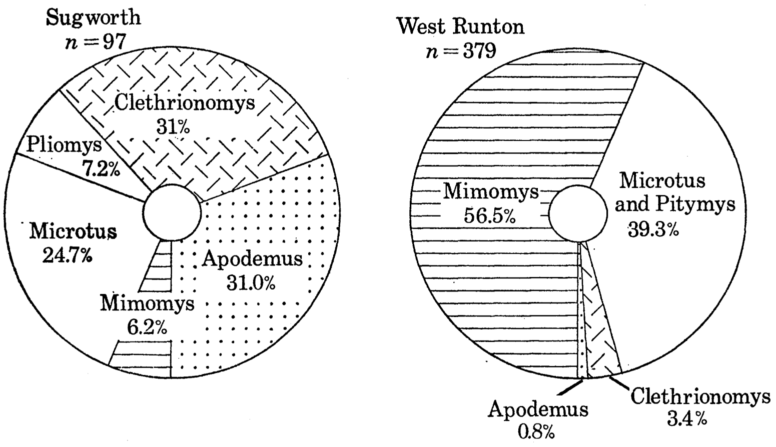

Figure 7. Pie diagrams showing relative abundance of small rodents at Sugworth compared with West Runton, as percentages of total molars.

Of the fourteen mammalian taxa recorded from Sugworth (table 1), nine are sufficiently well identified to make useful comparisons with the Cromerian Zone Cr II assemblages from West Runton (Stuart 1975). Of these nine taxa, six occur at West Runton; the exceptions being *Sorex* cf. *minutus*, *Beremendia* cf. *fissidens* and *Pliomys episcopalis*. The West Runton mammal fauna is much better known, but the absence of pine voles, *Pitymys* spp., from Sugworth seems significant since these are fairly abundant in the samples of the Upper Freshwater Bed examined by Stuart (1975). The relative abundance of rodent taxa, based on properties of molars, at Sugworth differs strikingly from that at West Runton (figure 7). At Sugworth, the characteristically woodland rodents *Apodemus sylvaticus* and *Clethrionomys glareolus* between them make up over 60 % of the total molars, compared with only 25 % for the grassland vole *Microtus* cf. *arvalis*. In contrast, at West Runton, molars of *Microtus* cf. *arvalis*, *Microtus oeconomus* and *Pitymys* spp. taken together greatly outnumber those of *Clethrionomys glareolus* and *Apodemus sylvaticus*. Most of the molars of *Microtus* spp. and *Pitymys* spp. are not usually identifiable to specific level, but analysis of the M_1 shows that *Microtus* cf. *arvalis* is the best represented taxon at West Runton (Stuart 1975). The relative numbers of incisors give a very similar picture; the figures for Sugworth are: *Mimomys savini*, 8.2 %; other voles, 53.0 %; *Apodemus sylvaticus*, 38.8 % ($n = 49$); and for West Runton (Stuart 1975): *Mimomys savini*, 60 %, other voles, 36.5 %, *Apodemus sylvaticus*, 2.6 % ($n = 115$).

The relative scarcity of *Mimomys savini* at Sugworth, less than 7 % of total molars, is very unusual in an assemblage from a temperate fluviatile deposit. For example, at West Runton *Mimomys savini* molars comprise about 60 % of the total, and at numerous sites of Hoxnian and Ipswichian age its probable descendant *Arvicola cantiana* (Hinton) is a prominent member of the fauna.

At West Runton (R. G. West, private communication) and at Sugworth (Gibbard & Pettit 1978), the pollen spectra and macroscopic plant remains in each instance indicate regional temperate forest, with alder fen carr and local herb communities close to the river. The differences in the composition of the small-mammal faunas from the two localities may reflect very local habitat differences, in particular the higher proportion of woodland rodents at Sugworth may indicate that here the forest approached closer to the river. If, as seems likely, *Mimomys savini* was an amphibious vole, resembling the modern water vole *Arvicola terrestris* L., its sparse occurrence at Sugworth may result from a local rarity of suitable habitat, i.e., slow-flowing or still water, not subject to marked fluctuations in level, with well-vegetated banks (Southern 1964). Another possibility is that the composition of the fossil small-mammal assemblages is seriously influenced by the activities of predators (see § 3). For example, predators may transport prey remains to the depositional site from some distance away, and may also preferentially select particular prey species. As discussed above (§3), much more work needs to be done on modern vertebrate taphonomy to properly evaluate the significance of the fossil assemblages.

5. Stratigraphical significance of the vertebrate fauna

The Sugworth vertebrate fauna (table 1) includes several taxa that do not occur in fossil assemblages later than Cromerian in age, but, since the British pre-Cromerian stratigraphical sequence is evidently incomplete, the vertebrate evidence alone cannot give an age more precise than Cromerian, or pre-Cromerian post-Pastonian.

The palaeontological evidence as a whole, however, points unequivocally to a Cromerian age for the Sugworth channel fill (Briggs *et al.* 1975; Shotton *et al.* 1980) and the palaeobotanical evidence (Gibbard & Pettit 1978) indicates pollen Zone Cr IIIb. This precise dating within the interglacial is very important for the reconstruction of the vertebrate faunal history of the Cromerian, since no adequate faunas from this subzone are available from the Cromer Forest Bed Series (C.F.B.S.) (A. J. Stuart, in preparation).

The stratigraphically significant vertebrate taxa are discussed below.

Dicerorhinus etruscus is recorded from a number of C.F.B.S. localities along the coasts of Norfolk and Suffolk, including the Pastonian and older deposits of East Runton, and the type Cromerian Upper Freshwater Bed of West Runton (Stuart 1974, 1975 and in preparation). It is also recorded from the cave or fissure deposits of Westbury-sub-Mendip, Somerset (Bishop 1974, 1975), which, on faunal grounds, may be of late Cromerian age (Stuart & West 1976), and is a characteristic species of the Lower and early Middle Pleistocene of Europe. Rhinoceros remains recorded from the Hoxnian of Swanscombe (Kent) and Clacton (Essex) are significantly larger and have been assigned to *Dicerorhinus hemitoechus* (Falconer) and *Dicerorhinus kirchbergensis* (Jäger) (Sutcliffe 1964).

Mimomys savini, a vole with hypsodont but rooted cheek teeth, occurs in the Cromerian Zone Cr II freshwater deposits at West Runton and also in the overlying marine gravel of Zone Cr III age (Hinton 1926; Stuart 1975). It appears to have been replaced by *Arvicola cantiana* (Hinton), its probable descendant, with rootless permanently growing cheek teeth, at some time during Zones Cr III and Cr IV, because the *Arvicola cantiana* material from Ostend (Norfolk) has recently been dated by pollen analysis and by stratigraphical position to Zone Cr IV (Stuart & West 1976). The latter species also occurs at Westbury (Bishop 1974) and at Hoxnian and Ipswichian sites. This agrees well with the pollen evidence for a pre-Zone Cr IV age.

Pliomys episcopalis has previously been recorded only once in Britain, at Westbury (Bishop 1974). It has also been recorded from many sites of early Middle Pleistocene age on the Continent, e.g., Vertesszöllös (Hungary), Episcopia (Roumania) (Kretzoi 1965), and Sudmer-Berg 2 (West Germany) (Koenigswald 1972), in association with either *Mimomys savini* or *Arvicola cantiana*.

Beremendia fissidens is also recorded from many European early Middle Pleistocene sites, but has not previously been found in Britain.

Sorex savini, as well as occurring at most Continental sites of broadly similar age, is recorded from West Runton, Zone Cr II (Hinton 1911; Stuart 1975), from Ostend, Zone Cr IV (Hinton 1911; Stuart & West 1976), and from Westbury (Bishop 1974).

I thank Dr Martin Bishop, Dr P. L. Gibbard and Dr D. F. Mayhew for their help in collecting small-vertebrate samples, and Dr A. Goudie and Dr H. A. Osmaston, who found large-mammal remains. I am also grateful to Dr P. L. Gibbard and to Mrs M. E. Pettit, who kindly allowed me to see their paper on the palaeobotany of the Sugworth deposits, before publication, to Dr A. van der Meulen, who confirmed the identification of *Beremendia*, and to Mr A. Lister, for help with identification of the deer.

This work formed part of a project on mammals of early Middle Pleistocene age that was supported by an N.E.R.C. research grant to Dr K. A. Joysey, and this support is gratefully acknowledged.

REFERENCES

Bishop, M. J. 1974 A preliminary report on the Middle Pleistocene mammal bearing deposits of Westbury-Sub-Mendip, Somerset. *Proc. speleol. Soc.* **13**, 301–308.

Bishop, M. J. 1975 Earliest record of man's presence in Britain. *Nature, Lond.* **253**, 95–97.

Briggs, D. J., Gilbertson, D. D., Goudie, A. S., Osborne, P. J., Osmaston, H. A., Pettit, M. E., Shotton, F. W. & Stuart, A. J. 1975 New interglacial site at Sugworth. *Nature, Lond.* **257**, 477–479.

Gibbard, P. L. & Pettit, M. 1978 The palaeobotany of interglacial deposits at Sugworth Berkshire. *New Phytol.* **81**, 465–477.

Hinton, M. A. C. 1911 The British fossil shrews. *Geol. Mag.* **8**, 529–539.

Hinton, M. A. C. 1926 *Monograph of the voles and lemmings (Microtinae), living and extinct.* London: British Museum, Natural History.

Koenigswald, W. von. 1972 Sudmer-Berg 2, eine Fauna des frühen Mittelpleistozäns aus dem Harz. *Neues Jb. Geol. Paläont Abh.* **141**, 194–221.

Kretzoi, M. 1965 Die Nager und Lagomorphen von Voigtstedt in Thüringen und ihre chronologische Aussage. *Palaontol. Abhandlung.* **213**, 587–661.

Mayhew, D. F. 1977 Avian predators as accumulators of fossil mammal material. *Boreas* **6**, 25–31.

Mellet, J. S. 1974 Scatological origin of microvertebrate fossil accumulations. *Science, N.Y.* **185**, 349–350.

Newton, E. T. 1882 The Vertebrata of the Forest Bed Series of Norfolk and Suffolk. *Mem. geol. Surv. U.K.*

Repenning, C. A. 1967 Subfamilies and genera of the Soricidae. *Prof. Pap. U.S. geol. Surv.* no. 565, pp. 1–74.

Shotton, F. W., Goudie, A. S., Briggs, D. J. & Osmaston, H. A. 1980 Cromerian interglacial deposits at Sugworth, near Oxford, England, and their relation to the Plateau Drift of the Cotswolds and the terrace sequence of the Upper and Middle Thames. *Phil. Trans. R. Soc. Lond.* B **289**, 55–86.

Southern, H. N. (ed.) 1964 *The handbook of British mammals.* Oxford: Blackwell.

Stuart, A. J. 1974 Pleistocene history of the British vertebrate fauna. *Biol. Rev.* **49**, 225–266.

Stuart, A. J. 1975 The vertebrate fauna of the type Cromerian. *Boreas* **4**, 63–76.

Stuart, A. J. & West, R. G. 1976 Late Cromerian fauna and flora at Ostend, Norfolk. *Geol. Mag.* **113**, 469–473.

Sutcliffe, A. J. 1964 In The Swanscombe Skull. A survey of research on a Pleistocene site (ed. C. D. Ovey). *Occ. Pap. anthrop. Inst.* no. 20.