

**Fossil remains of shrews (Soricomorpha: Soricidae)  
and desmans (Talpidae: Desmaninae) from Norfolk, England,  
with biostratigraphic implications  
for the Plio-Pleistocene boundary in East Anglia**

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Received: 28 November 2008

Accepted: 20 January 2009

HARRISON D. L., PARFITT S. A. 2009. Fossil remains of shrews (Soricomorpha: Soricidae) and desmans (Talpidae: Desmaninae) from Norfolk, England, with biostratigraphic implications for the Plio-Pleistocene boundary in East Anglia. *Acta zoologica cracoviensia*, **52A**(1-2): 61-79.

**Abstract.** Rare remains of soricids and desmans from the Plio-Pleistocene of Norfolk are described. Three soricid taxa are identified, comprising *Sorex* (*Drepanosorex*) *praeareaneus*, *Beremendia fissidens* and *Sorex* cf. *minutus*. At least one other is suspected. Palaeoecology and correlation with continental sites is discussed. Comparison is made with the Tegelen fauna of The Netherlands and the water moles of genera *Galemys* and *Desmana* are considered to be of prime stratigraphic importance in correlating the British sequence with the late Tiglian.

**Key words:** Soricomorpha, Soricidae, *Drepanosorex*, *Beremendia*, *Sorex*, *Desmana*, *Galemys*, Late Pliocene, Early Pleistocene, England.

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## I. INTRODUCTION

Remains of soricids and desmans are exceedingly rare in the nearshore marine Plio-Pleistocene deposits of East Anglia. Recent intensive bulk sieving has nevertheless recovered identifiable material from several localities (West Runton, East Runton and Sidestrand) between Weybourne and East Runton on the north Norfolk coast (Fig. 1). Deposited in a high energy, shallow marine environment, the fossils found are often highly mineralised, dark in colour, with a marked glossy patina. The remains consist of isolated teeth and damaged mandibular rami in which few teeth are retained *in situ*; natural pigmentation of the teeth is only very rarely retained.

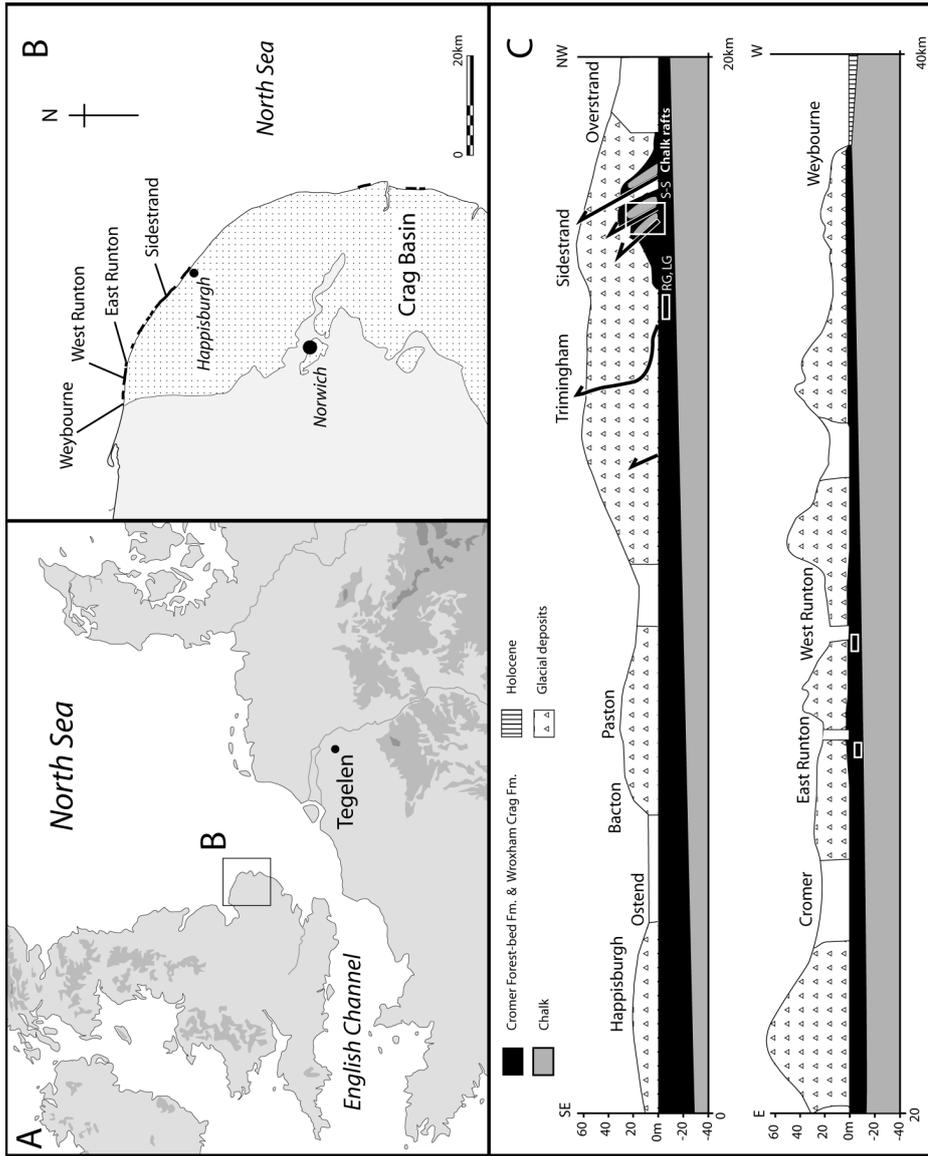


Fig. 1. A – Location of sites in eastern England and The Netherlands mentioned in the text; B – Location of sites in north Norfolk with sordic material and the extent of the Pliocene – early Middle Pleistocene Craggs and the Cromer Forest-bed Formation; C – Schematic drawing of the coastal sections between Weybourne and Happisburgh showing the position of the sample localities (white rectangles) at East Runton, West Runton and Sidestrand in relation to the glacial succession and other sites along the Norfolk coastline (adapted from LEE et al. 2004).

Although terrestrial vertebrates have long been known from the Crag deposits of East Anglia, it is only recently that concerted efforts have been made to recover small mammal remains from secure stratigraphic sequences, which can be related to the detailed sedimentological and palaeobotanical work undertaken by WEST (1980) and others. The youngest Crag in north Norfolk is associated with quartz- and quartzite-rich gravels and a characteristic marine molluscan fauna dominated by *Macoma balthica*, which distinguish it from all earlier Crag faunas (GIBBARD et al. 1990). In the East Runton area, micromammals have been sieved from grey shelly sands with flint pebbles (Weybourne Crag of REID 1882) exposed on the surface of the chalk at low tide. A similar sequence can be observed on the foreshore at nearby West Runton, where the sediments have also been assigned to the Pre-Pastonian Stage on the basis of palynology (WEST 1980; MAYHEW & STUART 1986). At West Runton, MAYHEW and STUART (1986) sieved samples of shelly marine sand and tidal silts exposed in trenches dug for the construction of coastal sea defences. Pollen spectra from the base of the West Runton sequence show a high non-arboreal pollen content indicative of a cold environment (Pre-Pastonian *a*, WEST 1980), whereas pollen spectra higher in the sequence are indicative of fully temperate conditions with deciduous woodland (Pastonian II, WEST 1980). Because the small mammals were collected from temporary and unstable sections, it was not possible to link them with the pollen biostratigraphy, but a Pre-Pastonian age seems likely for most of the remains.

Whereas the Crag at East Runton and West Runton is confined to the foreshore, at Sidestrand and Overstrand, large chalk rafts with drapes of Crag have been tilted by glacial deformation to a maximum elevation of 14 m above beach level (Figs 1C and 2). Although the cliffs are unstable and prone to catastrophic collapse, they have been the focus of intensive geological and palaeontological work (see for example NORTON 1967; WEST 1980; HARRISON et al. 1988; PREECE et al. in press). Directly overlying the chalk is a massive flint pebble lag ('Stone Bed') and up to 1.8 m of sand and gravel with marine shells. Pollen spectra indicate largely treeless, herbaceous vegetation ('park – tundra') and a cold climate. These spectra are correlated by WEST (1980) to the Pre-Pastonian *a* substage and sub-arctic marine conditions indicated by Foraminifera and an impoverished, shallow-marine molluscan fauna (NORTON 1967). The cold-stage Crag deposits are sharply delimited from the cross-bedded sands above, which contain pollen indicative of a warmer climate and dominant *Pinus* – *Quercus* – *Ulmus* – *Carpinus* woodland with areas of fen and swamp (WEST 1980). WEST (1980) correlated these spectra with the interglacial sequence at Paston and suggested that the sequence at Sidestrand recorded deposition through much of the interglacial cycle.

Some of the insectivore remains from Sidestrand have been obtained by excavation of foreshore Crag (e.g. S-S D) and are therefore not well stratified. Others however, are from samples taken from the cliff at Sidestrand and are well stratified (Fig. 2) and can be linked to the stratigraphy recorded by WEST (1980) at section SSV. Three of the sites (S-S 1, S-S 2 and S-S 3) are from the basal Crag (Pre-Pastonian of WEST 1980), while S-S 4 is located within the cross-bedded sands correlated by WEST (1980) with the Pastonian.

Shrew and desman remains have also been recovered from the 'Weybourne Crag' at the northern edge of the Crag Basin at Weybourne, but the mandibles are fragmentary and not sufficiently characteristic to be identified to genus or species (MAYHEW & GIBBARD 1998).

In this paper we take the widely adopted position of the Plio-Pleistocene boundary at approximately 1.8 Ma, although this may be revised with strong arguments in favour of placing the base of the Pleistocene at about 2.6 Ma (GIBBARD et al. 2005). The subdivision of the north Norfolk Plio-Pleistocene sequence is also the subject of intense debate. Most workers recognised a bipartite subdivision. The basal shelly sands and gravels were termed the Weybourne Crag by REID (1882, 1890), but reclassified as Norwich Crag Formation (Sidestrand Member) and assigned to the Pre-Pastonian *a* Cold Stage by WEST (1980). WEST (1980) believed there was a substantial time gap (~ 1Ma) between the Pre-Pastonian *a* Substage and later substages of the Pre-Pastonian and the succeeding Pastonian Temperate Stage. He assigned these younger sediments to the Cromer Forest-



Fig. 2. A—Lower part of the cliff at Sidsstrand showing Crag sediments sandwiched between tilted rafts of Maastrichtian Chalk and the position of Site S-S-1, S-S-2 (note people for scale) and Site S-S-4; B—Section showing the location of Site S-S-2 (photographs taken in 1986 by Martin WARREN); C—Close-up of the sequence at Site S-S-2, showing the basal pebble bed ('Stone Bed') resting on Chalk, Crag with pointer marking sampled deposits and cross-bedded sand (Pastonian of WEST 1980). Scale with 0.10 m divisions.

bed Formation. However, MAYHEW and STUART (1986) demonstrated on the basis of the vole assemblages that the Pre-Pastonian and Pastonian were closely linked in time, but separated from Cromerian and earlier Norwich Crag sites (e.g. Bramerton) by substantial periods of time. Although we use the terms Pre-Pastonian and Pastonian in this paper, there is evidence to suggest that these stages may subsume additional climatic oscillations (see Discussion).

**M e a s u r e m e n t s.** Measurements taken according to the method of REUMER (1984: Fig. 4). All measurements are given in mm. DRm2 int.: depth of the ramus internally, below middle of m2; DRm3 int.: depth of the ramus internally, below middle of m3; Lp4-m3: length of p4-m3; Lm1-m3: length of m1-m3; L: crown length; TRI L: length of trigonid; TRI W: trigonid width; TAL L: talonid length; TAL W: talonid width; H: height of the coronoid process; HC: height of the condyle; LLF: length of condylar lower facet; LUF: length of condylar upper facet.

**A b b r e v i a t i o n s.** HZM = Harrison Institute, Sevenoaks, Kent; RG, LG = Green private collection.

## II. SYSTEMATIC PALAEONTOLOGY

Family **Soricidae** FISCHER VON WALDHEIM, 1817

Subfamily **Soricinae** FISCHER VON WALDHEIM, 1817

Tribe **Soricini** FISCHER VON WALDHEIM, 1817

Genus **Sorex** LINNAEUS, 1758

**Sorex (*Drepanosorex*) *praeareneus*** KORMOS, 1934

1934. KORMOS, T. Földtani Közlöny, 64: 296-321, Fig. 32 Villany Kalkberg (= Vi 3) Hungary. Tiglian = Late Villanyian (MN 17).

**H o l o t y p e.** Skull with partial dentition, coll MAFI no. Ob 3681 (REUMER 1984: Pl. 9, Fig. 1)

**D i a g n o s i s.** See REUMER (1984: 40).

**M a t e r i a l.** **Sidestrand:** Right ramus with m2 and alveoli of m1 and m3 (HZM 1.17608), Site S-S 4, about 1 m above Crag; left ramus with alveoli of m1-3 (doubtful referral HZM 4.18309), Sidestrand Crag; right ramus with alveoli of m1-3 and mental foramen (HZM 3.18076), Site S-S 1; right ramus with alveoli of m1-3 (HZM 2.17817), Site S-S D, foreshore Crag; left ramus with alveoli of m2-3 (RG 2.4), foreshore Crag; left ramus with alveoli of p4 – m3 and mental foramen, (LG 1.1), Site LG, foreshore Crag; left ramus with m1-3 (RG 2.1), Site RG, foreshore Crag; right ramus with talonid of m1 (HZM 5.18375), Site S-S 3.

**East Runton (foreshore Crag):** Isolated right m1 (HZM 8.23346); left ramus with talonid of m1 (HZM 7.23345); distal fragment of left i1 sin (HZM 9.23347); left ramus with coronoid, condyle and alveoli of m1-3 (HZM 6.23344); partial left ramus with alveoli of m2-3 (HZM 11.23349); left mandibular condyle (HZM 10.23348).

## III. DESCRIPTION AND MEASUREMENTS

Available measurements are in mm. (Abbreviations are as in Table 1.)

1. HZM 1.17608, right ramus with m2 and alveolus of m3 (Fig. 3A-D).

The size of this fragment, with DR m2 int. of 1.44 mm, conforms well with the range of 1.36-1.48 mm (n = 45) of the population from the late Pliocene (MN 17) site of Zamkowa Dolna



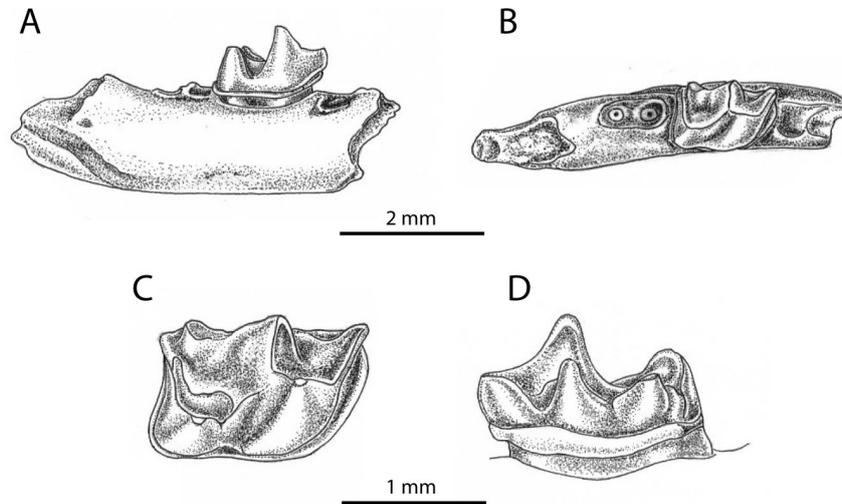


Fig. 3. *Drepanosorex praeearaneus*: A-D – HZM 1.17608, right ramus with m2, alveoli of m1 and m3 from Sidstrand (Site S-S 4), Norfolk. A – buccal view; B – occlusal view; C – m2 in occlusal view; D – lingual view.

Cave A, Poland (RZEBIK-KOWALSKA 1991: Table XXV) as well as with a series of thirteen specimens from the early Biharian site of Żabia Cave, Poland in the HZM collection referred to this species (Table I) with DR m2 int. = 1.28-1.92 mm, mean = 1.47. The coronoid, condyle and mental foramen are missing.

The m2 is well preserved and with only very light wear of the cusp tips. Its size (Length = 1.38 mm, TAW = 0.99 mm) conforms well with the comparative material from Żabia Cave, although the TAW is very slightly larger, and its morphology agrees closely. Particularly noteworthy is the marked convexity of the buccal face of the protoconid, a feature noted by REUMER (1984: 42) as characteristic of this species and leading to the exoedaenodonty observed in later members of the *Drepanosorex* lineage (e.g. *S. (D.) savini*). Other features are the moderately high entoconid crest; the entoconid situated far posteriorly, but with a distinct ‘gutter’ separating it from the postcristid, which declines steeply at a point internal to the entoconid cusp. This feature is also present in the m1 and m2 of the Żabia specimens. The cingulum is developed all round the tooth, most prominent mesially. The cristid obliqua is attached slightly buccal to the apex of the trigonid notch, as in the Żabia Cave material.

2. HZM 8.23346, isolated right m1 (Fig. 4D-F).

This tooth is also well preserved and only differs from the m2 described above in its more elongated form, with the trigonid distinctly longer than the talonid, a feature present in the Żabia Cave material, and clearly visible in the descriptions of RZEBIK-KOWALSKA (1991; Fig. 12) and REUMER (1984: Pl. 11). It is otherwise morphologically identical. L = 1.73, TRI W = 0.96, TALW = 0.96 mm.

3. RG 2.1, left ramus with m1 – m3.

The m1 is cracked transversely across the distal trigonid and the lingual part of m3 is missing. The cusps are so heavily worn that little cusp structure remains. The size of the teeth, their cingula and position of attachment of the cristid obliqua are, however, fully consistent with this species.

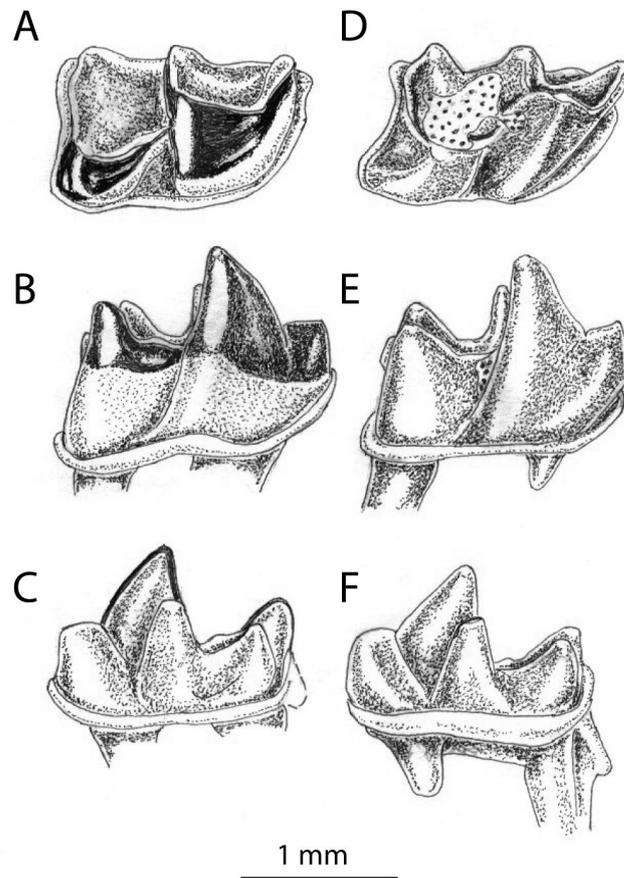


Fig. 4. *Drepanosorex praeearaneus*: A-C – HZM 2.23764, right m1 from Żabia Cave, Poland; D-F – HZM 8.23346, right m1 from East Runton (foreshore Crag), Norfolk. A and D – occlusal view; B and E – buccal view; C and F – lingual view.

The mental foramen is situated below the trigonid of m1, which has been slightly elongated as a result of the cracked trigonid.

4. HZM 6.23344, left ramus with coronoid and condyle intact; alveoli of m1-m3 (Fig. 5A-C).

The coronoid process is typically tall and narrow, the coronoid height (4.10 mm) is slightly less than in the Żabia Cave population. The narrowness of the coronoid compares well with the population from Zamkowa Dolna Cave A (RZEBIK-KOWALSKA 1991). As in that population the coronoid spicule is well developed and the coronoid process is vertically hollowed along its distal border, reaching downwards to the upper condylar facet. The internal temporal fossa is deep, but extends only halfway up the coronoid process, not to the tip, as noted by KORMOS (1934) in his original description of the species. The opening of the mandibular foramen is situated below the mid-point of the internal temporal fossa, similar to the Żabia Cave population (Fig. 5E). The shape and size of the condyle and its upper and lower articular surfaces also conform closely to the Żabia Cave material (Fig. 5F). H = 4.10, LLF = 1.15 (estimated), LUF = 0.83 mm.

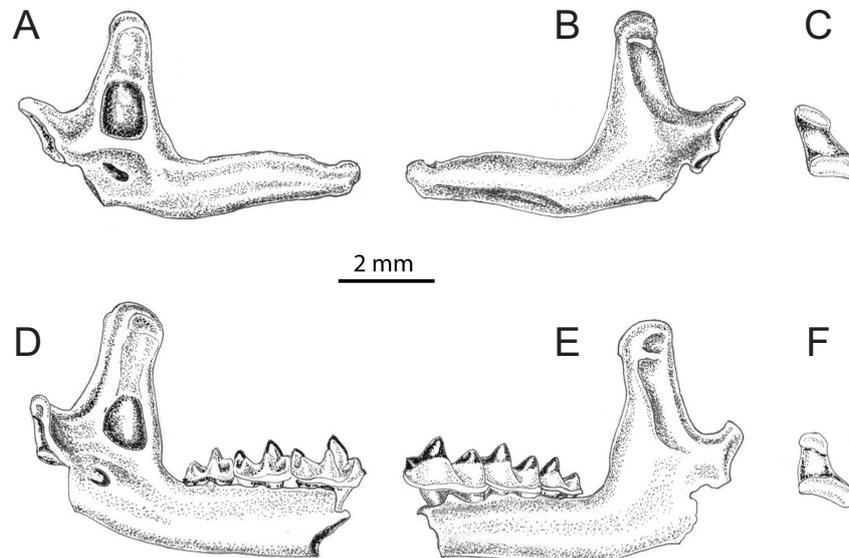


Fig. 5. *Drepanosorex praeearaneus*: A-C – HZM 6.23344, edentulous left ramus from East Runton (foreshore Crag), Norfolk; D-F – HZM 2.23764, right ramus with m1-3 from Żabia Cave, Poland. A and D – lingual view; B and E – buccal view; C and F distal view of condyle; D-F inverted.

##### 5. HZM 10.23448, left mandibular condyle.

This specimen is an intact condyle with part of the angular process attached. It is marginally larger (HC = 1.86 mm) than the Żabia Cave specimens (HC = 1.47-1.82 mm). It is however, very much smaller than the condyle of *Sorex (D.) savini*, but similar in shape and closely resembles the Żabia Cave specimens in its morphology. LLF = 1.15, LUF = 0.90 mm.

##### 6. Miscellaneous specimens.

A number of rami have been recovered, which have been referred to this species on account of their size, but are completely edentulous or have minimal dental relicts. HZM 7.23345 is a left ramus with the talonid of m1 in situ, subsequently lost, but with TAW = 0.93 compatible with this species. HZM 5.18375 is a similar right ramus with the worn talonid *in situ* and measurements compatible with this species. Edentulous soricid rami tentatively referred here on account of their size include HZM 2.17817, HZM 3.18076 and LG 1.1 with the mental foramen between m1 and p4, and HZM 11.23349 and RG 2.4.

Two incomplete lower i1s are referred here by comparison with intact examples from Żabia Cave (Fig. 6A) on account of their size and notably bulbous cuspules. RG 2.2 basal part right i1 with cuspules 2 and 3 from the foreshore Crag at Sidestrand (Fig. 6B) and HZM 9.23347, a distal fragment of left i1 with cuspules 2 and 3 (Fig. 6C). Both agree closely with specimens from Żabia Cave (Fig. 6A).

**Systematic position and comparisons.** We have followed the opinion of REUMER (1985) here in according subgeneric status to *Drepanosorex*. REUMER (1985) recognized a succession of chronospecies in the lineage, with progressive exoedaenodony and increas-

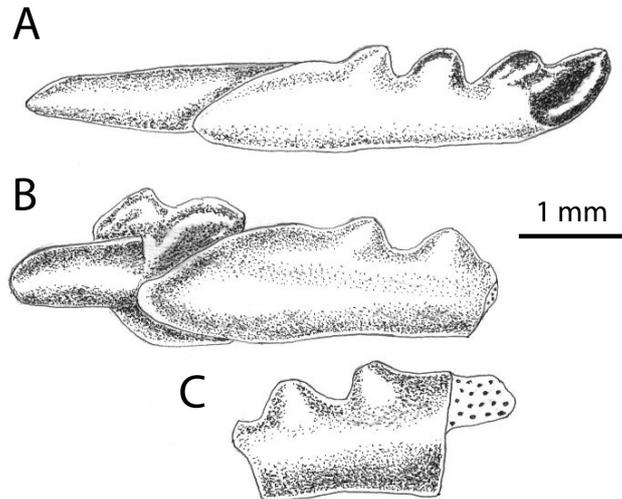


Fig. 6. *Drepanosorex praeareaneus*: A – HZM 10.23786, right i1 from Żabia Cave, Poland; B – RG 2.2, part of right i1 from Sidestrand (foreshore Crag), Norfolk; C – HZM 9.23347, part of left i1 from East Runton (foreshore Crag), Norfolk.

ing size from the late Pliocene until the end of the Cromerian Complex. It is certainly arguable that the degree of morphological difference from true *Sorex* is not great in the older more primitive Late Pliocene forms of *Drepanosorex* (a view taken by RZEBIK-KOWALSKA 1991 and originally by REUMER 1984), but the later more derived Pleistocene forms of the lineage *Sorex (D.) praeareaneus* – *margaritodon* – *savini* – *austriacus* could be argued to warrant full generic distinction for the lineage. For discussion of the possible bifurcation of this lineage and survival into the Late Pleistocene and even Holocene see RZEBIK-KOWALSKA (1991).

It is noteworthy that RZEBIK-KOWALSKA (1991) suspected the presence of *Sorex (D.) praeareaneus* at Żabia Cave, previously recorded as *Sorex (D.) pachyodon* by BOSÁK et al. (1982). The material studied here certainly confirms its presence at Żabia Cave.

This is the first record of *Sorex (Drepanosorex) praeareaneus* from Britain, where it seems to have been the dominant soricid in the Norfolk Crag fauna. A comparison of our measurements (Table I) with data presented by MAUL et al. (2007) shows that the material from the Crag is small and matches that of Tegelen (Fig. 9), currently the oldest and most primitive member of the subgenus.

#### IV. OTHER SORICID TAXA FROM THE PLIO-PLEISTOCENE OF BRITAIN

##### *Beremendia fissidens* (PETÉNYI, 1864)

**East Runton (foreshore Crag):** Incomplete right upper incisor, talon missing (HZM 17.23334)

This specimen, described and figured by HARRISON and CLAYDEN (1993), remains the only certain evidence of *Beremendia* in the British fossil record, since other previously referred large soricid teeth were reidentified as *Macroneomys* (HARRISON et al. 2006).

*Beremendia fissidens* is listed as occurring in the Tegelen fauna (VAN DEN HOEK OSTENDE & DE VOS 2006: 300).

**Soricidae** gen. et sp. undet.**Sidestrand (foreshore Crag):** Right edentulous ramus fragment (LG 1.2).

This specimen is unusually large, (DR m2 int. = 2.11 mm), clearly exceeding the largest specimens of *Sorex (D.) praeearaneus* (DR m2 int. = 1.92 mm) from Żabia Cave and Zamkowa Dolna Cave A (DR m2 int. = 1.68 mm; RZEBIK-KOWALSKA 1991: Table XXV). It does not, however, attain the rather massive depth and thickness of the ramus in *Beremendia fissidens* and its identity remains obscure pending collection of more material. The population of *Sorex (D.) praeearaneus* from the Plio-Pleistocene of Norfolk averages larger than that of Zamkowa Dolna Cave A and it is not impossible that this ramus could simply be a large individual or some other as yet unidentified Plio-Pleistocene shrew in Britain.

*Sorex* cf. *minutus* LINNAEUS, 1766

*West Runton:* Right ramus with alveoli of m1-m3 (Zoology Museum, Cambridge University, registered as WRC 87, sample G3).

This minute edentulous soricid ramus (DR m2 int. = 1.02 mm) is most probably referable to *Sorex minutus*, corresponding in size to the sample from Zamkowa Dolna Cave C (DR m2 int. = 0.93-1.10 mm, mean = 1.01, n = 36; RZEBIK-KOWALSKA 1991: Table III). The only other Plio-Pleistocene species which is at all likely to be confused is *Sorex minutissimus* ZIMMERMANN, 1780. This species is in fact even smaller (DR m2 int. = 0.85-0.90 mm, mean = 0.88, n = 10, Kozi Grzbiet (Poland), RZEBIK-KOWALSKA 1991: Table V). *Sorex minutissimus* is known to occur from the end of the Early Pleistocene at Cave 15-I of Temnata-Prohodna Cave System, Bulgaria (POPOV 1994) and cannot therefore be dismissed as a possible soricid in the Norfolk Plio-Pleistocene.

## V. DISCUSSION

**P a l a e o e c o l o g y.** Table II lists the insectivores currently known from the Pre-Pastonian and Pastonian at Sidestrand, East Runton, West Runton and Weybourne. Of these sites, Sidestrand has yielded the largest collection of insectivore remains so far obtained from any Crag locality. This collection is of particular importance because the small mammal assemblages have contextual information and a direct association with other biological proxies, allowing an assessment of the palaeoenvironment. As stressed by MAYHEW et al. (2008), the presence of terrestrial mammals in the marine Crag suggests either they were washed into the marine environment or may have been reworked from pre-existing terrestrial deposits during transgressive-regressive cycles. It is currently not possible to gauge whether reworking is a significant factor in the taphonomy of the assemblages, and the following discussion is based on the assumption that the small mammal remains are broadly contemporaneous with the marine deposits in which they are found.

At Sidestrand, *Sorex (D.) praeearaneus* is the dominant soricid, occurring in samples from foreshore exposures and at several levels in the cliff exposures. The palaeobotanical research of WEST (1980) has revealed that the Pre-Pastonian Crag (beds a, b and c) was deposited during a cold climatic phase, with a dominant 'Pinus – Gramineae – Ericales' vegetation (Biozone a of WEST (1980: 52), while the overlying (Pastonian) sequence includes deposits laid down during a warmer climatic phase with dominant Pinus – Quercus – Ulmus – Carpinus p.a.b., together with vegetation associated with fen and swamp conditions. A further indication of the severity of the climate during the deposition of the Pre-Pastonian sediments is provided by molluscan and foraminiferal assemblages recovered from the same deposits (NORTON 1967). Significantly, *Sorex (D.) praeearaneus* is present in both the cold-stage and the warm-stage deposits, as are several of the vole species that also continue into at least the early part of the ensuing warm stage. Significant components of the associated vole assemblage are *Lemmus kowalskii* (not found in the warm-stage deposits) and *Borsodia new-*

Table II

Comparison of micromammal fauna from Tegelen (The Netherlands) with those from Pre-Pastonian and Pastonian deposits at Sidestrand, East Runton, West Runton and Weybourne (Norfolk). Tegelen list from VAN DEN HOEK OSTENDE and DE VOS 2006; Norfolk lists based on MAYHEW and STUART 1986, MAYHEW and GIBBARD 1998, and HARRISON et al. 1989 (with revised taxonomy)

	Tegelen	Sidestrand	East Runton	West Runton	Weybourne
MAMMALIA					
<b>Soricomorpha</b>					
<i>Desmana thermalis</i>	+	+ <sup>b,c</sup>	+		+
<i>Galemys kormosi</i>	+	+ <sup>a-c</sup>	+	+	
<i>Talpa minor</i>	+	+ <sup>b,c</sup>			
<i>Beremendia fissidens</i>	+		+		
<i>Petenya hungarica</i>	+				
<i>Sorex (Drepanosorex) praeearaneus</i>	+	+ <sup>a-c</sup>	+		
<i>Sorex minutus</i>	+			cf.	
Soricidae gen. et sp. undet.		+ <sup>a</sup>			+
<b>Rodentia</b>					
<i>Hylopetes debruijini</i>	+				
<i>Castor fiber</i>	+		+		
<i>Trogontherium cuvieri</i>	+	+ <sup>a</sup>	+	+	
<i>Dicrostonyx</i> sp. <sup>d</sup>	+				
<i>Lemmus kowalskii</i>		+ <sup>a-b</sup>	+		
<i>Clethrionomys kretzoi</i>	+	+ <sup>b,c</sup>			
<i>Mimomys pliocaenicus</i>	+	+ <sup>a-c</sup>	+	+	+
<i>Mimomys reidi</i>	+	+ <sup>a-c</sup>	+	+	+
<i>Mimomys tigliensis</i>	+	+ <sup>a-c</sup>	+	+	+
<i>Pitymimomys pitymyoides</i>	+	+ <sup>a-c</sup>	+	+	
<i>Ungaromys nanus</i>	+				
<i>Borsodia newtoni</i>		+ <sup>a-c</sup>	+	+	+
<i>Micromys</i> sp.	+				
<i>Apodemus</i> cf. <i>sylvaticus</i>	+				
<i>Muscardinus pliocaenicus</i>	+				
<i>Glirulus pusillus</i>	+				
<i>Hystrix refossa</i>	+				

<sup>a</sup> Foreshore Crag exposures (HARRISON et al.'s site S-S D, GREEN's sites RG and LG), Pre-Pastonian (WEST 1980).

<sup>b</sup> Cliff Crag exposures (HARRISON et al.'s site S-S1 and S-S3), Pre-Pastonian (WEST 1980).

<sup>c</sup> Cliff sand exposure (HARRISON et al.'s site S-S4), Pastonian Stage (WEST 1980).

<sup>d</sup> Recorded in faunal list published by HOEK OSTENDE and DE VOS (2006), but details of stratigraphical provenance have not been published.

*toni*. The latter species appears to be associated with steppe conditions, and significantly, neither *Lemmus* nor *Borsodia* are present in the extensive collections from temperate stage deposits at Tegelen (MAYHEW 2008).

The functional morphology and palaeoecology of *Sorex (D.) praeearaneus* have been discussed by REUMER (1984), who argued that dental specializations suggested that its diet may have included hard-bodied, possibly molluscan prey. Furthermore, REUMER (1984: 124) suggested that *Drepanosorex* preferred moist environments such as deciduous forest, marsh or even open water. The fact that *Sorex (D.) praeearaneus* is the dominant soricid in the Norfolk Crag fauna as well as Tegelen during phases with contrasting environmental conditions indicates that it was probably a climatically tolerant species.

**C o r r e l a t i o n.** The nomenclature, age and correlation of the youngest pre-glacial marine deposits in north Norfolk are much disputed (see GIBBARD et al. 1990; GIBBARD et al. 1998; PAWLEY et al. 2008). The insectivores described in this paper provide additional evidence for the relative age of the deposits and their correlation with sequences on the European mainland. Key biostratigraphically significant elements in the insectivore assemblages include, *Desmana thermalis* KORMOS, 1930, *Galemys kormosi* (SCHREUDER, 1940), *Beremendia fissidens*, and *Sorex (Drepanosorex) praeearaneus*. These are associated with a diverse and characteristic assemblage of microtine voles, reviewed by MAYHEW and STUART (1986) and now including *Lemmus kowalskii* CARLS & RABEDER, 1988 (HARRISON et al. 1988, 1989), *Mimomys pliocaenicus* FORSYTH MAJOR, 1902, *M. reidi* HINTON, 1910, *Pitymimomys pitymyoides* (JÁNOSSY & VAN DER MEULEN, 1975), *M. (Tcharinomys) tigliensis* TESAKOV, 1998 (recently distinguished from *M. blanci* VAN DER MEULEN, 1973), *Borsodia newtoni* (FORSYTH MAJOR, 1902) and *Clethrionomys kretzoi* (KOWALSKI, 1958). Other small mammals include, *Talpa minor* FREUDENBURG, 1914 and *Sorex* cf. *minutus* LINNAEUS, 1766, *Trogontherium cuvieri* (FISCHER VON WALDHEIM, 1809) and *Mustela praeivalis* KORMOS, 1934.

Comparison of this Crag fauna with that of Tegelen reveals strong similarities (Table II). Of the Tegelen shrews, only *Petenya hungarica* KORMOS, 1934 is not represented in the Crag, and could possibly yet be found there. *Desmana thermalis* and *Galemys kormosi* are well represented in both (HARRISON et al. 1988; VAN DEN HOEK OSTENDE & DE VOS 2006: 299).

REUMER and HORDIJK (1999: 279) consider *Galemys kormosi* to be a particularly significant stratigraphical marker, occurring also in Beremend 4 and 5 in Hungary, Rębielice Królewskie and Weże 1 in Poland and Baza in Spain (RÜMKE 1985; JÁNOSSY 1986; RZEBIK-KOWALSKA 1994). They note that Tegelen is the youngest locality from which it has been recorded. It is therefore noteworthy that this species was found by HARRISON et al. (1988) both in the Pre-Pastonian ('Weybourne Crag') at Sidestrand sites S-S 1 and S-S 3, as well as in the Pastonian sediments at site S-S 4 (Fig. 7A-C). An intact left m1 of *Desmana thermalis* is additionally reported here (HZM 3.17616 (Fig. 7D-F). L = 3.36; TRI W = 2.37; TAL W = 2.94 mm), as well as the trigonid of a left m2 (HZM 5.18212 (Fig. 7G-H). TRI W = 2.50 mm), both of which were recovered from Site S-S 4. The existence of these desmanine species both in the basal part of the 'Weybourne Crag' and the overlying Pastonian sediments, together with the associated microtine rodent species, strongly supports correlation with the late Tiglian.

REUMER and HORDIJK (1999) have listed the insectivores found in a series of boreholes in Zuurland (near Rotterdam, The Netherlands), derived from strata of Tiglian age. These species, including *Galemys kormosi*; *Desmana thermalis*; *Talpa minor*; *Sorex* cf. *casimiri* RZEBIK-KOWALSKA 1991; *Sorex minutus*; *Sorex (Drepanosorex) praeearaneus*; *Beremendia fissidens* and *Petenya hungarica*, clearly show close affinity with the insectivores known from the 'Weybourne Crag'. REUMER (2005) lists other presumed Tiglian sites in The Netherlands containing one or several of these species including Brielle, Dordrecht, Gorkum (Gorinchem), Oosterschelde, Wassenaar, as well as the famous Russel – Tiglia – Egypte clay-pit at Tegelen.

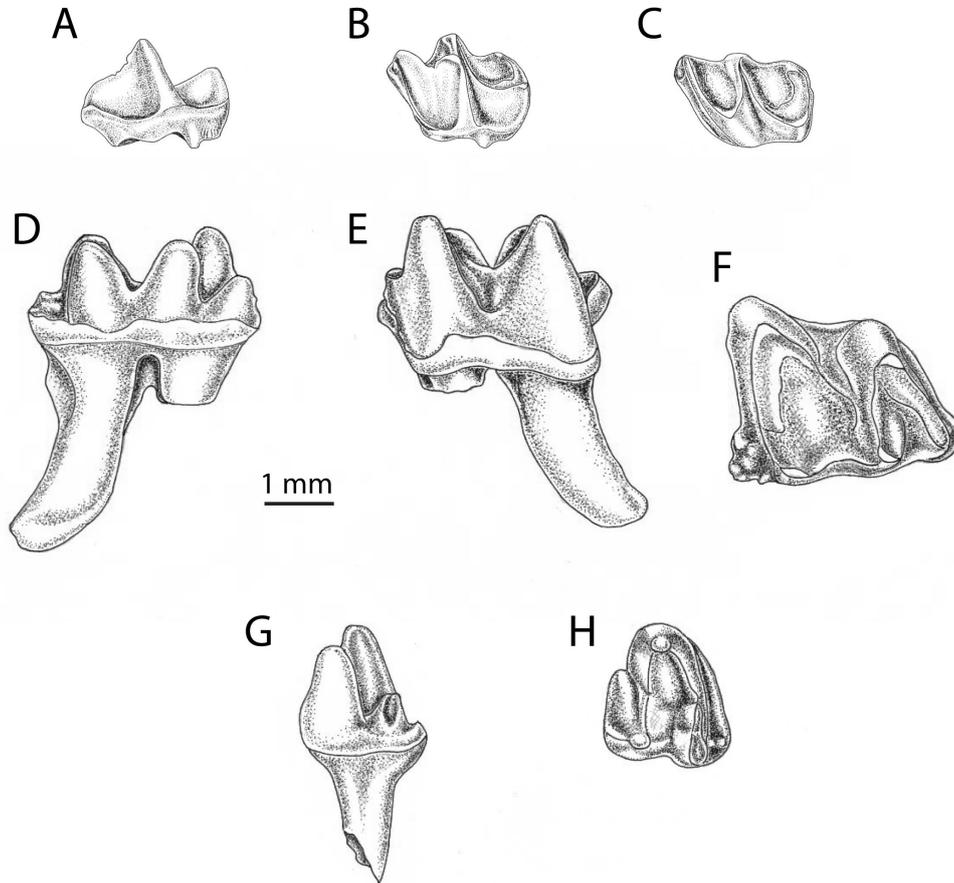


Fig. 7. A-C – *Galemys kormosi*: HZM 5.17969, left m3 from Sidestrand (Site S-S 3), Norfolk; A – oblique buccal view; B – buccal view; C – occlusal view (after HARRISON et al. 1989). D-H – *Desmana thermalis*: D-F – HZM 3.17616, left m1 from Sidestrand (Site S-S 4). D – occlusal view; E – buccal view; F – lingual view. G-H – HZM 5.18212, left m2 fragment from Sidestrand (S-S 4), Norfolk. G – distal view; H – occlusal view.

The known Crag insectivore species, although less abundant, show a remarkable similarity to the distinctive Tiglian insectivore fauna of The Netherlands outlined above.

The rodent fauna of Tegelen also shows a striking similarity in the microtine assemblage, differing only in the absence of *Lemmus kowalskii*, recorded from the 'Weybourne Crag' at Sidestrand (HARRISON et al. 1989) and *Borsodia newtoni* at Tegelen. *Lemmus kowalskii* is known in the Early Pleistocene continental faunas of Poland (KOWALSKI 1977) and Bavaria (CARLS & RABEDER 1988), but *Borsodia newtoni* appears to have been restricted to steppic environments and would be out of place in the Tegelen fauna. The extinct Giant Beaver (*Trogotherium cuvieri*) is present in both faunas, while European Beaver (*Castor fiber* LINNAEUS, 1766) is also known in the Crag, but only at East Runton.

The remaining rodent fauna of Tegelen is for the most part associated with warmer climatic conditions and a more forested environment. These species include *Hylopetes debruijini* REUMER and

Plio-Pleistocene Soricidae and Desmaninae from England

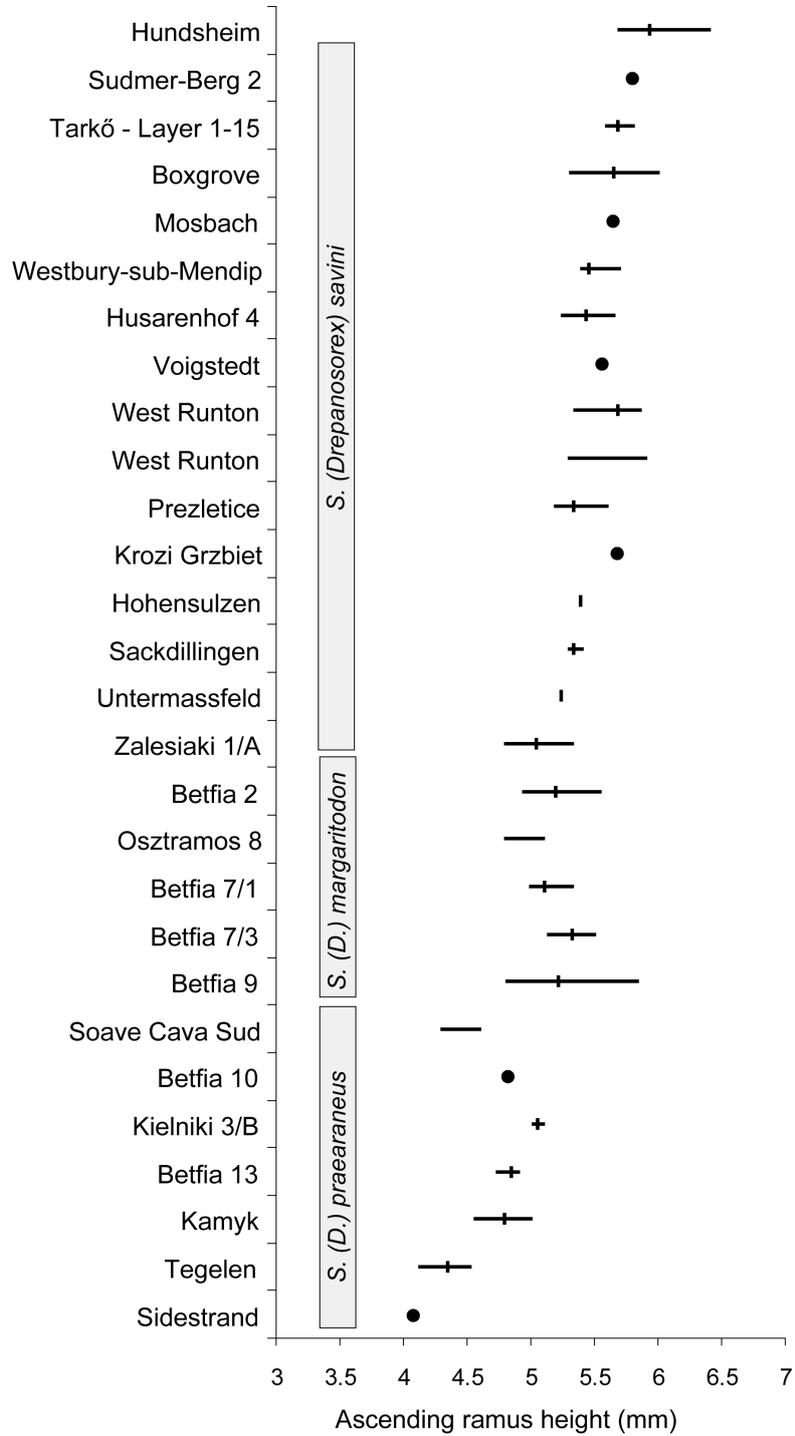


Fig. 8. Size change in the lineage *Sorex (D.) praeearaneus* – *S. (D.) margaritodon* – *S. (D.) savini* – *S. (D.) austriacus* (from Hundsheim). Minimum – (vertical line = Mean) – Maximum diagram of the coronoid height of *Sorex (Drepanosorex)* spp. from selected European Pliocene and Pleistocene assemblages (plotted from data in MAUL et al. 2007: Table 3).

VAN DEN HOEK OSTENDE, 2003, *Muscardinus pliocaenicus* KOWALSKI, 1963, *Glirulus pusillus* (HELLER, 1936), *Micromys* sp., *Apodemus* cf. *sylvaticus* (LINNAEUS, 1758) and *Hystrix refossa* (VAN WEERS, 1994). These species are all essentially members of the rich Pliocene rodent fauna, as known for instance at Podlesice, Poland (NADACHOWSKI 1989: Table II). Whether they ever occurred in the British Pliocene is unknown, but it seems probable that none of them occur in the 'Weybourne Crag' fauna. These differences between the British faunas and that of Tegelen are more likely to reflect environmental disparity rather than geographical separation. Even during periods of elevated sea levels, it is likely that the British Isles were fully connected to the European mainland allowing free interchange of terrestrial biota at this time (Fig. 9).

An anomalous feature of the Tegelen rodent fauna is the presence of *Dicrostonyx*, a vole usually associated with very cold arctic climate and tundra habitat. Curiously it is absent in the 'Weybourne Crag', although it is abundant in later Pleistocene cold stage faunas in Britain. VAN DEN HOEK OSTENDE and DE VOS (2006) have discussed the strong probability that elements of Tegelen fauna are derived from different time frames, but the exact circumstances of the discovery of these specimens is unclear and mixing seems the most plausible explanation for the presence of Collared Lemming.

MAYHEW and STUART (1986), on the basis of the 'Weybourne Crag' vole faunas, made a direct correlation with the late Tiglian (TC5-6) of Tegelen. Subsequently, LISTER (1998) provided a revised interpretation and correlation, noting the mismatch between the cool climate of the Pre-Pastonian and the fully temperate and wooded conditions at Tegelen. He suggested a more likely correlation was between the cold Pre-Pastonian and Tiglian TC4c and between the succeeding tem-

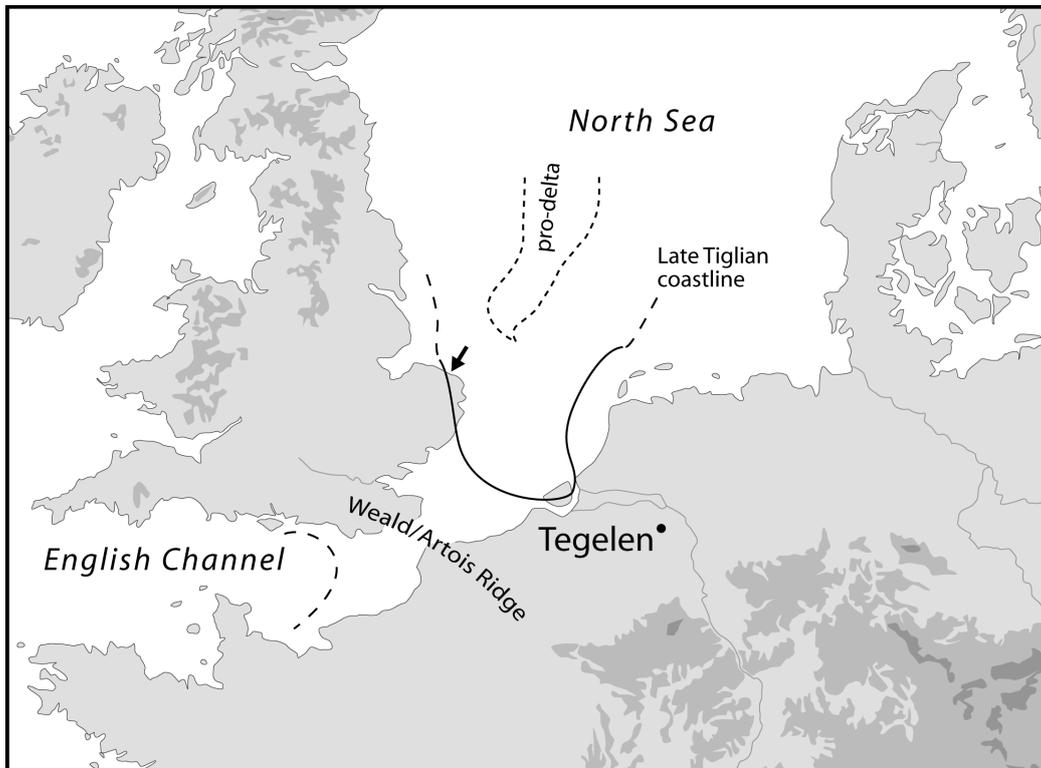


Fig. 9. The palaeogeography of northwestern Europe during the Late Tiglian with the location of the East Anglian sites (arrow) and Tegelen. The heavy line and dashes show the inferred position of the Late Tiglian coastline during a period of maximum transgression (adapted from FUNNELL 1996). Note the position of the postulated Weald – Artois land bridge.

perate Pastonian and TC5-6, a conclusion in concordance with the available palaeomagnetic and molluscan information (LISTER 1998: 275). Although these arguments are compelling, it can no longer be assumed that deposits correlated with either the Pre-Pastonian or Pastonian are all contemporary and that they necessarily represent only two climatic phases. MAYHEW (1990) has already shown that there are clear differences in crown height of key vole species between samples from West Runton, East Runton, Sidestrand and Weybourne. If these differences reflect stratigraphical age, then the small mammal assemblages from Sidestrand and Weybourne could be younger than Tegelen, whereas East Runton and West Runton could represent earlier episodes. Currently, it is unclear whether the small mammals in the marine Pre-Pastonian *a* deposits have been re-worked from different aged deposits by a single marine transgression. Alternatively, the marine deposits resting on the Chalk between Weybourne and Sidestrand may represent different marine transgressions that are currently subsumed within a single Pre-Pastonian sub-stage.

Although it may not be possible to resolve these issues from the vertebrate evidence alone, the small mammals nevertheless support a correlation with the occurrence of *Mimomys pliocaenicus* in MN 17 (Late Pliocene, late Villanyian European Land Mammal Age). We postulate that the north Norfolk Crag faunas fall into this time frame, although the precise correlation between the Norfolk and Continental sites remains unclear at present.

**A c k n o w l e d g e m e n t s.** We are much indebted to John CLAYDEN, who collected and donated a number of the shrew specimens described here, as well as to Paul BATES, the Honourable Sally BALCON and Richard PREECE for help with the fieldwork. Nigel LARKIN is thanked for providing a GPS survey of the Sidestrand localities. Ricky GREEN has provided further shrew material included here. Our colleagues in Poland, the late Kazimierz KOWALSKI and Barbara RZEBIK-KOWALSKA provided generous hospitality and help in the field during visits of the Harrison Institute to Poland, without which this research would not have been possible. Martin WARREN kindly gave most helpful advice interpreting stratigraphy at Sidestrand and provided photographs of the cliff sections. Malcolm PEARCH, of the Harrison Institute has kindly assisted with light macrographs and computer graphics. Further assistance with illustrations was provided by Derek ADAMS (Natural History Museum, London) and Silvia BELLO (Ancient Human Occupation of Britain Project, Natural History Museum, London). We are indebted to the Leverhulme Trust for financial support to the Ancient Human Occupation of Britain (AHOB) project.

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