

The palaeontology and dating of the ‘Weybourne Crag’, an important marker horizon in the Early Pleistocene of the southern North Sea basin

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Highlights

An updated account of the Mollusca and mammals from the Weybourne Crag in the UK and NL.

A *Macoma balthica*–*Mya arenaria* concurrent range zone is defined, tracable across the North Sea.

The small mammals from the Weybourne Crag and its correlatives belong to Mammal biozone MNR1.

Details of the first British records of the voles *Mimomys hordijki* and *Ungaromys dehmi* are provided.

Amino acid dating supports the contemporaneity of the *Macoma balthica*–*Mya arenaria* concurrent range zone.

Amino acid data indicate that the Baventian cold stage post-dates the Bramertonian.

The Baventian and ‘Pre-Pastonian a’ (Weybourne Crag) appear to be distinct cold stages.

Revised age for the ‘Weybourne Crag’ has implications for the duration of the Norwich Crag and the Tiglian.

Abstract

In the North Sea basin the marine bivalve *Macoma balthica* first appears within the Early Pleistocene 'Weybourne Crag', which forms an important biostratigraphical datum. Here we review the fossil assemblages from sites of this age, prompted by new discoveries from Sidestrand, Norfolk, UK. The molluscan assemblages from this horizon are dominated by intertidal species with some colder/deeper water taxa and a few temperate non-marine species. A high boreal/low arctic marine environment with reduced salinities is indicated. An extensive assemblage of small mammals dominated by voles includes two species (*Mimomys hordijki* and *Ungaromys dehmi*) previously unknown from the British Pleistocene. The assemblage can be assigned to Tesakov's Mammal Biozone MNR1 (=MN17, Middle Villafranchian), which according to current estimates corresponds to a date of ~2.2-2.1 Ma (MIS 84-79). It matches another assemblage from -61 m to -65 m in the Zuurland-2 borehole in The Netherlands, and is similar to that from the Dutch Tiglian type site at Tegelen, although this has more temperate elements. A late Tiglian age is consistent with the co-occurrence of the marine bivalves *Macoma balthica*, *Mya arenaria* and the freshwater gastropod *Viviparus glacialis* in the Zuurland-2 borehole and in a North Sea borehole (BGS 52-02-472). A *Macoma balthica* – *Mya arenaria* Concurrent Range Zone is defined for this assemblage, which can be traced across the North Sea basin. Amino acid dating provides strong independent support for these correlations and indicates that the Baventian cold stage post-dates the Bramertonian (Norwich Crag). It also confirms that Early Pleistocene molluscan assemblages with *M. balthica* are younger than those without it. The correlation of this marine marker horizon with Mammal Biozone MNR1 provides a secure link between continental and marine sequences during the Early Pleistocene. It also provides a basis for dating events in the pre-glacial fluvial drainage history and linking it to the East European mammal zonation.

Keywords

Weybourne Crag, Wroxham Crag, Norwich Crag, Baventian, Early Pleistocene, Molluscs, Mammals, The Netherlands, Amino acid dating

1. Introduction

Establishing secure links between marine and terrestrial sequences is a major objective of Quaternary research, but is frustrated by the limited opportunities of doing so. The delivery of pollen into the deep sea environment, such as happens off Portugal (e.g. Tzedakis et al., 2015), has been crucial in enabling correlation of the terrestrial pollen record with the marine isotope stratigraphy and in understanding phase relationships between the two (e.g. Donders et al., 2018). Shallow-marine sequences also offer opportunities for linking marine biostratigraphical schemes with terrestrial records, such as those based on mammal biostratigraphy.

The Early Pleistocene (Gelasian) succession in the North Sea basin is complex and consists of various laterally discontinuous units with poor age constraints. The shallow marine Plio-Pleistocene crags of East Anglia, UK, have a succession of molluscan faunas (cf. Harmer, 1900), the youngest of which comes from the so-called ‘Weybourne Crag’. This important horizon is characterized by the appearance of the bivalve *Macoma balthica*, which like many of the molluscs in the crags had origins in the Pacific Ocean. The ‘Weybourne Crag’ is also the last appearance datum of another bivalve, *Mya arenaria*, which became extinct in the North Sea basin until its reintroduction during the late Holocene. In this paper we characterise the fauna of the ‘Weybourne Crag’ and define the *Macoma balthica*–*Mya arenaria* Concurrent Range Zone, which can be used to correlate sites in eastern England with sites across the North Sea basin into the Netherlands. Vertebrate assemblages recovered from this horizon enable correlation with the East European Mammal Zonation (Tesakov, 2004), thereby allowing integration of biostratigraphical schemes from both marine and non-marine successions. Independent support for these correlations is provided by amino acid dating. An updated revision of the Early Pleistocene Gelasian succession in the North Sea basin is proposed.

2. Methods

2.1. Sediment sampling and analysis

Large bulk-samples from the ‘Weybourne Crag’ at Sidestrand (sites RG and LG, Fig. 1, Fig. 2, Fig. 3), weighing many tens of kilograms, were wet-sieved (0.85 mm mesh) in the sea and the residues dried and sorted for vertebrates. Subsamples from these dried residues were subsequently analysed for molluscs. A smaller (9 kg) sample of raw

sediment was also sieved using a finer (0.5 mm) mesh-size to recover smaller species, which were sorted using a binocular microscope. This mesh-size was also used in the analyses of shells from the borehole samples (Zuurland-2 and BGS 52-02-472). Minimum total of shells were estimated using the standard procedure of counting apices and hinge fragments of bivalves (cf. Norton, 1967). The new molluscs from Sidestrand are archived in the University Museum of Zoology, Cambridge, but the vertebrates have been deposited in the Natural History Museum, London. Molluscs from North Sea borehole BGS 52-02-472 are archived in the Naturalis Biodiversity Center, Leiden, and material from the Zuurland borehole is retained in the private collection of Mr Leen Hordijk.

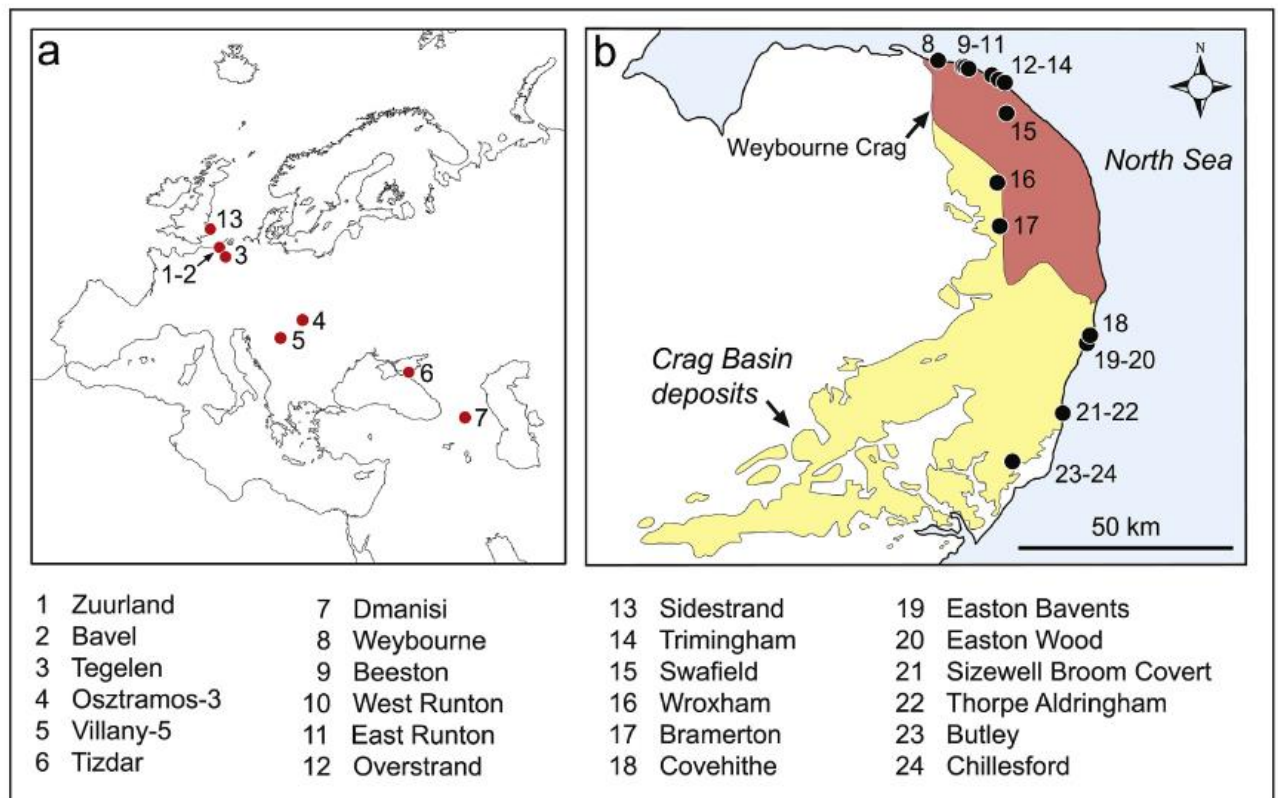


Fig. 1. a. Map of Europe showing sites mentioned in the text. b. Location of critical sites in East Anglia in relation to the Crag basin. Depositional area of the 'Weybourne Crag' (Wroxham Crag Formation) modified from Riches (2012, Fig. 6.8).

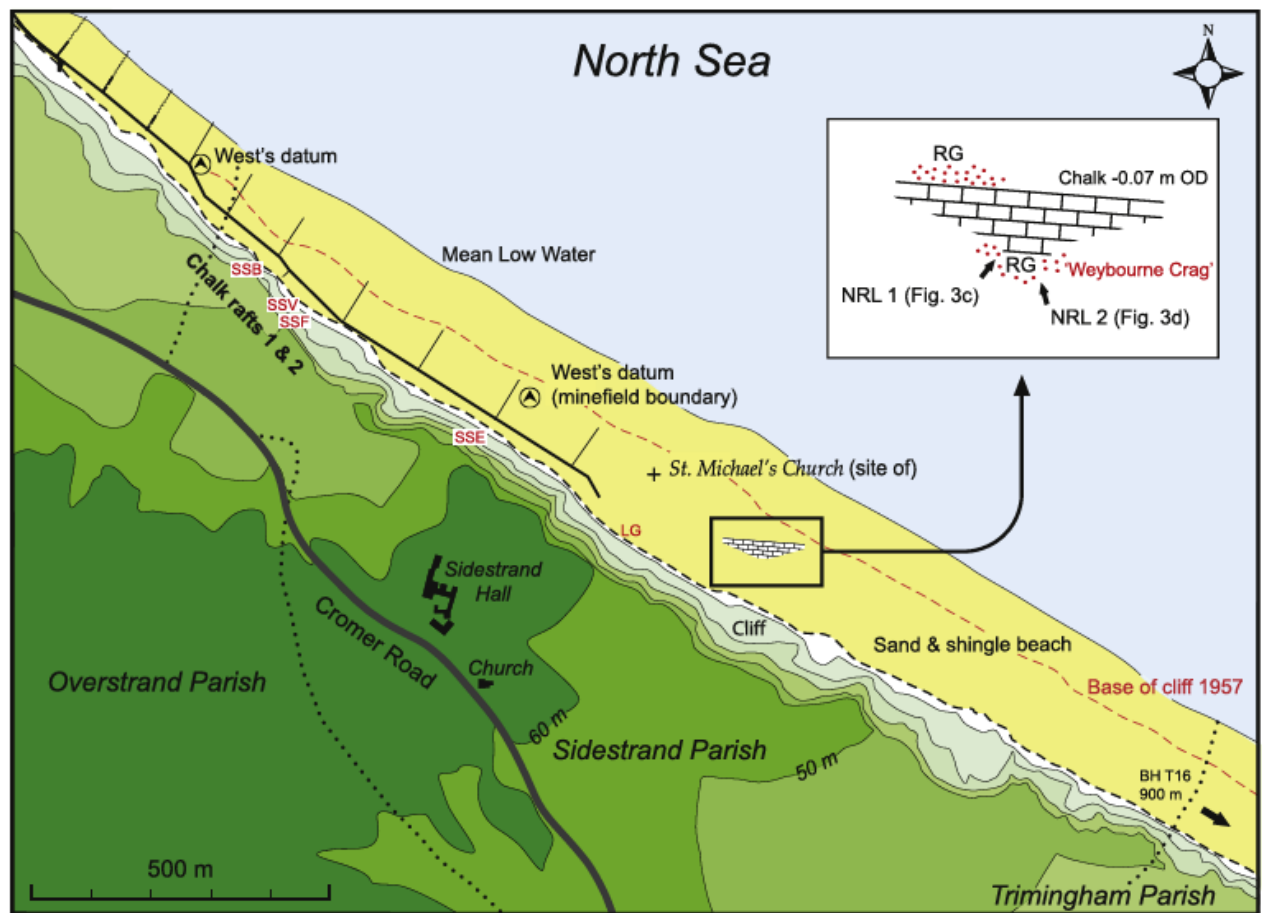


Fig. 2. Map of the coastline between Overstrand and Trimingham showing the location of West's sites SSB, SSV, SSF, SSE (all sampled for pollen and forams), Borehole BHT 16 and our sites RG, LG and NRL 1 and NRL 2 (inset). Norton's samples came from a site south-eastward from the end of Overstrand promenade (TG 252410), where the Crag and Chalk have been displaced by glacitectonic deformation.



Fig. 3. Photographs of the exposures of the 'Weybourne Crag' at Sidestrand. a. The 'Weybourne Crag' occurs on the surface of the Chalk rafts displaced by glaciotectionics. Height of cliff about 60 m (photograph by Martin Warren); b. View of the foreshore looking north-west showing the location of NRL 1 (c) and NRL 2 (d); c. Site NRL 1 showing organic mud (dark grey) overlying the 'Weybourne Crag'; d. Close-up of the 'Weybourne Crag' at NRL 2 showing bedding and characteristic fossils (inset). Photographs b-d taken by Nigel Larkin. For precise locations see Fig. 2.

2.2. Measurements of teeth

Where necessary, specimens were viewed under alcohol or acetone to visualize the enamel-free areas. Measurements followed the method of Tesakov (2004), and were taken on digital images using TpsDig software (Rohlf, 2015).

2.3. Amino acid analysis

To test the correlation between the British and continental sequences, amino acid analyses were undertaken from several critical sites. Newly-developed protocols were used to analyse the intra-crystalline components of the opercula of the freshwater gastropod *Bithynia*, which are composed of calcite, and shells of the marine Dog-whelk *Nucella lapillus*, which are predominantly composed of calcite (Penkman et al., 2008, 2011; 2013; Demarchi, 2009; Demarchi et al., 2014). All samples were prepared using the procedures of Penkman et al. (2008) to isolate the intra-crystalline protein by bleaching. Two subsamples were then taken from each shell/operculum; one fraction was directly demineralised and the free amino acids analysed (referred to as the ‘free’ amino acids, FAA, F), and the second was treated to release the peptide-bound amino acids, thus yielding the ‘total’ amino acid concentration, referred to as the ‘total hydrolysable amino acid fraction’ (THAA, H*). During preparative hydrolysis, both asparagine and glutamine undergo rapid irreversible deamination to aspartic acid and glutamic acid respectively (Hill, 1965). The DL ratios of aspartic acid/asparagine, glutamic acid/glutamine, serine, alanine and valine (D/L Asx, Glx, Ser, Ala, Val), as well as the [Ser]/[Ala] value for the opercula, were then assessed to provide an overall estimate of intra-crystalline protein decomposition (IcPD).

3. Regional stratigraphy

During the Early Pleistocene (~2.6–1.8 Ma), a series of marine sediments was laid down in the North Sea basin, overlying thick Neogene deposits, particularly towards the centre of the basin (Rijsdijk et al., 2005; Kuhlmann et al., 2006; Lee et al., 2015). In Britain, the highstand marine sediments of these sequences exposed onshore and in coastal sections constitute the later part of the Red Crag Formation, the Norwich Crag Formation, and the ‘Weybourne Crag’, an unofficial term retained for the youngest division of the crags. This is now included as part of the Wroxham Crag Formation (Table 1). Offshore the sediments form the Yarmouth Roads and Winterton Shoal Formations (Rijsdijk et al., 2005). In the Netherlands, the marine deposits from the same period generally occur at depth due to subsidence of that part of the basin. They constitute the Maassluis Formation, which includes a number of

climate-forced depositional cycles (Meijer et al., 2006; Slupik et al., 2007). Towards the end of the Early Pleistocene the southern part of the North Sea basin gradually filled with sediment, which enabled the major rivers to flow northwards over this land, connecting fluvial systems on either side of the basin (Meijer and Preece, 1995; Overeem et al., 2001).

Formation	Member	Sites discussed	Events	Regional stages/ages	
Happisburgh Formation			First of a series of major ice advances	Anglian (cold) 478-424 Ka (MIS 12)	MIDDLE PLEISTOCENE
Cromer Forest-bed Formation	Mundesley Member* ('Mya bed')	West Runton	Marine highstand	? (cold)	
	West Runton Member (West Runton Freshwater bed)		Freshwater sedimentation	Cromerian (temperate) 621-563 Ka (?MIS 15)	
				Pastonian and other stages	EARLY PLEISTOCENE (GELASIAN)
Wroxham Crag Formation	Various Members ('Weybourne Crag')	Sidestrand Weybourne East Runton West Runton Wroxham ('Bure Valley Beds') Swafeld borehole (25.9-26.3 m)	Major input of quartz-rich gravels FAD of <i>Macoma balthica</i>	Pre-Pastonian a (cold) 2.2-2.1 Ma	
Norwich Crag Formation	Westleton Member		Marine highstand (regressive)	?Baventian (cold) Baventian (cold)	
	Easton Bavents Member	Covehithe			
	Chillesford Member		Marine highstand	Bramertonian (temperate) 2.44-2.20 Ma	
	Chillesford Church Member				
		Bramerton (lower levels)			
		Thorpe Aldringham			
				Ludhamian (~2.45 Ma) and other stages	
Red Crag Formation	Sizewell Member	Butley	Marine highstand	Pre-Ludhamian (cold) ~2.7-2.45 Ma	

Table 1. Stratigraphical context of the British onshore sites discussed here. This simplified scheme essentially follows Bowen (1999). *assigned to the CF-bF by West (1980) but would be included within the Wroxham Crag Formation according to the definition of Rose et al. (2001). Meijer et al. (2006) tentatively linked the Ludhamian with transition of MIS 97 to MIS 96 (~2.45 Ma). Other ages are based on the estimated duration of the mammal biozones defined by Tesakov (2004) and on MIS boundaries defined by Lisiecki and Raymo (2005). The stages fall within these temporal limits rather than occupying the full range.

In Britain, Early Pleistocene sediments occur intermittently around the coast of Norfolk and Suffolk (Mathers and Zalasiewicz, 1988; Zalasiewicz et al., 1988; Hamblin et al., 1997; Gibbard et al., 1998), where they can be seen directly overlying Chalk bedrock on the foreshore or in cliff sections affected by glaciotectonic deformation (Lee, 2009; Burke et al., 2009; Lee et al., 2013; Phillips and Lee, 2013). The first major study of the youngest of these deposits was undertaken by Reid (1882, 1890), who attributed them to the 'Weybourn[e] Crag', which in representative sections between Cromer and Overstrand he described as a "Greenish loam, clay, and clay-ironstone, full of casts of marine shells" (Reid, 1890: 160). These sediments occurred above a Stone Bed that rested on the Chalk but beneath his Lower Freshwater Bed, Forest-bed (estuarine) and Upper Freshwater Bed, which are now all

included in the Cromer Forest-bed Formation (CF-bF). West (1980) described a similar sequence from foreshore exposures between West Runton and Trimingham (Fig. 1). Reid's Stone Bed (West's bed b) and the 'Weybourne Crag' (bed c) yielded pollen spectra that West (1980) attributed to the 'Pre-Pastonian a' cold substage. West assigned these sediments to the Sidestrand Member of the Norwich Crag Formation (but see discussion below). Following an unconformity, a horizon of cemented ferruginous gravels with clay pebbles (bed e) included silty-clay laminae, which produced pollen assigned to the Pastonian temperate stage, now also recognized as of Early Pleistocene age (Gibbard et al., 1991). West (1980) assigned these deposits, which correspond to part of Reid's 'Forest-bed (estuarine)', to the Paston Member of the CF-bF, but later these marine sediments, and the 'Weybourne Crag' itself, were included as part of the Wroxham Crag Formation defined by Rose et al. (2001). The Wroxham Crag consists of the quartz-bearing shallow-marine deposits in northern East Anglia that outcrop between the Norwich Crag Formation and the glacial Happisburgh Formation. It includes the 'Bure Valley Beds' (see below), marine elements of the CF-bF and quartz-bearing sands and gravels previously attributed to the Kesgrave Thames (Rose et al., 2001).

The Wroxham Crag Formation is underlain by the Norwich Crag Formation, which in turn rests on the Red Crag Formation (Table 1). The Red and Norwich Crag formations are readily separable in southern and central East Anglia, but the sediments become more variable northwards and the distinction is not always straightforward (Gibbard et al., 1998). In southern East Anglia, the Norwich Crag Formation has been divided into two members (Mathers and Zalasiewicz, 1988; Bowen, 1999): the Chillesford Church Member (formerly Chillesford Sand Member) and the Chillesford Member (formerly Chillesford Clay Member). The former is represented by fine-to medium-grained well-sorted sand that is generally unfossiliferous except for occasional pockets of shell. Sedimentary structures and trace fossils suggest deposition in a tidal-flat environment. At its type site at Chillesford Church pit (TM 382523), foraminifera and pollen assemblages have been recovered that are similar to those from the lower sediments at Bramerton (see below), the type site of the Bramertonian temperate stage (Funnell et al., 1979). In the Aldeburgh-Orford region in southeast Suffolk, the sands forming the upper part of the Chillesford Church Member grade into silty-clays of the Chillesford Member. These have yielded cold climate assemblages of pollen, foraminifera and molluscs similar to those of the Easton Bavents Clay (West and Norton, 1974; Zalasiewicz et al., 1991). The Easton Bavents Clay that forms the Easton Bavents Member is exposed in coastal sections between Easton Bavents and Covehithe (see below). These

sections constitute the stratotype of the Barentian cold stage. The Easton Barents Clay resembles the Chillesford Clay and has also yielded a cold stage assemblage (West et al., 1980).

The Westleton Beds (now Westleton Member) are gravels that unconformably overlie the Easton Barents Clay (type Barentian). They are exposed in coastal sections at Easton Barents and Covehithe and at inland localities in north-east Suffolk (Hey, 1967, 1976). The gravels are composed almost exclusively of rounded flints and have consequently been taken to represent the uppermost part of the Norwich Crag Formation (Mathers and Zalasiewicz, 1996). The clast lithology of the gravels suggests derivation from the north by longshore drift (Hey, 1967, 1976 but see Hamblin et al., 1997) with probable input from the early Thames from the south (Gibbard et al., 1998). The gravels are generally unfossiliferous but occasional casts of marine shells and other fossils have been found (Richards et al., 1999). They have been assumed to be of late Barentian to 'Pre-Pastonian a' age (Gibbard et al., 1998).

The flint-rich character of the Westleton Beds contrasts sharply with later marine gravels assigned to the Wroxham Crag Formation (but see Mottram, 2017). The latter includes the 'Weybourne Crag', which has a clast lithology containing a high proportion (typically 30%) of far-travelled lithologies, in addition to the dominant flint of the underlying bedrock. The far-travelled rocks consist of quartz, quartzite, hard sandstone, and Carboniferous, *Rhaxella* and Greensand cherts, slate, granite, basalt, dolerite and porphyry. All except the quartzose rocks and Carboniferous chert occur at very low frequencies (Green and McGregor, 1990, 1999; Pawley et al., 2004). Although the precise details of the pre-Anglian drainage pattern in East Anglia cannot be determined because of subsequent glacial erosion, it has been possible, on the basis of clast lithology, to relate the influx of distinct fluvial inputs from the Thames, Bytham and other river systems into the biostratigraphical framework of the East Anglian succession (Green and McGregor, 1999; Rose et al., 2001, 2002; Rose, 1994; Rose, 2009). The precise dating of the 'Weybourne Crag' would therefore form an important link in this correlation.

There are also important palaeontological differences between the Norwich Crag Formation and the so-called 'Weybourne Crag', especially the occurrence in the latter of the marine bivalve *Macoma balthica*. Harmer (1900, 1905) considered that the 'Weybourne Crag' (Zone of *Tellina balthica*) formed the youngest division (the Weybournian) of the East Anglian Crags. Some later authors, however, have regarded the 'Weybourne Crag' as merely a

marginal facies of the Norwich Crag (see Gibbard et al., 1998: 249), disregarding the differences in clast lithology mentioned above. Moreover, Norton (2000) demonstrated a stratigraphical relationship between the two in the Swafeld borehole (see below). The term ‘Weybourne Crag’, distinguishable from the classic Norwich Crag by clast lithological differences and the occurrence of the bivalve *Macoma balthica* therefore remains useful and we retain it here as an informal name, used in the way defined by Reid (1890) and Harmer (1900, 1905).

3.1. The critical sites (Fig. 1 and Table 1)

Listed below are nine Early Pleistocene sites that have yielded *Macoma balthica*. Six of these have been assigned to the ‘Weybourne Crag’, including the stratotype of this unit at Weybourne Hope. Two other sites are from the southern North Sea that have also yielded *M. balthica* in Early Pleistocene levels, whereas Zuurland is a borehole in which the appearance of *M. balthica* can be identified, as at Swafeld, within the Early Pleistocene succession.

In order to put the data from these ‘Weybourne Crag’ sites into perspective, comparisons need to be made with data from sites of known age. Four Early Pleistocene marine sites lacking *Macoma balthica* range from the Red Crag Formation (Butley) to the Baventian cold stage (Covehithe). These comparisons should enable the relationship of the ‘Weybourne Crag’ to the Norwich Crag Formation and Baventian to be established.

The third group of sites include stratotypes of two Dutch Early Pleistocene stages (Tiglian and Bavelian) and an early Middle Pleistocene marine horizon at West Runton, Norfolk, UK, immediately overlying the Cromerian interglacial succession. These sites provide valuable points of reference.

3.1.1. Sites with *Macoma balthica*

3.1.1.1. Sidestrand, Norfolk (52° 54' 32" N, 1° 21' 56" E)

Important exposures of the ‘Weybourne Crag’ occur in the vicinity of Sidestrand, also referred to Overstrand and Trimingham in the literature. West described several sampling localities at this site (Fig. 2, Fig. 3, Fig. 4) from which pollen, molluscs and foraminifers were recovered (West, 1980; Norton, 1967, 1980; Funnell, 1961). Reid (1890: 138-139) also recorded small mammals from both the ‘Weybourne Crag’ and from a ferruginous

conglomerate with clay-pebbles, lignite and cakes of peat, which he included in his Forest-bed (estuarine). Remains of large mammals have also been collected from the foreshore along this stretch of coast and Lister (1993, 1996; 1998) has provided a detailed review of these, distinguishing, where possible, remains from the Early Pleistocene and those from the early Middle Pleistocene. However, it is the small mammals that provide the best biostratigraphical evidence for the age of the deposits (Mayhew and Stuart, 1986; Mayhew, 2015; Harrison et al., 1988a, Harrison et al., 1988; 1989; Harrison and Parfitt, 2009). The Early Pleistocene sediments at Sidestrand have normal palaeomagnetic polarity (Maher and Hallam, 2005).

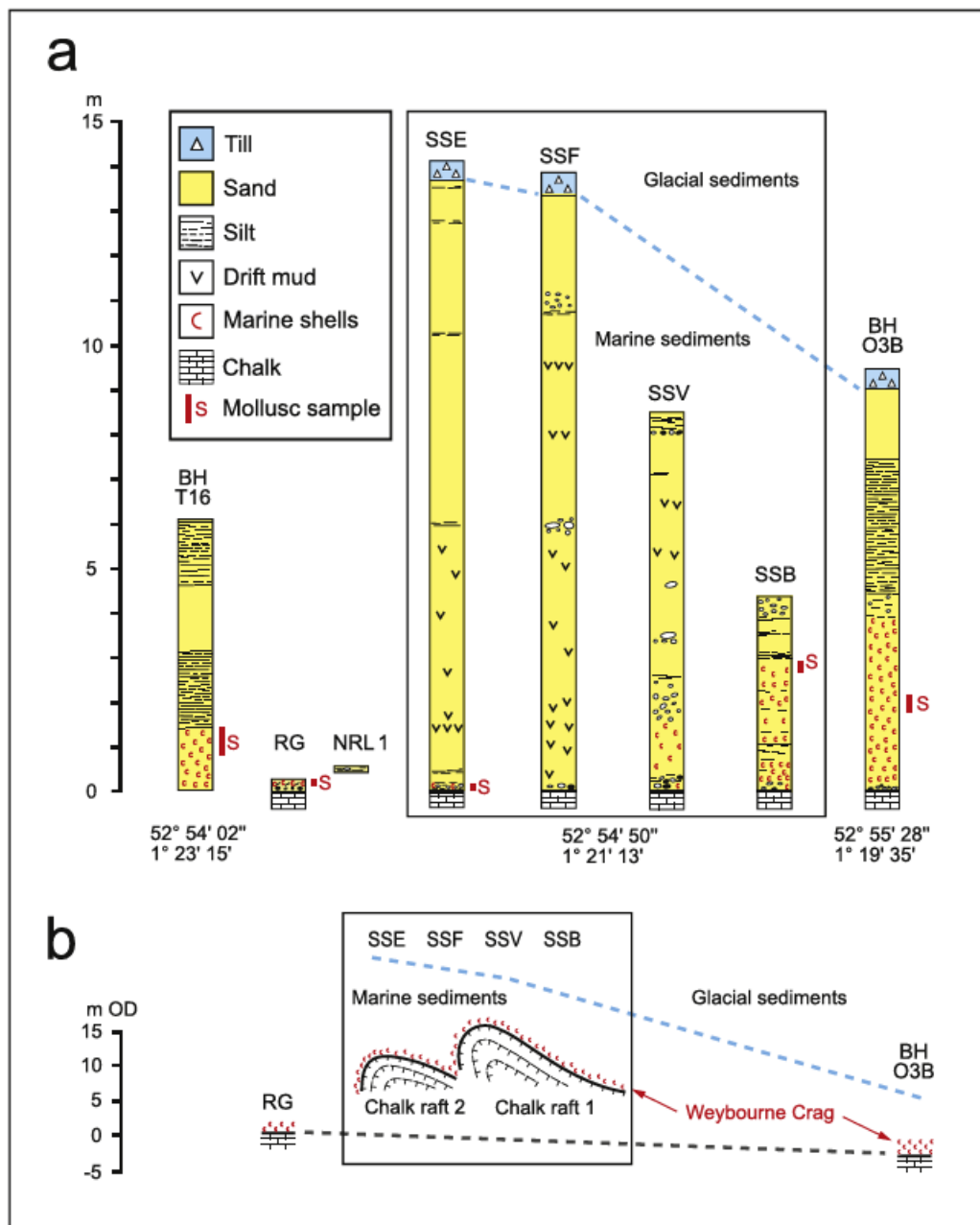


Fig. 4. a. Stratigraphical logs of various pre-glacial Pleistocene sequences between Trimingham (BH T16) and Cromer (BH O3B), showing the position of sampled horizons in the ‘Weybourne Crag’ (site codes follow West (1980), except for RG and NRL, which are described herein). b. Location of some of the critical sampling horizons in relation to elevation (height in m O.D.). The Chalk occurs on the foreshore at sites RG and BH O3B but has been severely displaced by glaciotectonics into massive rafts at intermediate locations (see Fig. 3a).

The new material from Sidestrand studied here was collected by Ricky Green in 1998–2000 and came from two discrete sites (RG) on the foreshore and a third (LG) at the base of the cliff about 150–200 m to the west. The RG sites were located on either side of a platform of Chalk dipping shoreward that runs obliquely across the beach and are extremely close to, and possibly contiguous with, sites NRL 1 and NRL 2 (Fig. 2), which are illustrated here (Fig. 3) and show an identical sequence. The basal unit, a stone bed consisting of large flint pebbles (‘bed a’ of West, 1980), rested directly on the Chalk and was overlain by highly fossiliferous shelly sands with silt laminae forming part of the ‘Weybourne Crag’ (bed b). The shelly deposits (Fig. 3d) are overlain by a unit of grey laminated silts (Fig. 3c) with seams of clay conglomerate. Pollen spectra from these silts were dominated by conifers but also contained a significant component of temperate taxa (S. Peglar, personal communication); the saltmarsh foraminiferid *Jadammina macrescens* was also recovered (J.E. Whittaker, personal communication). This appears to match the sequence reported from site SSB at Sidestrand by West (1980: 50).

The stratigraphy of the deposits overlying the ‘Weybourne Crag’ at Sidestrand is complex and has been described in a number of recent papers (Preece et al., 2009; Lee, 2009; Burke et al., 2009; Lee et al., 2013; Phillips and Lee, 2013; Larkin et al., 2011, 2014).

3.1.1.2. Weybourne, Norfolk (52° 56′ 55″ N, 1° 08′ 33″ E)

The ‘Weybourne Crag’ was the name applied by Reid (1882) to shallow-marine shelly sands with laminated clay resting on the Chalk surface at its type locality at Weybourne Hope. These deposits can be traced in cliff sections from their feather-edge at Weybourne Hope to Skelding Hill and Sheringham, where a more complete and thicker sequence (up to 4 m) includes interbedded laminated clays, silts, sands and gravels (West, 1980; Mayhew and Gibbard, 1998; Pawley et al., 2004). The gravels include a significant far-travelled

component carried by rivers flowing through central and northern England as well as a contribution from the Thames catchment to the south (Pawley et al., 2004).

Small mammal remains were first described from Weybourne Hope by Mayhew and Gibbard (1998) and more recently from another locality about 700 m to the east ('Weybourne 2' of Mayhew, 2015). In addition to rare insectivore remains (*Desmana thermalis* and a soricid), the assemblages comprise an abundant and diverse assemblage of voles (*Lemmus kowalskii*, *Borsodia newtoni*, *Pitymimomys pitymyoides*, *Clethrionomys kretzoi*, *Mimomys pliocaenicus*, *M. tigliensis*, *M. reidi*). Pollen spectra associated with the small mammals at Weybourne Hope were obtained from clasts of grey silt within the marine sediments. These indicate pine woodland and grassland communities and a cold climate, whereas a second spectrum is more temperate in character and indicative of cool temperate to boreal coniferous woodland (Mayhew and Gibbard, 1998). The source of the clasts is likely to be the *in situ* laminated silty-clay horizons that occur beneath Skelding Hill. These horizons contain comparable pollen assemblages and are reworked locally to produce a clay conglomerate and clay pebbles within the cross-bedded sands (West, 1980). The laminated clay unit overlying the 'Weybourne Crag' at Skelding Hill, assigned to the Pastonian temperate stage, has a reversed palaeomagnetic signal (Hallam and Maher, 1994).

3.1.1.3. East Runton, Norfolk (52° 56' 15" N, 1° 16' 28" E)

At East Runton, the Chalk surface and associated ferruginous stone bed and 'Weybourne Crag' are exposed on the foreshore at low-tide. Most of the larger mammals (antlers and elephant teeth) recovered from this site came from a bed of ferruginous conglomerate with clay pebbles overlying the 'Weybourne Crag' rather than from the 'Weybourne Crag' itself (Reid, 1890: 157-158; Lister, 1996: 32). Silty-clay laminae from this upper unit (bed e of West) produced pollen that West (1980) assigned to the Pastonian Stage. Indeed, West (1980: 114-116) concluded that much of the large mammal fauna from the foreshore in the East Runton area is of Pastonian age, although Lister (1993, 1996: 40) highlighted the unusually high diversity of deer species (3 or possibly 4 species) raising suspicions that the East Runton mammal fauna may be composite. In contrast to the large mammals, almost all of the small mammals (and molluscs and ostracods) from East Runton seem to have come from the 'Weybourne Crag'. Mayhew and Stuart (1986) recorded *Borsodia newtoni*, *Pitymimomys pitymyoides*, *Mimomys pliocaenicus*, *M. tigliensis* and *M. reidi* as constituents of the 'Weybourne Crag' at this locality. Associated ostracods are indicative of shallow polyhaline

waters and suggest that “sea temperatures at depth were 2 ± 2 °C colder than present” (Wood, 2009).

3.1.1.4. Beeston, Norfolk (52° 56' 40" N, 1° 13' 51" E)

At a point midway between Beeston Regis Hill and a stream about 500 m to the east, Reid (1890: 155) reported an assemblage of marine shells from the ‘Weybourne Crag’ that included *Macoma balthica* and *Mya arenaria*.

3.1.1.5. Dobbs Plantation, Wroxham, Norfolk (52° 41' 32" N, 1° 21' 37" E)

In the early literature (summarized by Cambridge, 1978), the fossiliferous pebbly sands and gravels of the Bure Valley (the ‘Bure Valley Beds’) were separated from the Norwich Crag by the occurrence of *M. balthica*. They have therefore been thought to correlate with the ‘Weybourne Crag’ of the North Norfolk coast. A section excavated at Dobb’s Plantation, Wroxham, a site in a tributary valley of the Bure, demonstrated 1.35 m of sandy gravels with several distinct shell-beds resting on Chalk. There have been problems relating to the identification of *M. balthica* at this site and some specimens named as such have proved to be poorly preserved specimens of *Macoma obliqua* (Riches et al., 2008: 96). However, *M. balthica* does occur at this site (identification confirmed by T. Meijer) together with *Mya arenaria* but *M. balthica* was recovered only from the uppermost levels (Cambridge, 1978). The fauna was dominated by intertidal species (Table 2). Funnell (1980) studied foraminiferal assemblages from the same section noting intertidal or shallow, temperate, open coast assemblages at the base and a boreal, increasingly cold intertidal or shallow subtidal assemblage in the upper levels.

	Weybourne	West Ranton	East Ranton	Sidestrand-Overstrand
Soricomorpha				
<i>Beremendia fissidens</i> (Pétenyi, 1864)	+		+	
<i>Sorex</i> (<i>Drepanosorex</i>) <i>praeearaneus</i> Kormos, 1934			+	+
<i>Sorex</i> cf. <i>minutus</i> Linnaeus, 1766		+	+	
Soricidae gen. et sp. undet.	+			
<i>Galenys kormosi</i> (Schreuder, 1940)	+	+	+	+
<i>Desmana thermalis</i> Kormos, 1913	+		+	+
<i>Talpa</i> sp.	+			+
Carnivora				
<i>Mustela praenivalis</i> Kormos, 1934				+
Proboscidea				
<i>Mammuthus meridionalis</i> (Nesti, 1825)	+	+		
Artiodactyla				
<i>Cervalces gallicus</i> (Azzaroli, 1952)			+	
<i>Eucladoceros tetraceros</i> (Dawkins, 1878)	cf			+
<i>Eucladoceros</i> cf. <i>sedgwicki</i> Falconer, 1868				+
Cervidae gen. et sp. indet.				+
Ovibovine (<i>Megalovis</i> / <i>Pliotragus</i> or <i>Caprovis savinii</i> Newton, 1882)				+
Rodentia				
<i>Trogotherium</i> sp.				+
<i>Ungaromys delhmi</i> Carls and Rabeder, 1988				+
<i>Clethrionomys kretzoi</i> (Kowalski, 1958)	+			+
<i>Mimomys pliocaenicus</i> Forsyth Major, 1902	+	+	+	+
<i>Mimomys hordijki</i> van Kolfschoten and Tesakov, 1998				+
<i>Mimomys reidi</i> Hinton, 1910	+	+	+	+
<i>Mimomys tigliensis</i> Tesakov, 1998	+	+	+	+
<i>Mimomys</i> sp. (large form)				+
<i>Pitymimomys pitymyoides</i> (Jánossy and van der Meulen, 1975)	+	+	+	+
<i>Borsodia newtoni</i> (Forsyth Major, 1902)	+	+	+	+
<i>Lemmus kowalskii</i> Carls and Rabeder, 1988	+			+

Table 2. Mammal remains recovered *in situ* from the ‘Weybourne Crag’.

The clast lithology of the upper levels also shows a marked change from a flint-dominated assemblage of the Norwich Crag to one with *Rhaxella* chert and white/colourless quartzose rocks. This change is broadly coincident with the appearance of *M. balthica* (Rose et al., 2001). This section has been designated as the type site of the basal Dobb’s Plantation Member of the Wroxham Crag Formation (Rose et al., 2001).

3.1.1.6. Swafeld borehole, Norfolk (52° 50’ 33’’ N, 1° 23’ 43’’ E)

In the late 1990s a borehole was drilled by the British Geological Survey (BGS) at Swafeld, Norfolk, an inland site about 8 km south of Sidestrand (Fig. 1). It recovered fossiliferous sediments to a depth of about 30 m but detailed analyses are not available. However, the interval 25.9–26.3 m yielded a molluscan assemblage containing species typical of the

‘Weybourne Crag’, whereas below (27.4–29.3 m) Norwich Crag assemblages lacking *M. balthica* were recovered (Norton, 2000). Apart from Wroxham (see above), this is the only other instance in Britain where these two assemblages occur in direct conformable superposition (Fig. 5).

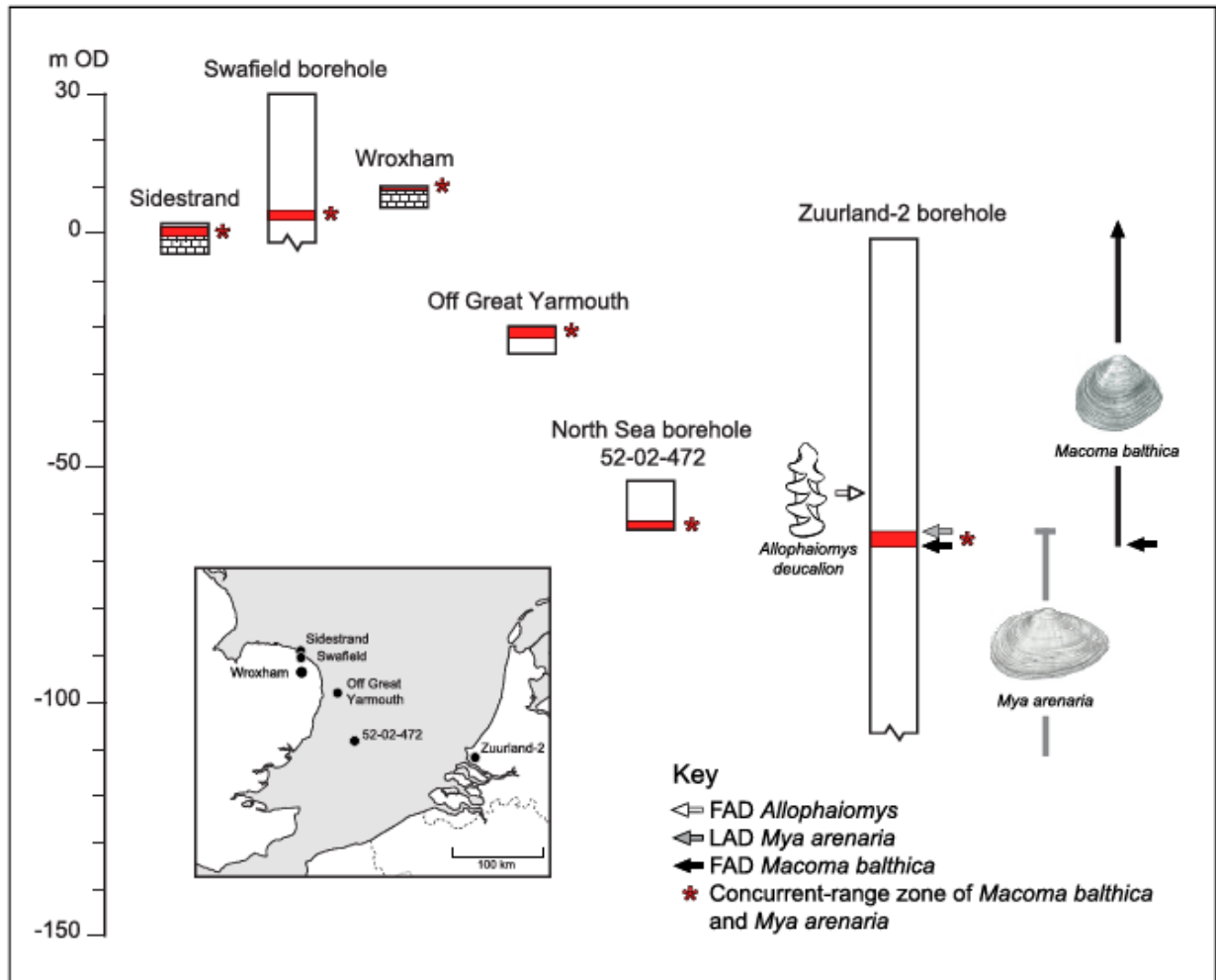


Fig. 5. Height relations of critical localities showing the First Appearance Datum (FAD) for *Macoma balthica*. The Last Appearance Datum (LAD) of *Mya arenaria* extends above this datum at all the sites (data from Swafield are not available) to form the *Macoma balthica* – *Mya arenaria* Concurrent Range Zone (see Appendix).

3.1.1.7. Yarmouth Roads Formation off Great Yarmouth (52° 30' N, 02° 00' E)

Fossils recovered from gravel dredged from the Early Pleistocene Yarmouth Roads Formation off Great Yarmouth (Fig. 5) included species relevant to this study. The water-depth in this area is about 25 m but the maximum dredge-depth below sea-bottom was unrecorded. Geological mapping has demonstrated about 10 m of Holocene and Late

Pleistocene deposits underlain first by the Early Pleistocene Yarmouth Roads Formation and then by the Winterton Shoal Formation (Cameron et al., 1984).

Until recently the ovibovine *Caprovis savinii* was previously only known from a single horn-core found at Overstrand (Newton, 1882: 49, pl. 10). De Wilde (2006), however, has reported two horn-cores of this species from Early Pleistocene sediment dredged from the same site off Great Yarmouth and another found at the Sorting Centre at Spaansen near Harlingen from material dredged from another location (52° 33' N, 02° 01' E at a sea-depth of approximately 20 m). The material from the second dredge-site is better localized and has yielded several hundred mammalian fossils, remains of *Mammuthus meridionalis* and antlers of *Eucladoceros ctenoides* accounting for more than half of the material collected (de Wilde, 2006).

3.1.1.8. North Sea borehole BGS 52-02-472 (52° 03' 00" N, 2° 16' 61" E)

Borehole BGS 52-02-472, located in the Southern Bight of the North Sea (Fig. 5), formed part of the geological mapping programme of the North Sea undertaken by the RGD (Rijks Geologische Dienst) and BGS. The borehole was recovered by the Geodoff coring system that made use of the straight flush method. It recovered a fossiliferous sequence comprising sand units separated by clays to a maximum depth of 10 m below the sea-floor.

3.1.1.9. Zuurland-2 borehole, The Netherlands (51° 53' 29" N, 4° 9' 39" E)

The Zuurland-2 borehole (registration code 37C554) was located south of Brielle, on the island of Voorne in the Province of Zuid Holland, in the southwestern part of the Netherlands (Fig. 1, Fig. 5). It is situated close to the southern boundary of the subsiding part of the North Sea basin and has recovered Quaternary sediments to a depth of 107 m (Fig. 5), although the base of the Quaternary infill has not been reached (Burger et al., 1988). The sediments were recovered by Leen Hordijk using a manual bailer coring system but only the upper 63 m have been analysed in detail (Van Kolfschoten and de Boer, 1988). The sediments were extremely fossiliferous throughout most of the sequence, and included remains of small mammals (Van Kolfschoten, 1988; Van Kolfschoten and Tesakov, 2010) and molluscs (Meijer, 1988). Analyses of the molluscs to a depth of –95 m have now been undertaken (section 4.2.3).

The small mammal assemblages recovered between –61 m and –66 m are relevant to this study (Van Kolfschoten and Tesakov, 1998; 2010; Van Kolfschoten et al., 2018; Tesakov and van Kolfschoten, 2011). The occurrence of *Borsodia newtoni* and *Mimomys*

pliocaenicus allows attribution to arvicolid biozone MNR1 of Tesakov (2004). *Mimomys hordijki* and *Phenacomys europaeus* were also recovered from this level. *Allophaiomys deucalion*, which first occurs in arvicolid biozone MQR11 (Tesakov, 2004) and is the basis of the division between the Villanyian and Biharian Land Mammal Ages (Van Kolfschoten and van der Meulen, 1986), does not occur until a higher level (−52 to −56 m) at Zuurland (Van Kolfschoten, 1998).

3.1.2. Sites without *Macoma balthica*

3.1.2.1. Bramerton, Norfolk (52°36'11.34"N, 001°23'31.79"E)

Two pits have been excavated into Early Pleistocene sediments at Bramerton, near Norwich (Riches et al., 2008). The pit at Bramerton Common has long been regarded as the type section for the Norwich Crag (Reid, 1890), whereas Blake's Pit, located about 300 m away, has been the focus of much of the recent research and is the source of the *Nucella* analysed here. At both localities, sands with lenses of shells and minor beds of silt and clay rest on Chalk at about 2–3 m O.D. The thickness of the sediments varies from about 6 m at Blake's Pit to 12 m at Bramerton Common. Pollen spectra from silt lenses in the basal 4 m at Blake's Pit belong to an *Alnus* – *Quercus* – *Carpinus* pollen assemblage zone (p.a.z.) representing the temperate Bramertonian Stage, with Blake's Pit as the type locality (Funnell et al., 1979). Cooler conditions are indicated by a *Pinus* – Ericales – Gramineae p.a.z. recovered from later sediments about 5 m above the Chalk. This later p.a.z. representing heath and herbaceous communities and a sharp deterioration of climate has been correlated with the 'Pre-Pastonian a' Substage of the Norfolk coast (Funnell et al., 1979). Marine shells are common but *M. balthica* does not occur (Norton, 1967; Funnell et al., 1979). The small mammals have been described by Mayhew and Stuart (1986) and include the vole *Mimomys praepliocaenicus*, indicating attribution to Tesakov's Mammal Biozone MNR2 (Mayhew, 2015).

3.1.2.2. Thorpe Aldringham, Suffolk (52°11'25.08"N, 001°36'18.09"E)

This Norwich Crag site has yielded pollen spectra now correlated with the Bramertonian Stage (Funnell et al., 1979). Marine shells were common but *M. balthica* did not occur (West and Norton, 1974). The *Bithynia* opercula analysed for amino acid dating came from the basal shell layer of the pit near Shell Pit Cottages noted by West and Norton (1974). The voles *Mimomys praepliocaenicus*, *M. reidi* and *Pitymimomys baschkiricus* have been found at this site (Mayhew, 2015), indicating attribution to arvicolid biozone MNR2.

3.1.2.3. Covehithe, Suffolk (52°20'54.60"N, 001°41'44.67"E)

The stratotype of the Baventian cold stage is located in the cliffs at Easton Bavents, north of Southwold on the Suffolk coast. The Baventian deposits can be traced in cliff sections between Southwold and Covehithe, and include at least 2 m of laminated blue and grey clays (Easton Bavents Clay) underlain by a thicker sequence of shelly Norwich Crag Formation and overlain by two lithologically-distinct gravel bodies, the Westleton Beds (Norwich Crag Formation) and Wroxham Crag Formation (Funnell and West, 1962; West, 1980; West et al., 1980; Hamblin and Rose, 2012). Pollen analyses of silt bands within the basal metre of crag at Easton Bavents indicate temperate forest with *Tsuga*. The deposits have been assigned to the Antian temperate stage defined from a level in the Ludham borehole (Funnell and West, 1962). A single pollen spectrum obtained from the upper part of the shelly crag is of intermediate character and was assigned to the early part of the Baventian. The marine molluscan assemblages record changes from open-coast littoral conditions at the base to sublittoral conditions towards the top (Norton and Beck, 1972). Temperatures throughout are interpreted as having been similar to those of the modern boreal region. Pollen spectra obtained from the laminated clays at Covehithe indicate a relatively open landscape dominated by grassland heath and stands of boreal trees (West et al., 1980). Moreover, these pollen spectra resemble those obtained from the type section of the Baventian at Easton Bavents with which the clays can be correlated. Foraminifera from the Easton Bavents Clay indicate a deteriorating cold climate in a sublittoral or low intertidal setting (Funnell and West, 1962). This climatic interpretation is supported by a low arctic molluscan assemblage of *Macoma calcaria*, *Serripes groenlandicus*, *Yoldia myalis* and *Ciliatocardium ciliatum* (Long, 1974, 2000) with low-diversity dinoflagellate (Head, 1998) and ostracod assemblages indicative of frigid, open-marine conditions (Lord et al., 1988; Wood, 2009). The Baventian sediments at Easton Bavents have normal palaeomagnetic polarity (Thompson, 1991).

Non-marine vertebrates occur sparsely in the shelly crag. Large mammals recorded from the 'Upper Shell Bed' at Easton Bavents (*Equus* cf. *stenonis*, *Mammuthus meridionalis*, *Eucladoceros falconeri* and *Anancus arvernensis*) are probably of early Baventian, or late Antian age (Larwood and Martin, 1953; Stuart, 1982). Relatively few small mammal remains were known until recently, when bulk sampling at Easton Wood (=Covehithe Warren, 52° 21' 52" N, 1° 42' 11" E, see Mayhew, 2013, 2015) yielded *Mimomys preapliocaenicus*, *M. tigliensis*, *Borsodia praehungarica cotolovinensis*, *Lemmus*

kowalskii and the recently described arvicolid species *M. glendae*, the probable precursor of *M. hordijki* known from the Zuurland-2 borehole and the ‘Weybourne Crag’ at Sidestrand.

3.1.2.4. Neutral Farm Pit, Butley, Suffolk (52°06′24.84″N, 001°27′42.14″E)

This pit has been known since the late nineteenth century for its rich and diverse marine molluscan fauna belonging to the Red Crag Formation (Dixon, 1977; Balson, 1999). The molluscan assemblages also include occasional terrestrial and freshwater species (Bell, 1871). Sections here reveal over 6 m of Red Crag consisting of two distinct units separated by a sharp horizontal truncation surface (Dixon, 1977, 1979). The lower unit is a cross-bedded shelly sand with sedimentary structures implying deposition in water-depths of about 10–20 m (Dixon, 1979). The higher unit of burrowed, trough-bedded sands grades to laminated silts and fine sands, reflecting a shallowing sequence from nearshore/onshore to foreshore sand flats at the top of the section. The molluscan succession similarly indicates a shallowing nearshore marine environment (Dixon, 1977). Foraminiferal assemblages from Neutral Farm Pit are similar to those from the Pre-Ludhamian Stage (Beck et al., 1972). Arctic species dominate the ostracod fauna (Lord et al., 1988) with further indications of high boreal and arctic marine conditions provided by several newly described ostracods that occur at Neutral Farm and at other Pre-Ludhamian localities (Wood, 2009). Neutral Farm Pit was selected as the type site for the ‘Butleyan’ division of the Red Crag (Harmer, 1900), which has been considered to equate broadly with the Praetiglian Stage of the Dutch sequence (Spaink, 1975). Meijer et al. (2006), however, have demonstrated that three cold episodes occurred within the Praetiglian Stage, which they tentatively correlated with MIS 100-96, so an age estimate for the Pre-Ludhamian sediments at Butley can currently only be given between broad limits (2.7–2.45 Ma).

3.1.3. Stratotypes for reference

3.1.3.1. Tegelen, Limburg, The Netherlands (51° 21′ N, 6° 10′ E)

For many years, fossils had been recovered from Early Pleistocene clays in the neighbourhood of Tegelen near Venlo, close to the Dutch – German border in Limburg. The sequences exposed in these clays pits are part of the Waalre Formation and are the type sections for the Tiglian C Substage of the Dutch Early Pleistocene succession (Zagwijn, 1963). Most of these former clay pits are now abandoned and inaccessible, including almost all of the most fossiliferous sites. In 1970, one of these former pits, Russel-Tiglia clay-pit Egypte, was reopened allowing renewed investigations (Freudenthal et al., 1976). Most of the new samples from this pit, including those used here for amino acid dating, came from a

clayey-sand filling a gully cut into the Tegelen Clay (see Van den Bosch, 2016; Fig. 4). The middle part of this gully was extremely rich in plant material. Extensive lists of the fauna and flora now exist for various pits around Tegelen and Maalbeek (e.g. Tesakov, 1998; Westerhoff et al., 1998; van den Hoek Ostende and de Vos, 2006; Villa et al., 2018). The small mammal assemblages include abundant remains of *Mimomys pliocaenicus* allowing attribution to arvicolid biozone MNR1. Westerhoff (2009: 95) undertook an extensive review of the geology of the Tegelen-Maalbeek area and concluded that the pollen sequences in this area are controlled largely by local sedimentary processes. He suggested that the sequence at the Russel-Tiglia Egypte pit represents only about 10–20 ka years, considerably shorter than the 200–400 ka generally proposed for the duration of the Tiglian C Substage, characterized by high values of *Pterocarya*. He discouraged further attempts to correlate small-scale fluctuations in climate with specific events, such as the cold phase TC4c, and recommended that the traditional division of the Tiglian into three phases (A–C) be abandoned. The age of the Tiglian Stage is therefore uncertain but most authors give 2.2–1.7 Ma as the best approximation (Westerhoff, 2009).

3.1.3.2. Bavel, Noord Brabant, The Netherlands (51° 35' 37" N, 004° 50' 05" E)

In the 1960s, clay pits in the vicinity of Bavel near Breda in the southwestern part of The Netherlands exposed fossiliferous sections belonging to an Early Pleistocene interglacial stage post-dating the Tiglian but pre-dating the Cromerian. The geology and palynology were described by Zagwijn and de Jong (1984), who defined this as the type site of the Bavel interglacial. They also defined the Bavelian Stage, which included this and a later temperate stage, the Leerdam interglacial, separated by the Linge glacial, and including a later cold stage, the Dorst glacial following the Leerdam interglacial.

The sediments at Bavel, which include clays, sands and gravels, are fluvial in origin and belong to the Stramproy Formation. Pollen from the clays reveals a vegetational succession leading to temperate forest in which *Tsuga* and *Carpinus* are characteristic components. The limited mammal fauna has been described by Van Kolfschoten (1990). The molluscan fauna, which includes a number of extinct species, was recovered from three adjacent pits. Detailed analyses have still to be published, although a preliminary list from pit 1 does exist (Spaink, 1968; see also Meijer and Preece, 1996). The *Bithynia bavelensis* opercula used for amino acid dating came from this site. A palaeomagnetic change from reversed to normal polarity occurs within the sequence at Bavel. This appears to represent the lower boundary of the

Jaramillo subchron (1.07–0.99 Ma), which, if correct, would imply that the Bavel interglacial equates with MIS 31 (cf. Lisiecki and Raymo, 2005).

3.1.3.3. West Runton, Norfolk (52°56'29.77"N, 001°15'12.08"E)

The West Runton Freshwater Bed (WRFB) exposed at the base of the cliffs here is the stratotype of the early Middle Pleistocene Cromerian Stage but earlier and later sediments are also visible. At the western end of the section Early Pleistocene sediments, including a sand with abundant *M. balthica* (bed c), occur above a stone bed resting on Chalk. This is the 'Weybourne Crag' but it is the marine sediments that immediately overlies the WRFB that we have targeted for amino acid dating in order to provide a known point of reference. These sediments contain marine molluscs including three species of bivalve (*Mya truncata*, *Astarte borealis* and *Yoldia myalis*) that occur with united valves in life-position (Lyll, 1863: 215; Reid, 1890). These are the most cold-resistant taxa represented. This is 'bed a' of the post-West Runton Freshwater Bed succession (West, 1980: 18) but it is also known as the 'Mya bed' or 'Leda myalis bed' (Reid, 1890), now assigned to the Mundesley Member of the Cromer Forest-bed Formation (West, 1980). *Mya arenaria*, a characteristic component of the earlier 'Weybourne Crag' assemblages, does not occur in this younger 'Mya bed' (Norton, 1980; Meijer, 1993). There appears to be a stratigraphical hiatus between the underlying interglacial freshwater deposits (WRFB) and these cold-water marine sediments (Preece, 2001), which appear to post-date the type Cromerian (as defined by West, 1980).

4. Results

4.1. Mollusca from the 'Weybourne Crag'

No details of the molluscan assemblages have previously been published from the foreshore exposures of the 'Weybourne Crag' at sites RG and LG at Sidestrand (Table 2). A revised and updated list of Mollusca from Sidestrand and other 'Weybourne Crag' sites is given in Table 2, together with counts obtained from other critical sites under discussion; full data from Zuurland-2 (61-65 m) is given in Supplementary Table 1. Notes on species of interest are provided as Supplementary data and selected species are illustrated in Fig. 6, Fig. 7, Fig. 8. Earlier lists of Mollusca have been published from various exposures of the 'Weybourne Crag' but they have usually been grouped together as a composite fauna (Reid, 1890; Harmer, 1905), although Reid (1882) does provide details from individual sampling sites. Foreshore sections at East Runton have hitherto furnished the richest assemblages. At Sidestrand, Norton (1967) described molluscan assemblages from the basal

20 cm of site SSE (Pa II), from shelly sands of 'Pre-Pastonian a' age (bed b) at site SSB, 3 m above the stone bed, and at site SSK just above the stone bed (Fig. 2, Fig. 4).

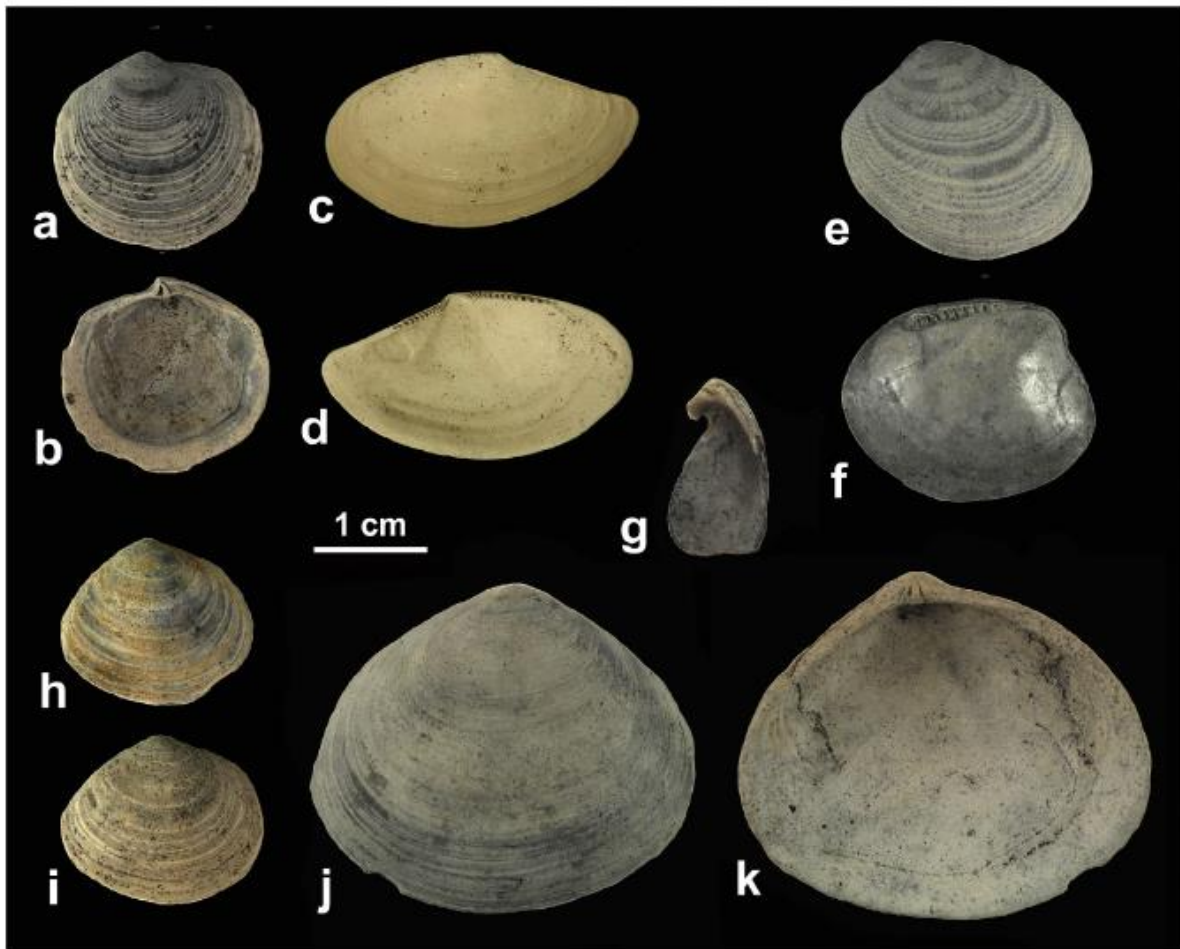


Fig. 6. Selected marine bivalves from the 'Weybourne Crag' at Sidestrand. a-b. *Lucinoma borealis* (Linnaeus). c-d. *Yoldia oblongoides* (Wood). e-f. *Acila cobboldiae* (Sowerby). g. *Mytilus* cf. *trossulus* Gould, umbonal fragment. h. *Macoma balthica*, small form. i. *Macoma balthica* (Linnaeus). j-k. *Macoma obliqua* (Sowerby).

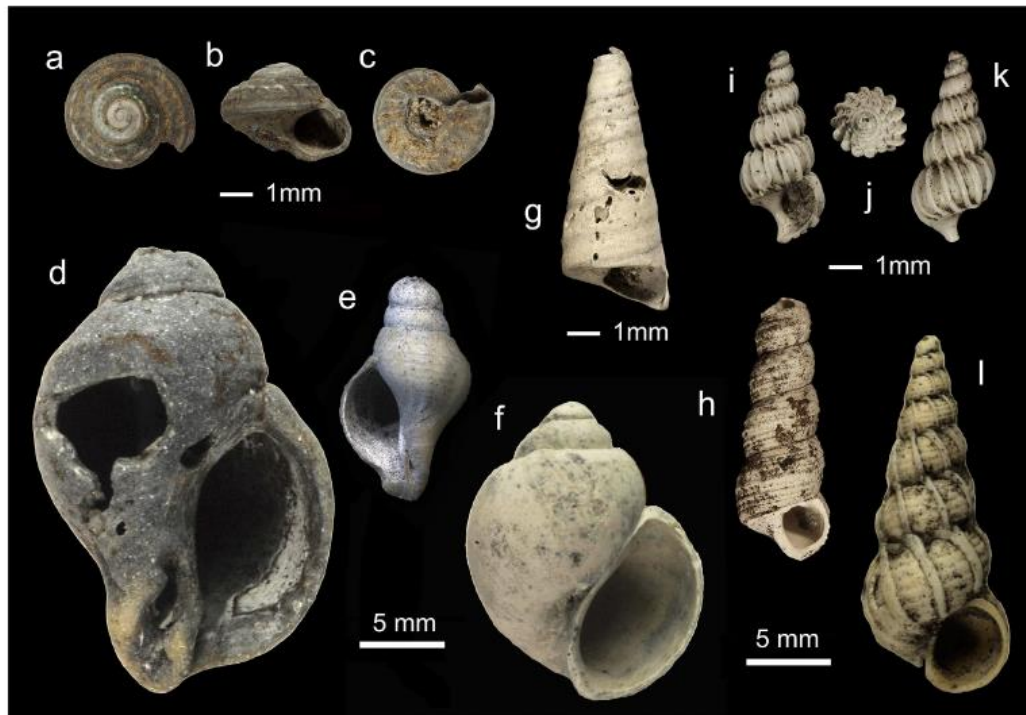


Fig. 7. Selected marine gastropods from the 'Weybourne Crag' at Sidestrand. a-c. *Solariella obscura* (Couthouy). d. *Nucella lapillus* (Linnaeus). e. *Neptunea inversa* Harmer), juvenile. f. *Amauropsis islandicus* (Gmelin). g. *Turritella incrassata* Sowerby. Reworked. h. *Turritella communis* Risso. i-k. *Epitonium clathratulum* (Kanmacher). l. *Boreoscala greenlandica* (Perry).

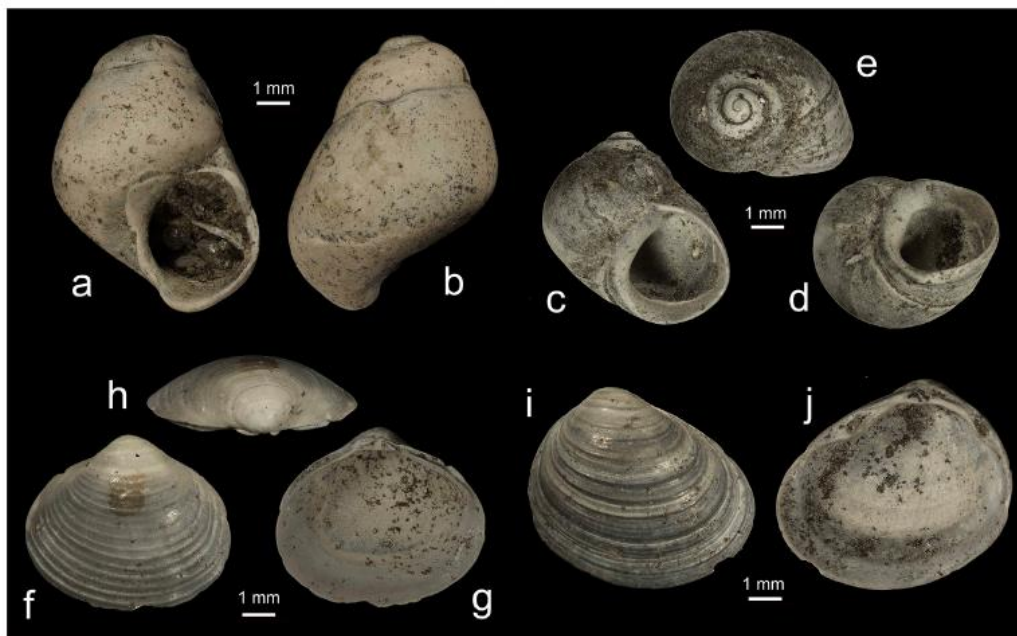


Fig. 8. Selected non-marine molluscs from the 'Weybourne Crag' at Sidestrand. a-b. *Viviparus glacialis* (Wood), juvenile. c-e. *Lithoglyphus jahni* Urbański. f-h. *Corbicula* sp., immature shell. i-j. *Pisidium clessini* Neumayr.

The molluscan assemblages from the ‘Weybourne Crag’ at Sidestrand comprise a mixture of ecologically incompatible species that cannot have formed a single living community. These shells must have accumulated from various sources but understanding the taphonomic processes involved in their accumulation presents a challenge. A few species, such as *Turritella incrassata* and *Euspira helicina hemiclausia*, are otherwise known only from older Pliocene sediments from which they must have been derived, a conclusion consistent with their poor preservation (Fig. 7g). Poor preservation, however, is not an infallible indication of derivation but it does give a general guide if an assessment is made of the whole assemblage (Supplementary data). The occurrence of bivalves with united valves in positions of life is critical in trying to establish the composition of the original living community. Reid (1890: 139) noted that between Cromer and West Runton, numerous specimens of *Mya arenaria*, *Macoma obliqua* and occasionally *M. balthica*, occurred in life-positions between the unworn flints of the stone-bed.

Despite variable preservation, the general condition of the shells at Sidestrand suggests that re-working from much older deposits (as with *T. incrassata*) has not been extensive. Several other extinct species are present including *Neptunea inversa* (Fig. 7e), *Acila cobboldiae* (Fig. 6e–f), *Macoma praetenuis* and *Yoldia oblongoides* (Fig. 6c–d), but these do not appear to have been derived. Most of the assemblage indicates intertidal or shallow subtidal soft-bottom environments but a few species (e.g. *Nucella lapillus* and *Littorina* spp.) prefer harder substrates. Reduced salinities can be inferred from the occurrence of euryhaline species characteristic of intertidal mudflats, such as *Peringia ulvae* and *Scrobicularia plana*. The extinct gastropod *Ellobium pyramidale* probably also belonged to this ecological group. *Mya arenaria* inhabits mud and muddy-sand in the intertidal zone, but can live at depths approaching 200 m. It can tolerate a wide range of salinities and temperatures and has high resistance to the presence of hydrogen sulphide (H₂S) and to oxygen deficiency (Strasser, 1999). *Macoma balthica*, another euryhaline bivalve, also lives in thick mud and muddy sand and gravel in shallow water, principally from the upper regions of the intertidal zone to low-water. It is the dominant species in the ‘Weybourne Crag’ (Table 2) but these specimens (Fig. 6h–i) are generally smaller and often have thicker shells than modern populations from the North Sea and they appear to have lived longer. Growth-bands indicate that the thicker-shell form lived for 11–24 years ($n = 18$), whereas the thin-shelled form appears to have lived for only 7–8 years ($n = 2$). Rib-counts in the cockle *Cerastoderma edule* can be used as an index of palaeochlorinity (Koulman and Wolff, 1977). In Sidestrand specimens the mean number of ribs was 22.4 ± 1.33 ($n = 30$),

which indicates a palaeochlorinity of ~13‰. This is low but similar to values from marine Tiglian deposits in the southern Netherlands, which had a reconstructed mean palaeochlorinity of ~14‰, ($n = 355$ from 21 sites; T. Meijer, unpublished data), compared with modern values from the Dutch coast of ~16‰ (Eisma, 1965; IDON, 2004).

Low temperatures are indicated by the occurrence of species with arctic circumpolar or northern modern ranges including *Amauropsis islandica* (Fig. 7f), *Solariella obscura* (Fig. 7a–c), *Boreoscala greenlandica* (Fig. 7l) and *Cryptonatica affinis*, which are confined to high latitudes today (Graham, 1988; Warén, 1993). The bivalves *Yoldia oblongoides* (Fig. 6c–d), *Ciliatocardium ciliatum*, *Astarte borealis*, *Macoma obliqua* (Fig. 6j–k), *Lucinoma borealis* (Fig. 6c–d) and *Mytilus trossulus* (Fig. 6g) would also belong in this category. Several other northern species are known from other ‘Weybourne Crag’ sites (Table 2). The assemblage therefore has a distinctly low arctic/high boreal character, a finding in keeping with earlier conclusions (Norton, 1967).

Both the coarse nature of the sediments and the composition of the contained molluscs indicate shallow-marine conditions. However, the new assemblages also include a few species, such as *Amauropsis islandica* (Fig. 7f) and *Epitonium clathratulum* (Fig. 7i–k), which do not live in intertidal environments but in much deeper water (>30 m). *Arctica islandica*, a bivalve that inhabits sublittoral sediments in water-depths reaching >450 m, is also common. Some mixing of different intertidal and deeper water habitats appears to have occurred but in high latitudes some typically ‘deep water’ species can live in much shallower water just below or even within the intertidal zone (Ocklemann, 1958). Such mixtures may therefore also point to cold surface water.

A more serious problem is the occurrence of some temperate non-marine shells. Their occurrence suggests deposition near the outflow of a relatively large stream or river, although such mixed assemblages may result from erosion in tidal channels and from bioturbation. Many of the freshwater species are fluvial, including *Pisidium amnicum* and *P. clessini* (Fig. 8i–j). However, given the thermophilous affinities of several of these species, such as *Corbiculasp.* (Fig. 8f–h), it is unlikely that they lived at precisely the same time as the low arctic/high boreal marine molluscan assemblages. However, *Corbicula* was also present in the Zuurland-2 borehole in levels containing *M. balthica* and other elements characteristic of the ‘Weybourne Crag’ (Meijer, 1988; see Fig. 9). One possibility is that these non-marine components (Fig. 8) have been re-worked from an earlier temperate period. However, the shells are reasonably well preserved and the fluvial species, which include *Viviparus*

glacialis (Fig. 8a–b) and *Lithoglyphus jahni* (Fig. 8c–e), are ecologically coherent and form part of a recognizable assemblage known from the Late Tiglian of The Netherlands (Meijer, 1988, 1990). *Borysthenia goldfussiana*, another extinct species, is also a component of this assemblage (see Fig. 9, Fig. 10), and is known from the ‘Weybourne Crag’ at Weybourne, East Runton and West Runton, although it still awaits discovery at Sidestrand. *Viviparus glacialis* is an extinct freshwater species known in England only from occasional shells from the ‘Weybourne Crag’ of Norfolk (East Runton and now Sidestrand) and from a few inland localities (Belaugh, Coltishall, Horstead and Rackheath). In The Netherlands, the only other country from which *V. glacialis* is known (Fig. 11 and Supplementary Table 2), it is far more common and occurs mainly in sediments of Praetiglian and Tiglian age (Meijer, 1990; Gittenberger et al., 1998). The co-occurrence of *V. glacialis*, *Macoma balthica* and *Mya arenaria* in the Late Tiglian (Fig. 11) has been used to correlate Early Pleistocene deposits across the North Sea basin (Gibbard et al., 1991).

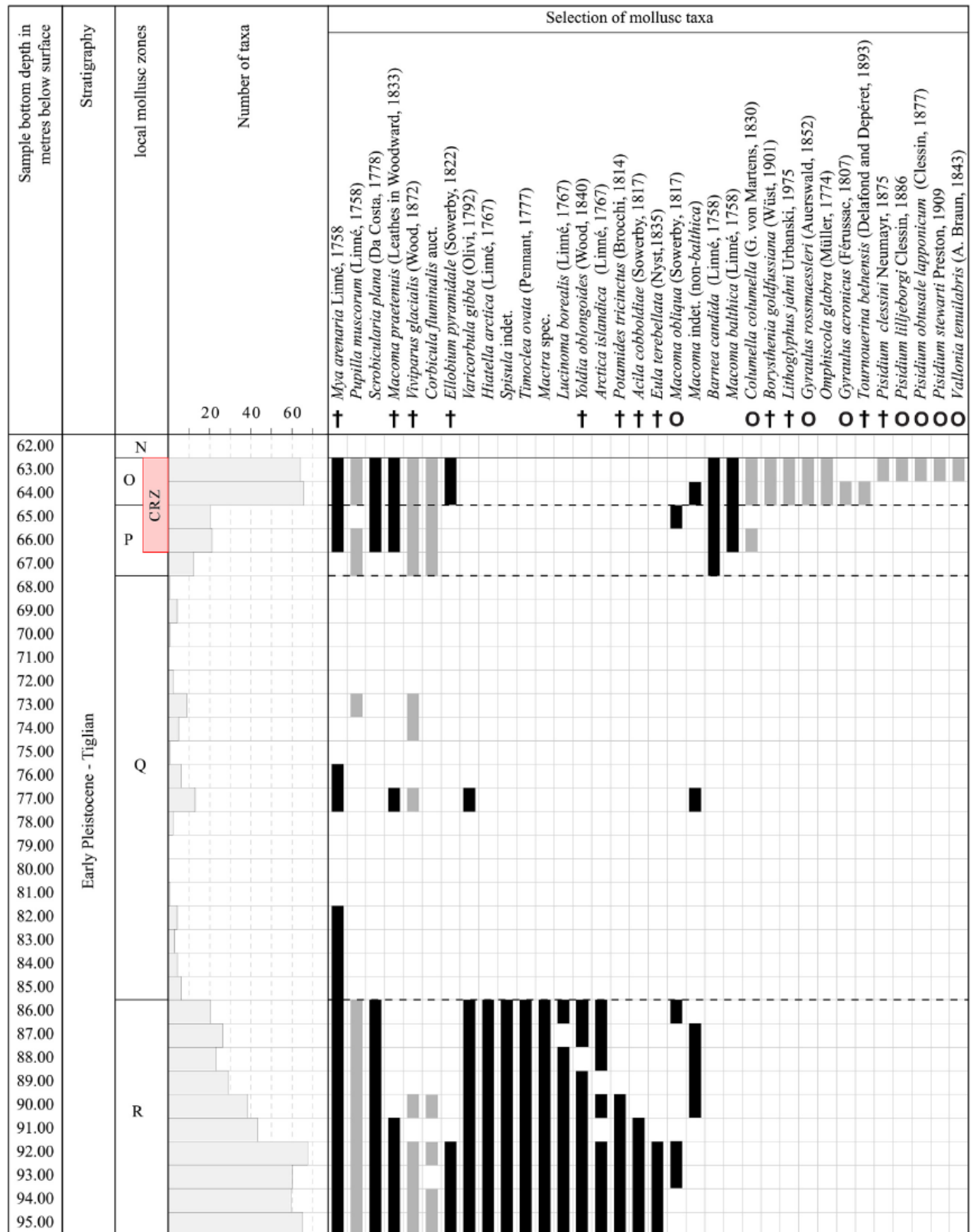


Fig. 9. Molluscan range chart for the Zuurland-2 borehole showing the occurrence of species between -62 m and -95 m (see Meijer (1988) for data from higher levels). The *Macoma balthica* – *Mya arenaria* Concurrent Range Zone (CRZ) is indicated. For details of other zones see text. † = extinct O = not living in or around the southern North Sea basin.

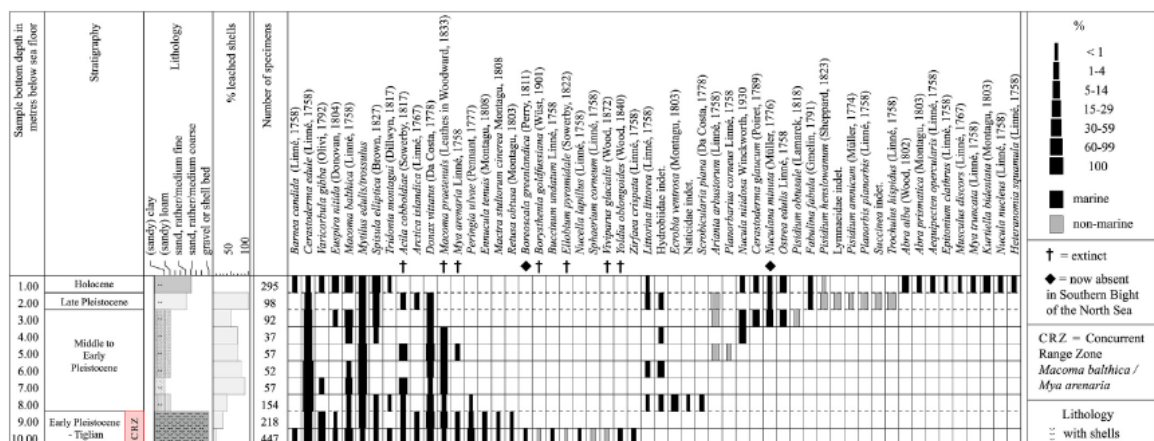


Fig. 10. Molluscan range chart for North Sea borehole BGS 52-02-472 showing a ‘Weybourne Crag’ assemblage at the base. The *Macoma balthica* – *Mya arenaria* Concurrent Range Zone (CRZ) is indicated.

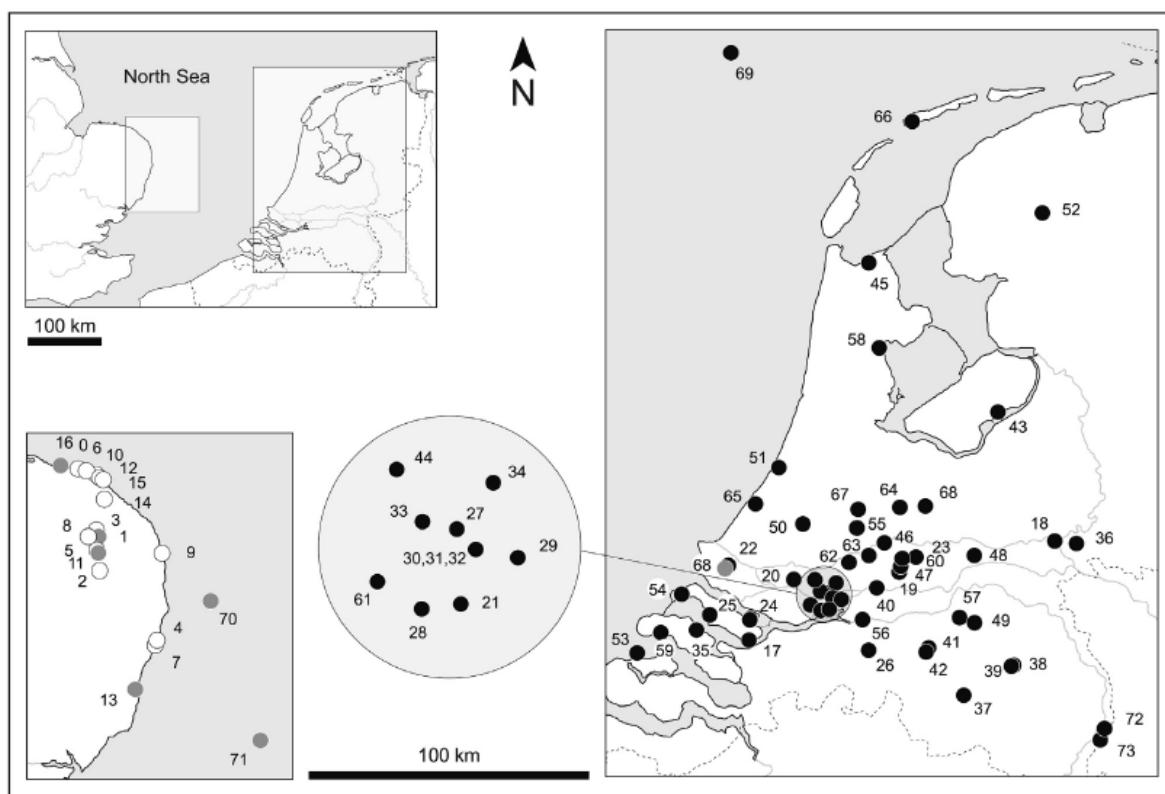


Fig. 11. Maps showing the occurrence of Early Pleistocene records of *Macoma balthica* and *Viviparus glacialis*. Open dots: *M. balthica* present, *V. glacialis* absent; Black dots: *V. glacialis* present, *M. balthica* absent; Grey dots: *V. glacialis* and *M. balthica* present. Zuurland-2 (site 68) is the only Dutch site where both these species co-occur; the other sites are either pre-Late Tiglian or else are exclusively non-marine. All British sites with *V. glacialis* also yield *M. balthica*. Supplementary Table 2 provides details of the sites.

4.2. Mollusca from horizons correlated with the ‘Weybourne Crag’

Similar molluscan assemblages to those of the ‘Weybourne Crag’ were recovered from the sediments dredged off Great Yarmouth, the basal levels of North Sea borehole BGS 52-02-472, the Zuurland-2 borehole (–62 m to –66 m), and also from the Swafeld borehole (25.9 m–26.3 m), although detailed information from this borehole is not available. There are also similarities with the molluscan assemblage from the Baventian clay at Covehithe, although *M. balthica* is conspicuously absent from that fauna (Table 2) consistent with an earlier age (West et al., 1980).

4.2.1. Yarmouth Roads Formation off Great Yarmouth (52° 30' N, 02° 00' E)

Samples of dredged material were collected from piles of dumped sediment awaiting processing by the Sorting Centre SVB (Vlissingen, The Netherlands). The samples included many species that occur in the ‘Weybourne Crag’, including *Macoma balthica*, *Mya arenaria* and *Viviparus glacialis* (Table 2). The last species was unusually common (Raad, 2008) but the samples had been picked by eye in the field rather than by sieving in the laboratory so the numbers in Table 2 are not comparable with those of the other samples. The specimens were slightly leached and had a bluish colour, reminiscent of the ‘Weybourne Crag’ (cf. Fig. 6, Fig. 7, Fig. 8).

4.2.2. North Sea borehole BGS 52-02-472 (52° 03' 00" N, 2° 16' 61" E)

The molluscan assemblages from this borehole (Fig. 10) indicate a sequence of Holocene sands overlying Middle to Early Pleistocene sediments (Sliggers, 1989). The lower 2 m are of particular interest since they contain *Macoma balthica*, *Mya arenaria* and *Viviparus glacialis* (Table 2).

4.2.3. Zuurland-2 borehole, The Netherlands (51° 53' 29" N, 4° 9' 39" E)

A series of local molluscan assemblage zones (A-O) has been previously been distinguished at Zuurland (Meijer, 1988). Here we extend this zonation scheme to include the interval between –63 m and –95 m, which has now been studied in outline (Fig. 9); detailed analysis awaits completion. Details of this extended zonation are as follows (including an overlap with zones N and O previously described):

Zone N: –60 m to –62 m. This is a quasi-sterile zone.

Zone O: –62 m to –64 m. This zone contains rich assemblages of marine and non-marine species in which temperate taxa dominate. It is characterized by *Viviparus glacialis*, *Borysthenia goldfussiana*, *Tournouerina belnensis*, *Ellobium pyramidale*, *Corbicula* sp., *Mya arenaria*, *Macoma balthica* and *Barnea candida*. *Macoma praetenuis* occurs in this zone but was not reported by Meijer (1988). In addition to these temperate species, several noteworthy high boreal to arctic non-marine species (*Columella columella*, *Vallonia tenuilabris*, *Pisidium stewarti* and *P. lilljeborgii*) also occur (Supplementary Table 1). The assemblages indicate a shallow-marine environment with a strong fluvial influence. The presence of cold-climate non-marine species may herald the colder conditions represented by the barren sediments between –60 and –62 m.

Zone P: –64 m to –67 m. This zone contains an impoverished subset of the species of Zone O but both temperate and cold-adapted species are already present. *Macoma balthica* appears.

Zone Q: –67 m to –85 m. Quasi-sterile zone with very few taxa occurring in low numbers.

Zone R: –85 m to –95 m. Marine assemblages of high diversity with few non-marine taxa. The diversity decreases toward the top of the zone. The assemblages are characterized by *Aequipecten opercularis*, *Arctica islandica*, *Lucinoma borealis*, *Timoclea ovata*, *Varicorbula gibba*, *Littorina littorea*, *Propebela turricula*, *Acteon* sp., *Epitonium clathratulum*, *Ptychopotamides tricinctus* and *Ringicula ventricosa*. These assemblages point to a deeper marine environment than those of the overlying deposits.

These sediments yielding zones R and Q belong to the Maassluis Formation and are Middle Tiglian, whereas zones P and O belong to the Waalre Formation and are assigned to the Late Tiglian. Besides these local assemblage zones, an additional *Macoma balthica*–*Mya arenaria* Concurrent Range Zone between –62 m and –66 m is proposed with this as the stratotype (see Appendix).

4.3. Mammal remains from the ‘Weybourne Crag’

The well-provenanced mammals from the ‘Weybourne Crag’ (Table 3 and Supplementary Table 3) enable correlation of marine and non-marine biostratigraphical schemes. The remains of large vertebrates are found regularly along the stretch of the Norfolk coast near Sidestrand (Lister, 1993, 1996, 1998) but only the following identifiable remains have been recovered *in situ* from the ‘Weybourne Crag’.

Taxa	1					5					9				
	Siderland Trimingham	Overstrand Ranton (East Ranton)	Sheringham	Weybourne	Bacton	Siderland Trimingham	Overstrand West Ranton, Site WRFO	West Ranton, Site WRF	West Ranton, Site WRAT	West Ranton East Ranton	Wivham	Croftville	North Sea borehole BGS 12-02-472, 8.10 m dissected off coast of Great Yarmouth	10	10
Polyplacophora															
<i>Chiton</i> sp.		2													
Marine gastropods															
○ <i>Auroroma candida</i> (Möller, 1842)												X			
○ <i>Admete viridula</i> (Fabricius, 1780)		1			x										
<i>Ananospis islandica</i> (Gmelin, 1791)		1	c	r	r	x	53				X	X	X		8
○ <i>Boreoscala groenlandica</i> (Perry, 1811)		c	vc	r	vr	x	69								152
○ <i>Boreoscala stans</i> (Sowerby, 1813)															1
<i>Boreostrophon clathratum</i> (Linnaeus, 1767)					x							X			
<i>Buccinum undatum</i> (Linnaeus, 1758)	r	r	vc	c	x	33						X	X		
○ <i>Cryptomica affinis</i> (Gmelin, 1791)					x	31									2
<i>Curatoma cf. trevelianae</i> (Turton, 1834)						31									X
<i>Ecrobia ventrosa</i> (Montagu, 1803)					x										
† <i>Elliptium pyramidalis</i> (Sowerby, 1822)					x	1									
<i>Epitonium clathratulum</i> (Kammacher, 1798)						1				X	X		X		
○ <i>Epitonium trevelianum</i> (Johnston, 1841)		2			x										
<i>Epitonium turtonis</i> (Turton, 1819)		2			x										
<i>Euspira catana</i> (da Costa, 1778)		2	vc	r	r	x									
† [<i>Euspira helicina hemiclausea</i> (J. de C. Sowerby, 1825)]						24									X
<i>Euspira cf. nitida</i> (Donovan, 1804)						6							X		X
<i>Euspira cf. pallida</i> (Broderick & Sowerby, 1829)															X
<i>Gibbula tunida</i> (Montagu, 1803) ?		3			x	X	346	X			X	X			156
<i>Littorina littorea</i> (Linnaeus, 1758)	vc	vc	vc	vc	vc	X					X	X			
<i>Littorina saxatilis</i> (Olivier, 1792)			r	r	r	x									
Naticidae (several sp.)						80									
<i>Neptunea antiqua</i> (Linnaeus, 1758)			vr	vr	x			X			X	X			X
† <i>Neptunea inversa</i> Harmer, 1918	r	r	vc	r	x	1					X				
<i>Neptunea</i> sp. indet. (dextral species)						2									2
<i>Nucella lapillus</i> (Linnaeus, 1758)	c	c	c	vc	vc	vc	X	X	X	X					134
<i>Peringia ulvae</i> (Pennant, 1777)					x	X	16	X	X	X			X		
<i>Propagella turriculata</i> (Montagu, 1803)	vr	c			x	18						X			X
○ <i>Propagella nobilis</i> (Möller, 1842)															X
<i>Propagella rufa</i> (Montagu, 1803)															X
<i>Raphitoma linearis</i> (Montagu, 1803)		2			x										2
<i>Rettus obtusa</i> (Montagu, 1803)		4				1							X		
<i>Rissoia parva</i> (Da Costa, 1778)					x				X						
○ <i>Solarisella obscura</i> (Couthouy, 1838)						19									
<i>Solarisella</i> sp.								X							
<i>Tectura virginea</i> (O.F. Müller, 1776)		1			x										
<i>Tornus subcarinatus</i> (Montagu, 1803)						X									
Turridae (several sp.)						9									X
<i>Turritella communis</i> Risso, 1826	vr	r			x	9									4
† <i>Turritella incrassata</i> Sowerby, 1814						3									
<i>Velutina velutina</i> (O.F. Müller, 1776)		1			x										
Marine bivalves															
† <i>Acanthocardia echinata</i> (Siggers)		3			x										
† <i>Acila cobboldiae</i> (Sowerby, 1817)	c	c	c	c	vc	x	X	182	X	X		X	X	X	3
<i>Aequipepon opercularis</i> (Linnaeus, 1758) ?		2				1			X						
<i>Arctica islandica</i> (Linnaeus, 1767)	vc	vc	c	vc	X	X	117	X	X	X		X	X	X	12
○ <i>Astarte borealis</i> (Schumacher, 1817)	vc	vc	vc	vc	vc	x	46				X	X			9
○ <i>Astarte subacutilatera</i> G.B. Sowerby II, 1854		1			x										
<i>Astarte elliptica</i> (Brown, 1827)															
○ <i>Astarte fusca</i> (Poli, 1791)		1													
<i>Astarte montagu</i> (Dillwyn, 1817)	vc	vc	vc	vc	c	X	x	X	305	X	X		X	X	16
<i>Astarte sulcata</i> (da Costa, 1778)	vc	vc	c	c	?	x			X						
<i>Barnea candida</i> (Linnaeus, 1758)						1									X
<i>Cerastoderma edule</i> (Linnaeus, 1758)	vc	c	vc	vc	vc	vc	X	x	X	319	X	X	X	X	16
<i>Ciliatocardium ciliatum</i> (Fabricius, 1780)						2									
<i>Donax vittatus</i> (Da Costa, 1778)						121			X	X		X	X	X	
<i>Emmella tenuis</i> (Montagu, 1808)															
<i>Fabulina fabula</i> (Gmelin, 1791)						2									
<i>Hiatella arctica</i> (Linnaeus, 1767)	r	c	r		x	27			X						
<i>Lacuna borealis</i> (Linnaeus, 1767)	c	c	r	r	2	x	90								
<i>Macoma balthica</i> (Linnaeus, 1758)	vc	vc	vc	vc	vc	X	x	X	1710	X	X	X	X	X	94
○ <i>Macoma balthica</i> (Linnaeus, 1758) small thick-shelled form	vc					25									
<i>Macoma calcarata</i> (Gmelin, 1791)	r	r	r		x										2
○ <i>Macoma obliqua</i> (Sowerby, 1817)	vc	vc	vc	vc	vc	vc	X	x	X	221	X	X	X	X	2
† <i>Macoma praetensis</i> (Leathes in Woodward, 1833)		2			x										148
<i>Macoma stultorum</i> (Linnaeus, 1758)		1			x	12									
○ <i>Macromeris polymya</i> (Stimpson, 1860)					X										
<i>Modiolus modiolus</i> (Linnaeus, 1758)						3									
<i>Mya arenaria</i> Linnaeus, 1758	c	vc	c	vc	vc	vc	X	x	X	52	X	X	X	X	19
<i>Mya truncata</i> Linnaeus, 1758	c	c	r	vr	x	36									
<i>Mytilus undata</i> (Pennant, 1777)						1									
<i>Mytilus edulis</i> (Linnaeus, 1758)	c	r	c	vc	r	r	x	X	776	X	X	X	X	X	1
○ <i>Mytilus cf. trossulus</i> Gould, 1850						5									
<i>Polistaptes rhomboides</i> (Pennant, 1777)															1
<i>Scrobicularia plana</i> (Da Costa, 1778)						13					X				2
○ <i>Serripes groenlandicus</i> (Möller, 1786)	vr	?			x										
† <i>Spionidius</i> sp.															
<i>Sphenia binghami</i> Turton, 1822															
<i>Spisula elliptica</i> (Brown, 1827)	c	c	c	vr	x	339									
<i>Spisula subtruncata</i> (Da Costa, 1778)									X						
<i>Spisula</i> sp.															
<i>Thracia phaeocolina</i> (Lamarck, 1818)															
<i>Thracia ovata</i> (Pennant, 1777)															
<i>Parvicardula gibba</i> (Olivier, 1792)	l	c	c	c	r	x	X	265	X	X	X		X	X	
<i>Venerupis decussata</i> (Linnaeus, 1758)															
† <i>Yoldia oblongoides</i> (Wood, 1840)	c	c	c	vc	r	c	x	X	496						
<i>Zidfaea crispata</i> (Linnaeus, 1758)															1
Non-marine gastropods															
<i>Antissa leucostoma</i> (Millet, 1813)						1									
<i>Arianta arbustorum</i> (Linnaeus, 1758)						4									
† <i>Borythania goldfussiana</i> (Wüst, 1901)										X	X	X		X	
† <i>Lithoglyphus jahnii</i> Urbanski, 1975						2									
<i>Oxytoma elegans</i> (Risso, 1826)						1									
<i>Planorbis planorbis</i> (Linnaeus, 1758)															
<i>Planorbis planorbis</i> (Linnaeus, 1758)						1									
<i>Papilla muscorum</i> (Linnaeus, 1758)															
<i>Succinea palustris</i> (O.F. Müller, 1774) s.l.						1									
<i>Succinea oblonga</i> (Draparnaud, 1801)															
<i>Trochulus hispidus</i> (Linnaeus, 1758)						4									
<i>Valvata piscinalis</i> (O.F. Müller, 1774)						1									
† <i>Viviparus glacialis</i> (Wood, 1872)						2									
† <i>Viviparus cf. medius</i> (S. Woodward, 1833)															
† <i>Viviparus viviparus gibbus</i> (Sandberger, 1880)															
Non-marine bivalves															
<i>Corbicula</i> sp.						3									
<i>Pisidium amicum</i> (O.F. Müller, 1774)						2									
† <i>Pisidium clesini</i> Neumayr, 1875						1									
<i>Sphaerium cornum</i> (Linnaeus, 1758)															

Table 3. Revised list of Mollusca from critical ‘Weybourne Crag’ sites and from other sites discussed. Sources: 1. Reid (1882), 1890; 2. Harmer (1905), 1914; 3. Norton (1967); 4. This paper; 5. Norton in West (1980); 6. Gibbard et al. (1991); 7. Cambridge (1978); 8. West et al. (1980), Long (2000); 9 and 10. This paper. Key: (†) extinct; (?) possibly extinct; O – not living in the southern North Sea. Frequency estimates from Reid (1890): vr = very rare; r = rare; c = common; vc = very common; X = present. Species in square brackets are probably derived. Data from the Zuurland-2 borehole are given in Supplementary Table 1.

The beaver-like rodent *Trogontherium* is represented by two mandibles from RG and a maxilla from LG. These are important additions to the Early Pleistocene record of *Trogontherium*, which in Britain is otherwise only known as *ex situ* finds from other sites at Sidestrand and nearby coastal localities (Mayhew, 1978).

An incomplete antler of the comb-antlered deer *Eucladoceros tetraceros* (Fig. 12a) was excavated from the shelly sand at locality RG. This specimen appears to represent the earliest known occurrence of this species, which is known principally from its type locality at Peyrolles, France (~1.46–1.47 Ma, according to Nomade et al., 2014, 2014b) and as *ex situ* finds from coastal sites in Norfolk. A second species of *Eucladoceros* tentatively referred to *sedgwicki* is represented by a broad and flattened antler tine very different from that of *E. tetraceros*. It was found in the ‘Weybourne Crag’ overlying a Chalk raft at Sidestrand (J. Andrews coll.).

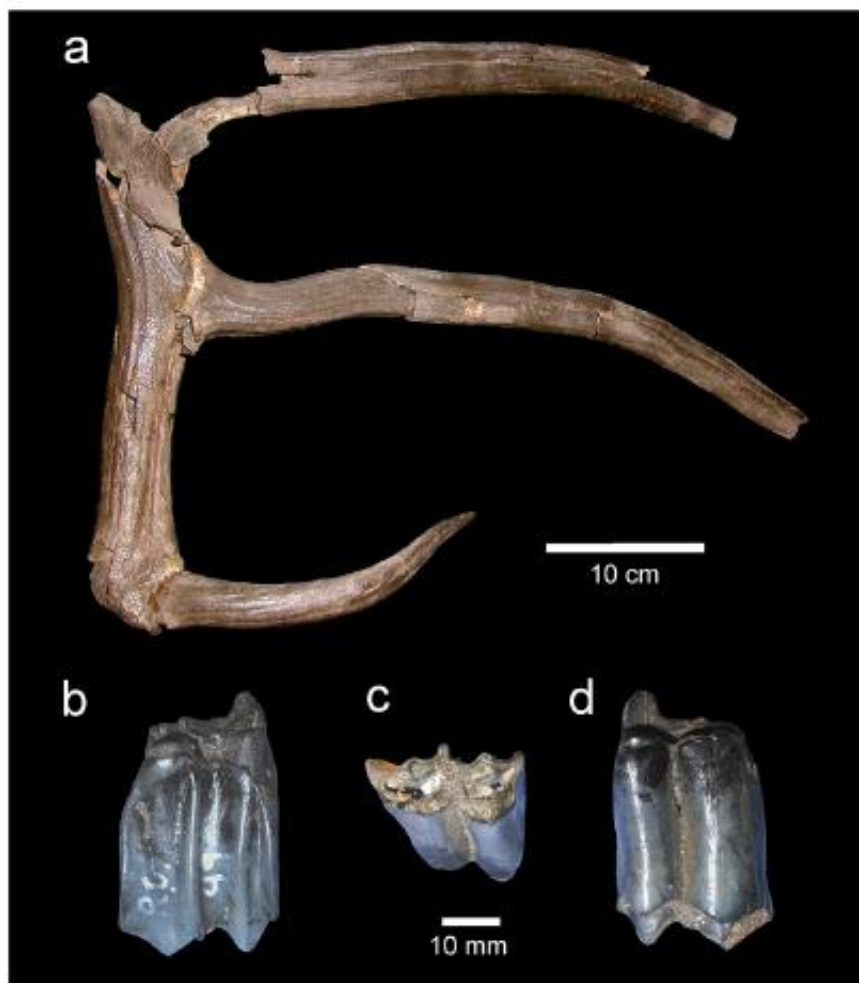


Fig. 12. Selected large mammals from the ‘Weybourne Crag’ at Sidestrand. a. *Eucladoceros tetraceros* Kunst, antler. b-d. Ovibovini, ?*Pliotragus* or *Megalovis* sp., upper molar.

An ovibovine is represented by an upper molar from Sidestrand (RG). This could be *Pliotragus* or *Megalovis* sp. (see Supplementary data for discussion on the nomenclature) or *Caprovis savinii*, originally described by Newton (1882: 49, pl. 10) from a single horn-core from Overstrand. The biological affinity of this taxon is obscure and it is unknown on the continent, but de Wilde (2006) reported a number of horn-cores that he assigned to this species dredged from the Early Pleistocene sediments off Great Yarmouth (Section 3.1.7).

A few other large mammals have been recovered from *in situ* ‘Weybourne Crag’ at other sites. Azzaroli (1953) mentioned a lower jaw of the elk *Cervalces gallicus* that was said to have been extracted from “shelly crag directly overlying the stone bed” at East Runton and West (1980: 27 and section Fig. 11) found a left lower M2 of *Mammuthus meridionalis* in his section BN cemented between the Stone Bed and ‘Weybourne Crag’ at West Runton. Material in private collections from Weybourne includes molars of *Mammuthus meridionalis* and antlers of *Eucladoceros* cf. *tetraceros* (Cruickshank collection, Reydon, Suffolk).

The R. Green collection from Sidestrand contains remains of marine and freshwater fish, and small mammals, with about 250 arvicolid remains identifiable to species (Supplementary Table 3). The teeth are mineralized and in some cases rolled and polished (Fig. 13). Additional material seen from Sidestrand (Supplementary Table 3) included the specimens figured in Mayhew and Stuart (1986), and specimens from the Harrison collection (see Harrison et al., 1988a, Harrison et al., 1988).

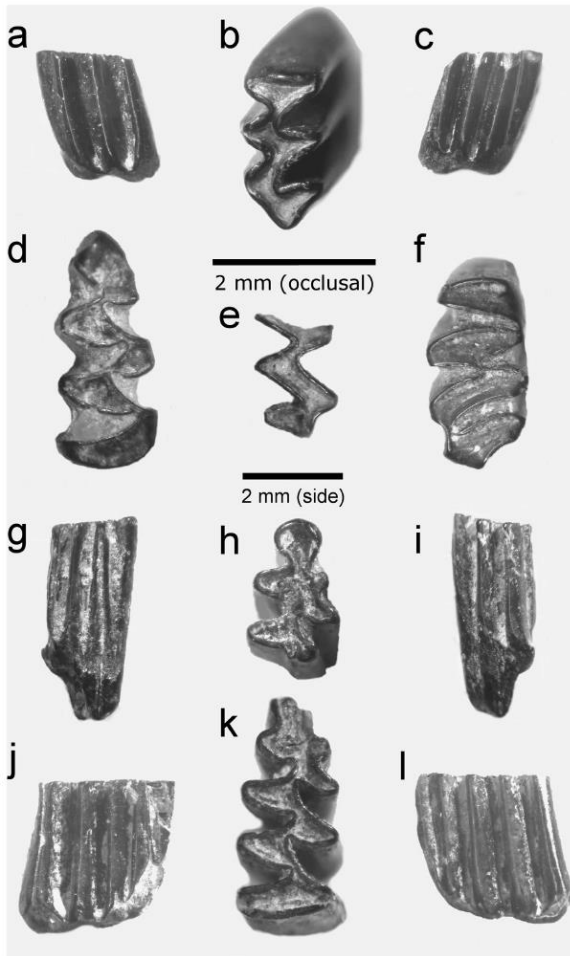


Fig. 13. Selected vole teeth from the ‘Weybourne Crag’ at Sidestrand. a-c M1 *Ungaromys dehmi* Carls and Rabeder; d. m1 *Lemmus kowalskii* Carls and Rabeder; e. M2 *Pitymimomys pitymyoides* (Jánossy and van der Meulen); f. M3 *Lemmus kowalskii* Carls and Rabeder; g-i. m1 anterior loop *Mimomys hordijki* van Kolfschoten and Tesakov; j-l. m1 *Mimomys hordijki* van Kolfschoten and Tesakov. Scale bars for side and wear surface views = 2 mm.

The arvicolids are assigned to *Mimomys pliocaenicus*, *M. reidi*, *M. hordijki*, *M. tigliensis*, *Pitymimomys pitymyoides*, *Borsodia newtoni*, *Clethrionomys kretzoi*, *Ungaromys dehmi*, *Lemmus kowalskii* (Fig. 13). Several of these species are indicative of open and/or steppic environments. The taphonomy clearly indicates fluvial transport into a shallow-marine environment, but the assemblage does not contain species indicating derivation from different biozones. Indeed, it is a typical assemblage found at other ‘Weybourne Crag’ sites in Britain (Table 3) and at localities in Europe assigned to arvicolid biozone MNR1 (=MN17, Middle Villafranchian). This attribution is based on the presence of *M. pliocaenicus* rather than the precursor *M. praepliocaenicus*, the presence of *M. hordijki*, *P. pitymyoides*, and *B. newtoni* (rather than the precursor *B. praehungarica*). Supplementary Fig. 1 shows the

context of the assemblage at Sidestrand, and some other British and Dutch localities, in relation to the East European arvicolid biostratigraphy (Tesakov, 2004).

Arvicolid biozone MNR1 spans several cold and temperate stages between 2.1 and 2.2 Ma and therefore might exhibit faunal and morphometric variations reflecting these different conditions. Assemblages from Tegelen, for example, indicate temperate conditions whereas those from the ‘Weybourne Crag’ sites are characteristic of steppic and arctic environments. The question then arises whether all the cold assemblages assigned to MNR1 are exactly contemporaneous. The progressive and marked increase in molar crown-height in Early Pleistocene arvicolids, particularly in the *Mimomys pliocaenicus* lineage, provide a means of testing the stratigraphical relations between putative ‘Weybourne Crag’ sites. Diagnostic measurements of molar teeth (Supplementary Tables 4 and 5) used to assess crown-height include the hypsodonty index, the length of the hyposinulid, the height of the enamel-free area in the upper third molar (M3) and the disappearance of enamel islets in the lower first molar in relation to crown-height. Fig. 14a compares the timing of the disappearance of enamel islets in the lower first molar of *M. praepliocaenicus* and *M. pliocaenicus* at various localities. This shows a clear distinction between *M. praepliocaenicus* from Bramerton and Thorpe (near Norwich), both therefore belonging to biozone MNR2, and *M. pliocaenicus* from MNR1 (‘Weybourne Crag’ sites and Dutch localities). Moreover, the data also show considerable variation between assemblages within MNR1, Sidestrand samples, for example, are significantly higher-crowned than those from the ‘Weybourne Crag’ at West Runton. This pattern is also reflected in the M3 with Sidestrand appearing to indicate a high-crowned, ‘advanced’ assemblage (Fig. 14b). This complexity suggests that although the ‘Weybourne Crag’ sites are close in age, they may not be precisely contemporary.

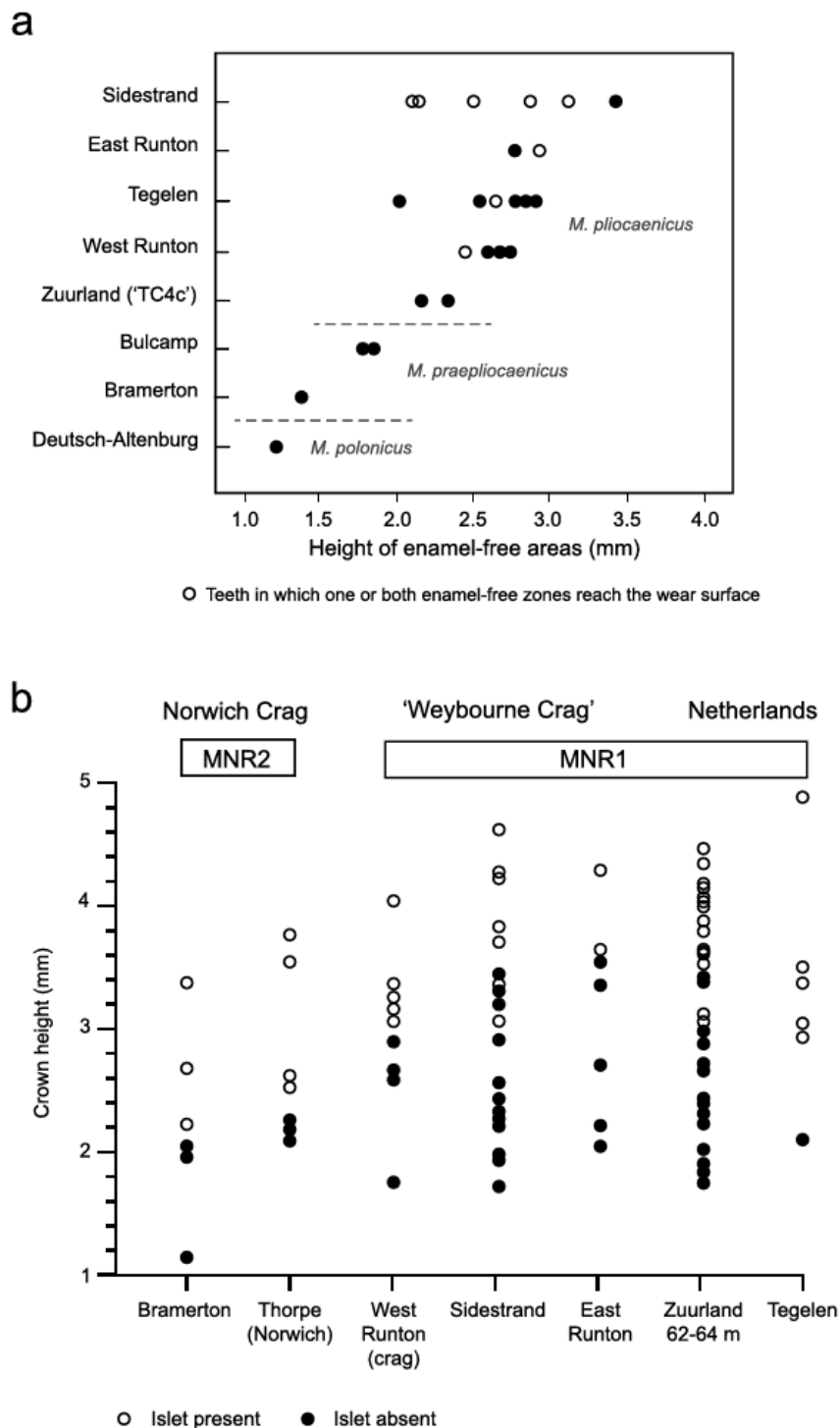


Fig. 14. a. Height of enamel-free area in the upper third molars of *Mimomys polonicus*, *M. praepliocaenicus* and *M. pliocaenicus* at various localities (Mayhew, 1990, Fig. 1, Fig. 2). b. Comparison of the timing of the disappearance of enamel islets in the lower first molar (m1) of *M. praepliocaenicus* and *M. pliocaenicus* at various localities. There is a clear distinction between *M. praepliocaenicus* from Bramerton and Thorpe (near Norwich), both therefore belonging to biozone MNR2, and *M. pliocaenicus* from MNR1 ('Weybourne Crag' sites and Dutch localities). The data also show considerable variation between assemblages within MNR1, suggesting that although close in age, the sites may not be exactly contemporary.

4.4. Amino acid dating

To test the correlations between the critical sequences, amino acid dating was undertaken from eleven Early Pleistocene sites, and one dating from the early Middle Pleistocene. These included one site from the Red Crag Formation (Neutral Farm, Butley), three from the Norwich Crag Formation (Thorpe Aldringham and Blake's Pit, Bramerton (Bramertonian temperate stage; Norwich Crag), a Baventian cold stage sequence at Covehithe), and three from the 'Weybourne Crag' (Sidestrand, Weybourne, East Runton), as well as three other sites correlated with this horizon (Great Yarmouth, Tegelen (type Tiglian), and -63 to -65 m in the Zuurland-2 borehole). In order to provide some additional points of reference, the type site of the late Early Pleistocene Bavel interglacial was also included, as was the early Middle Pleistocene 'Mya bed' immediately overlying the type Cromerian West Runton Freshwater Bed (WRFB).

The *Bithynia* opercula samples from Zuurland-2 (-63 m to -65 m) show high levels of intracrystalline protein decomposition (IcPD), with all samples indicating a pre-Bavelian age, as expected (Fig. 15, Supplementary Table 6). Valine is the most useful indicator for samples of this age, as it is a slow racemiser, although Ala and Glx also gave the same result. Opercula of both *B. tentaculata* and *B. Troschelii* were analysed from Weybourne but the data from the two species did not cluster tightly. Data from the single *tentaculata* from Weybourne plotted close to the Val D/L values obtained from *B. troschelii* at Tegelen (type Tiglian), whereas data from the two *troschelii* opercula plotted with the cluster from -63 m to -65 m in the Zuurland-2 borehole (Fig. 15). In previous studies on late Middle Pleistocene opercula of *Bithynia*, little difference in the rate of racemization was found to exist between these species (Penkman et al., 2013), so the differences observed in the 'Weybourne Crag' samples were unexpected. However, in this situation, where re-working has occurred (i.e. terrestrial material into a marine deposit), our approach has been to assume that the youngest values are a better reflection of the true age. We therefore conclude that the *Bithynia* opercula from the 'Weybourne Crag' at its type site are the same age as those from -63 m to -65 m in the Zuurland-2 borehole, whereas those from Tegelen appear to be slightly older. The IcPD data from *Bithynia* opercula (species undetermined) from the Norwich Crag at Thorpe Aldringham demonstrate an age older than those from Weybourne, Zuurland-2 (-63 m to -65 m) and Tegelen, whereas the data based on *B. bavelensis*, an extinct species known only from the Bavel interglacial at its type site, indicate its much younger age; the IcPD from both these sites are therefore consistent with the current stratigraphical interpretation.

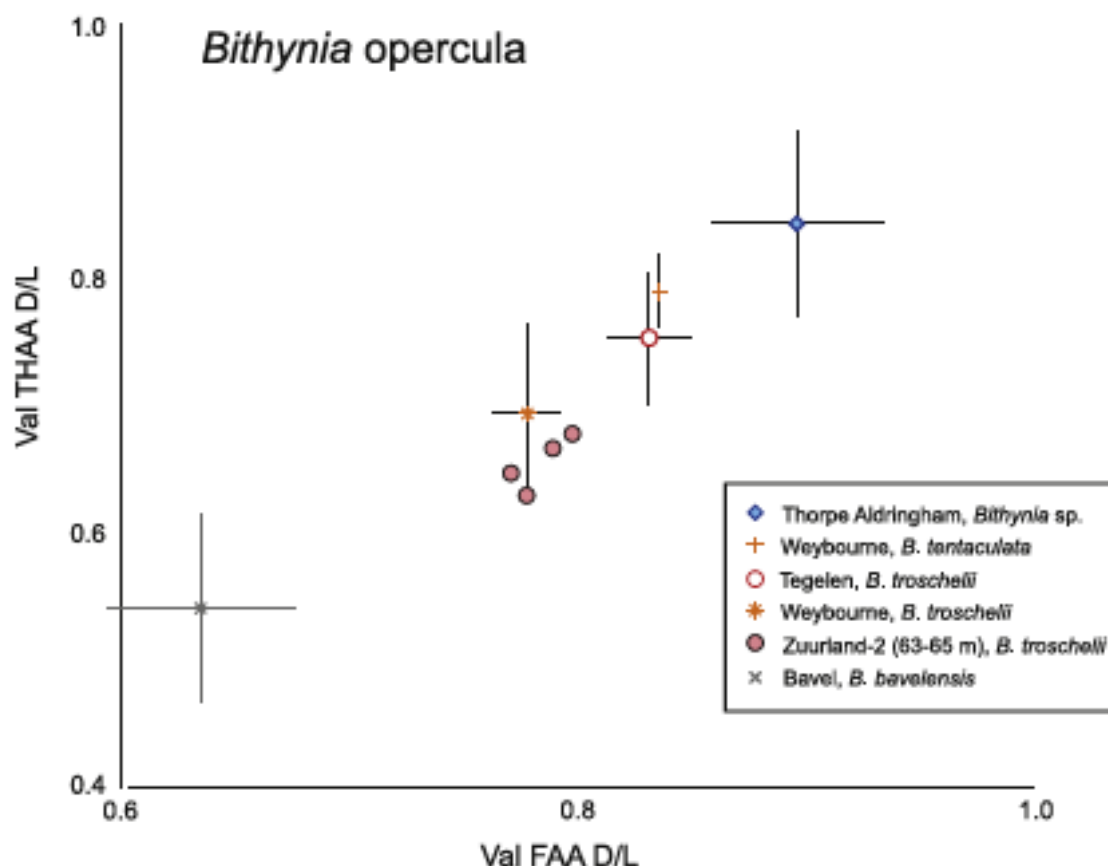


Fig. 15. Intra-crystalline free amino acid (FAA) vs total hydrolysable amino acid (THAA) D/L for valine in *Bithynia opercula* from Zuurland-2 (–63 m to –65 m), plotted with comparable data from the Bavel interglacial (~1.1 Ma) at Bavel, Weybourne (‘Weybourne Crag’), Tegelen and Thorpe Aldringham (Norwich Crag).

The mineral component of the shells of the marine Dog-whelk *Nucella lapillus* consists predominantly of calcite, although aragonite occurs in the apical and apertural regions and in the inner homogeneous layer of the shell (Demarchi et al., 2014). This predominantly calcite mineralogy offers an advantage for amino acid studies, as it is less subject to mineral diagenesis compared to shells composed entirely of aragonite (Penkman et al., 2007, 2010), and is therefore more likely to maintain the closed system of intra-crystalline protein. This is borne out in the emerging dataset now available for *Nucella lapillus*, which appears to provide a coherent aminostratigraphic framework (Demarchi, 2009; Davies et al., 2009). Consequently, shells of this species were analysed from critical horizons in the British sequence, but the comparison could not be extended to most of the Dutch sites because of their non-marine character.

IcPD data from *Nucella lapillus* (Fig. 16, Supplementary Table 6) show a clear separation of the sites belonging to the Red Crag (oldest), Norwich Crag, and ‘Weybourne Crag’ (youngest). Comparable data from the Baventian site at Covehithe, that lacks *M. balthica*, are similar to those from Bramerton (Norwich Crag) but they are slightly lower, consistent with a slightly younger age. The data therefore do not support the correlation of the Baventian with the ‘Pre-Pastonian a’ (‘Weybourne Crag’). The *Nucella* data show significant differences between Sidestrand and Bramerton for THAA D/Ls for Ala, Val and Glx (Bonferroni-Holm posthoc test, although the equal variance test was passed for Ala only). FAA vs THAA plots for Glx and Val (Fig. 16b) reinforce this, with D/L values from Sidestrand consistently lower than those from Bramerton, although much higher than those from the ‘Mya bed’ at West Runton. Ser D/Ls and [Ser]/[Ala] values provided limited resolution for *Nucella* shells of these ages and are therefore not reported.

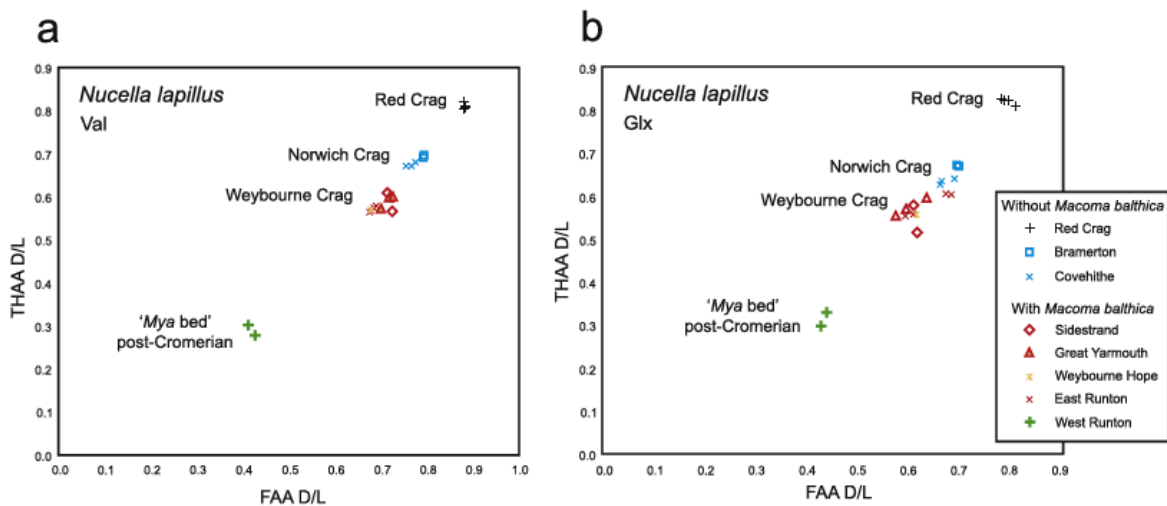


Fig. 16. Amino acid data from the shells of *Nucella lapillus* from various sites studied here. a. Intra-crystalline free amino acid (FAA) vs total hydrolysable amino acid (THAA) D/L for valine. b. Intra-crystalline free amino acid (FAA) vs total hydrolysable amino acid (THAA) D/L for glutamic acid.

The *Nucella* D/L values for valine are remarkably similar from all the putative ‘Weybourne Crag’ sites analysed (Sidestrand, Weybourne, East Runton and Great Yarmouth), indicating that they are very similar in age (Supplementary Table 6). They form a distinct group that is clearly separable from Bramerton and Covehithe, sites without *M. balthica*, which are clearly older. For all the amino acids analysed, the samples from the Early Pleistocene sites lacking *M. balthica* are always more degraded than those with *M. balthica* (Fig. 17). This supports the hypothesis that the ‘Weybourne Crag’ is stratigraphically younger than the Norwich Crag, rather than just a facies of it.

Nucella lapillus

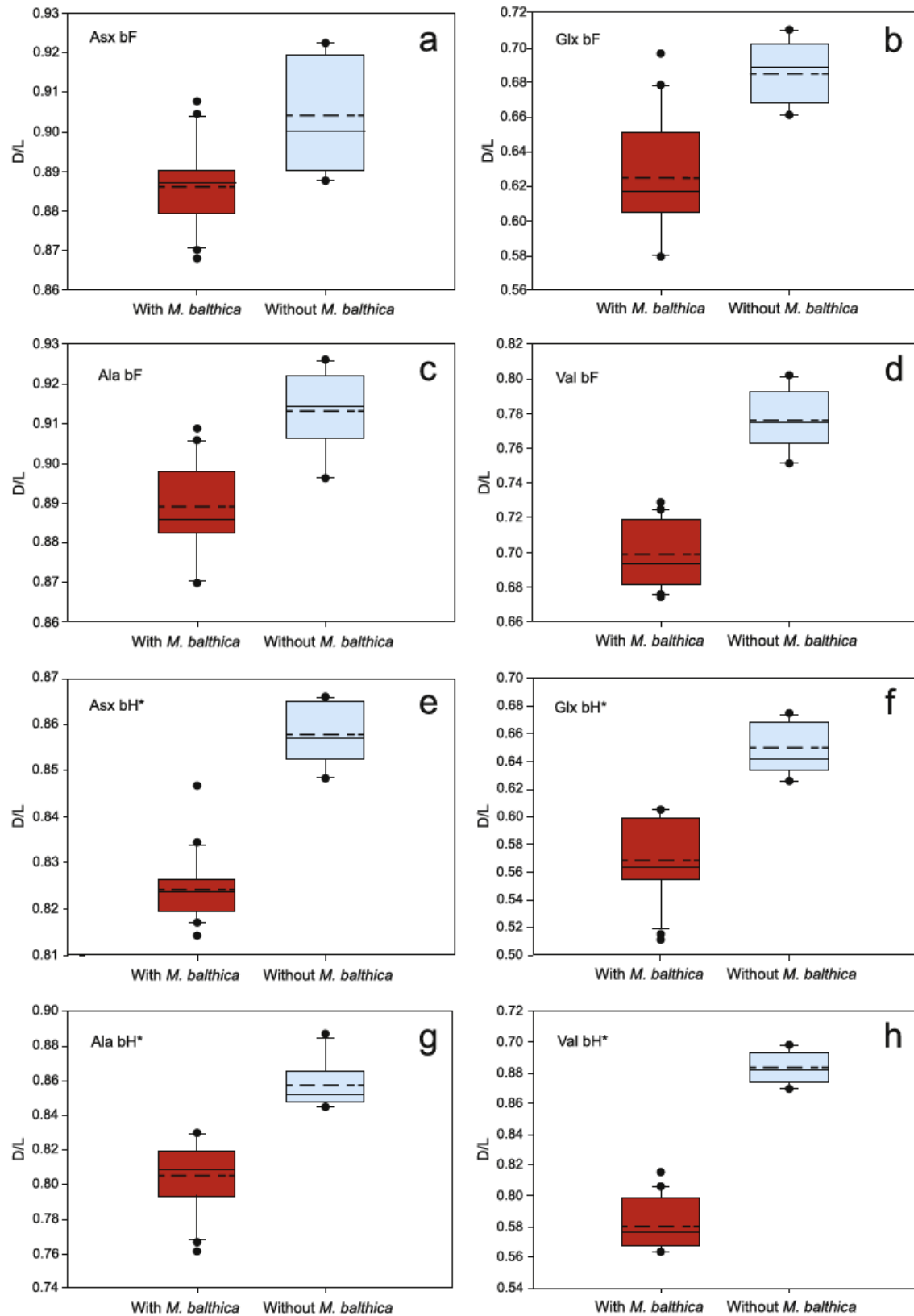


Fig. 17. Comparisons of amino acid data from the shells of *Nucella lapillus* from assemblages with (Sidestrand, Weybourne Hope, East Runton) and without (Bramerton, Covehithe) *Macoma balthica*. a-d. D/L values of Asx, Glx, Ala, Val for the free amino acid

(FAA; F) fraction. e-h. D/L values of Asx, Glx, Ala, Val for the total hydrolysable amino acid (THAA; H) fraction. For each group, the base of the box indicates the 25th percentile. Within the box, the solid line plots the median and the dashed line shows the mean. The top of the box indicates the 75th percentile. Where more than nine data points are available, the 10th and 90th percentiles can be calculated (shown by lines below and above the boxes respectively). The results of each duplicate analysis are included in order to provide a statistically significant sample size. Note different scales on the y-axes.

The precise age of the ‘*Mya* bed’ that directly overlies the WRFB at West Runton is uncertain. West (1980) believed that it formed part of the type Cromerian succession but the marine molluscs from it, including *Yoldia* (= *Leda*) *myalis*, are cold-water species, suggesting attribution to a subsequent cold stage (Preece, 2001). More data from other British early Middle Pleistocene sites with *Nucella* are needed to enable critical comparisons with the British aminostratigraphy based on *Bithynia* opercula.

5. Discussion: significance of the ‘Weybourne Crag’ for the European Early Pleistocene

The ‘Weybourne Crag’ is an important marker horizon in the southern North Sea basin that allows linkage between marine and terrestrial Early Pleistocene sequences across the North Sea. Below we discuss its depositional environment, its palaeontology, including the definition of the *Macoma balthica* – *Mya arenaria* Concurrent Range Zone, its correlation with the East European mammal zonation and the implications arising from its revised age.

5.1. Palaeoenvironment of the ‘Weybourne Crag’

The molluscan assemblages from the ‘Weybourne Crag’, and marine horizons in the southern North Sea correlated with it, consist mostly of marine molluscs that indicate high boreal/low arctic conditions predominantly of shallow-water with reduced salinities. A range of soft-bottom intertidal habitats are represented, including mudflats, but harder substrates were also present. Species from deeper subtidal marine habitats are also known from several sites. The occurrence of non-marine components (molluscs and vertebrates) at low frequency at several sites suggests deposition close to the outflows of rivers. At Zuurland (Zone O), these non-marine elements included several arctic molluscs but other species (e.g. *Corbicula* sp.) occurred suggestive of much warmer conditions (Meijer and Preece, 2000). *Corbicula*, for example, is known from the ‘Weybourne Crag’ at Sidestrand and East Runton, and occurred both in the sediment dredged off Great Yarmouth and in Zone O in the Zuurland-2 borehole. Foraminiferal assemblages from Sidestrand analysed by Funnell (1961, 1970) were impoverished, dominated by *Elphidiella hannai*, and contained only cold-tolerant species.

Pollen assemblages from ‘Weybourne Crag’ sites indicate open environments (West, 1980: Table 15), a conclusion supported by the mammalian and terrestrial molluscan fauna. Additional evidence for the severity of the prevailing climate is provided by penecontemporaneous ice-wedge casts in East Anglia (Funnell and West, 1962) and The Netherlands (de Mulder et al., 2003) and seismic reflection data indicating that ice sheets and icebergs repeatedly entered the North Sea, south of 60°N, from 2.53 Ma ago (Rea et al., 2018).

5.2. Arrival of *M. balthica* and definition of the *Macoma balthica* – *Mya arenaria* concurrent range zone

The opening of the Bering Strait between Alaska and Siberia towards the end of the Miocene at 5.32 Ma provided an opportunity for cool-temperate and polar marine species to move between the North Pacific and Arctic-Atlantic basins (Gladenkov et al., 2002). These movements were highly asymmetrical, Vermeij (1991) estimating that of 295 molluscan species that participated in trans-arctic migrations, 261 were of Pacific origin, whereas only 34 were of Arctic-Atlantic origin. Vermeij (1991) analysed the dynamics of this biotic exchange and provided a full list of these taxa, together with details of their geological occurrence in different regions. Many of the species encountered in the Early Pleistocene Crags of East Anglia had Pacific origins, including *Mya arenaria*, *Macoma balthica* and *Littorina* spp. *Mya arenaria* originated in the Pacific during the Miocene and dispersed into the Atlantic either through the Panamanian region (before the isthmus formed) or via a route across the Arctic once the Bering Strait had opened (Strasser, 1999). In the North Sea basin it occurred from the Late Pliocene to the Early Pleistocene, after which it became extinct in this region. Modern populations of this species in the eastern Atlantic appear to have arisen from re-introduction, possibly by the Vikings (Petersen et al., 1992). Recent molecular phylogenetic studies suggest that *M. balthica* (which may be a species complex) spread from the Pacific in a series of trans-arctic migrations to reach the North Sea and north-east Atlantic coasts during the Early Pleistocene (Väinölä, 2003; Nikula et al., 2007). The occurrence of *M. balthica* at Kap Kopenhagen in northern Greenland at ~2.4 Ma (Símonarson et al., 1998) is consistent with this suggestion, although the dating is uncertain.

There is ecophenotypic variation in the shape of *M. balthica* shells in modern populations, leading Riches (2010) to query the species definition used to distinguish crag fossils. While a detailed morphometric study of fossil samples would be worthwhile, we feel that his conclusion that the current palaeontological definition of *M. balthica* should not be relied on

as the basis for a First Appearance Datum (FAD) in the southern North Sea basin is unduly pessimistic. The present populations of *M. balthica* that inhabit the North Sea may well be genetically distinct from those that occurred there during the Early Pleistocene and indeed there are suggestions that different populations may even be represented within these (see earlier comments). However, this does not alter the fact that the arrival of this taxon in the fossil record is marked and can be recognized throughout much of the basin (Fig. 5). In our view the FAD of *M. balthica* remains an important biostratigraphical marker horizon (Spaink and Norton, 1967; Norton and Spaink, 1973). This species is absent from older crag deposits and is one of the characteristic fossils of the 'Weybourne Crag' in which it first occurs, often in considerable abundance. *Littorina saxatilis*, again absent from the Norwich Crag, also appears for the first time in the 'Weybourne Crag'. Most of the 'Weybourne Crag' records of *M. balthica* are from coastal sites in Norfolk (Fig. 11) but it occurred with other characteristic 'Weybourne Crag' species in the Swafeld borehole in levels (25.9–26.3 m) above those yielding typical 'Norwich Crag' molluscan assemblages (27.4–29.3 m) in which it did not occur (Norton, 2000). In The Netherlands, this species is absent from most of the Maassluis Formation (equivalent to the Norwich Crag Formation) assigned to the Middle Tiglian and occurs for the first time during the Late Tiglian when it became abundant (Meijer, 1988, 1993). This is clearly seen in the Zuurland-2 borehole where fossiliferous marine sediments lacking *M. balthica* below 75 m have been assigned to the Middle Tiglian but those above 66 m (–66 m to –75 m are unfossiliferous) contain *M. balthica* and have been attributed to the Late Tiglian (Meijer, 1988, Fig. 9).

A number of species occur throughout the Middle Tiglian but have their Last Appearance Datum (LAD) in the Late Tiglian (Meijer, 1988). Of these, *Mya arenaria* and *Viviparus glacialis* are the most relevant. Indeed, the co-occurrence of the freshwater gastropod *V. glacialis* with the marine bivalve *M. balthica* was a critical element in the correlation of the 'Weybourne Crag' ('Pre-Pastonian a') of East Anglia with the Late Tiglian of The Netherlands (Gibbard et al., 1991). However, in The Netherlands this co-occurrence was previously only known from the Zuurland-2 borehole, so the association of these critical species, together with *M. arenaria* in North Sea borehole BGS 52-02-472 (Fig. 10), is important. All of the other Dutch Late Tiglian localities with *V. glacialis* (Fig. 11) are fluvial with no marine influence. The co-occurrence of these two marine bivalves (with *V. glacialis*) in Early Pleistocene sequences has been recognized at sites on both sides of the North Sea basin, prompting us to define the *Macoma balthica* – *Mya arenaria* Concurrent Range Zone (see Appendix).

5.3. Link to the East European mammal zonation

The small mammal assemblages from Sidestrand, East Runton and Weybourne clearly belong to the *Borsodia newtoni* – *Mimomys pliocaenicus* biozone (MNR1), which can therefore now be linked to the *Macoma balthica* – *Mya arenaria* Concurrent Range Zone. In Zuurland-2, the FAD of *M. balthica* occurs at –66 m and the LADs of *M. arenaria* and *V. glacialis* occur at –62 m. Small mammal assemblages from –61 m to –65 m also belong to arvicolid biozone MNR1 (Mayhew, 2015), which is again associated with *M. balthica*, *M. arenaria* and *V. glacialis*. This suggested correlation is supported by amino acid data from *Bithynia* opercula showing similar IcPD values between Zuurland (–63 m to –65 m) and the ‘Weybourne Crag’ at its type locality. Moreover, it is noteworthy that *M. hordijki*, reported here from Sidestrand (its first British record), was originally described from –61 m to –65 m in the Zuurland-2 borehole (Van Kolfschoten and Tesakov, 1998). Teeth of another significant vole, *Phenacomys*, have also recently been reported from the same levels in the Zuurland-2 borehole (Van Kolfschoten et al., 2018). This genus has North American origins, suggesting the existence of a Holarctic component in the Early Pleistocene mammal fauna of northern Eurasia. If so then the opportunity for long-distance correlations between Europe and North America may eventually be possible (Van Kolfschoten et al., 2018).

The non-marine character of the sediments at Tegelen precludes linkage of these two biozones at this locality. However, *Viviparus glacialis* and *Lithoglyphus jahni* are both present in an assemblage that reflects more temperate conditions than those reconstructed from the ‘Weybourne Crag’ (Freudenthal et al., 1976; Westerhoff et al., 1998). The small mammal assemblage lacks open steppic species, such as *Borsodia newtoni*, but *Mimomys pliocaenicus* does occur, allowing attribution to arvicolid biozone MNR1 (Tesakov, 1998; Mayhew, 2015).

5.4. Relevance to Early Pleistocene stratigraphy and its chronology

The ‘Weybourne Crag’ was assigned by West (1980) to the ‘Pre-Pastonian a’ Substage but there has been considerable debate as to whether this cold episode is identical to that represented by the type Baventian at Easton Bavents in Suffolk, which Funnell (1995) thought occurred during the Olduvai Subchron (1.77–1.97 Ma), or whether it represents a different event. The current consensus seems to be that the ‘Pre-Pastonian a’ merely forms a later part of the same cold stage as that represented by the Baventian (Funnell, 1987; Zalasiewicz et al.,

1991; Gibbard et al., 1998; Lee et al., 2015) and that this occurred during the later part of the Tiglian (Gibbard et al., 1991).

Evidence for a cold episode at Tegelen within the Late Tiglian (attributed to Substage TC4c) was originally suggested on the basis of a thin layer of fine sand generally lacking pollen, except for *Pinus*, which dominated (Zagwijn, 1963). This cold TC4c Substage that Funnell (1996) thought equated with MIS 68 became part of the stratigraphical template of the Dutch Quaternary, which itself became the standard framework for much of NW Europe (Zagwijn, 1985). Any cold event in the late Early Pleistocene was consequently correlated with TC4c including periglacial features at Öbel, Germany (Gibbard et al., 1995), the Westleton Beds (Richards et al., 1999), the Baventian/‘Pre-Pastonian a’ (Gibbard et al., 1998) and regressive (low sea-level) sequences with periglacial features (frost-cracks and cryoturbation) in the Beerse area of northern Belgium (Kasse, 1993). A recent reappraisal of the type sequences, however, suggested that this sand body in the Russel-Tiglia Egypte pit at Tegelen formed during the onset of local crevassing, casting serious doubt on its significance as an indicator of (supra)regional climatic deterioration (Westerhoff, 2009). On the other hand, evidence for two cold episodes within ‘Tiglian C’ has been reported from Belgium (Kasse and Bohncke, 2001), the first correlated with TC4c and a second (assigned to ‘TC5b’) somewhat later, although precisely how these relate to the standard Dutch sequence in the light of recent re-interpretations is unclear.

Returning to the British sequence, much of the debate here depends on the veracity of the proposed correlation of the Chillesford Clay with the Easton Bavents Clay and thence with ‘Pre-Pastonian a’ deposits (Zalasiewicz et al., 1991). If this correlation was correct, it follows that the Baventian and the ‘Pre-Pastonian a’ represent successive parts of a single cold episode, the Baventian succeeding the Bramertonian rather than preceding it (contra Funnell et al., 1979). However, as highlighted by Zalasiewicz et al. (1991), there are problems with such an interpretation including differences in foraminiferal and dinoflagellate assemblages, differences in height (+14 m to +10 m O.D. for the Chillesford Clay vs 0 to +2 m O.D. for the Easton Bavents Clay) and the recognition of possible Baventian foraminifera and pollen assemblages beneath undoubted Bramertonian sediments at Sizewell. Riding et al. (1997) also reported differences in derived palynomorphs between Baventian clays at Easton Bavents/Covehithe and the Chillesford Clay, indicating different provenances and pathways into the Crag basin. In this case, correlation of these ‘Baventian’ assemblages with those of ‘Pre-Pastonian a’ are precluded both by the occurrence of *M. balthica* in the latter and the

fact that the small mammals from Bramerton and from 'Pre-Pastonian a' deposits ('Weybourne Crag') belong to different mammal biozones (Mayhew and Stuart, 1986; Mayhew, 2013, 2015). Indeed, at Covehithe, Suffolk, the only site to have yielded both molluscs and foraminifers from the Baventian clay, the similarity between the arctic molluscan assemblages there and those from the 'Weybourne Crag' at Sidestrand and in North Sea borehole BGS 52-02-472 is remarkable, the critical difference being the absence of *M. balthica* at Covehithe (West et al., 1980).

Our new IcPD data based on *Nucella* shells has a direct bearing on these discussions, and indicates that the Baventian sediments at Covehithe post-date the Norwich Crag at Bramerton (Bramertonian) but are older than the 'Weybourne Crag' ('Pre-Pastonian a') at the various sites analysed. The extent of racemization between the Covehithe samples and those from the 'Weybourne Crag' are enough to suggest that they are unlikely to belong to the same cold stage, as has been suggested.

Arvicolid biozone MNR1 spans a number of climatic cycles between MIS 84 and MIS 79 (Supplementary Fig. 1, Fig. 18). Assemblages from this interval are therefore likely to reflect both temperate and cold environments. The assemblages from Tegelen, for example, include many species with thermophilous affinities (e.g. Westerhoff et al., 1998; van den Hoek Ostende and de Vos, 2006). Indeed, a recent palaeoclimate reconstruction based on the herpetofauna of Tegelen indicated a humid subtropical climate with a mean annual temperature of 13.4 ± 0.3 °C and a mean annual precipitation of 542 ± 50 mm (Villa et al., 2018). This forms a marked contrast to the high boreal/low arctic conditions reconstructed from the marine assemblages of the 'Weybourne Crag' and the open/steppic environments indicated from the contemporary small mammals. The next question to consider is whether all the 'Weybourne Crag' assemblages belong to a single stage. Morphometric comparisons of the molars of arvicolids such as *Mimomys pliocaenicus* reveal differences between sites (Fig. 14), hinting that although close in age, they may not be exactly contemporary. This possibility merits further work.

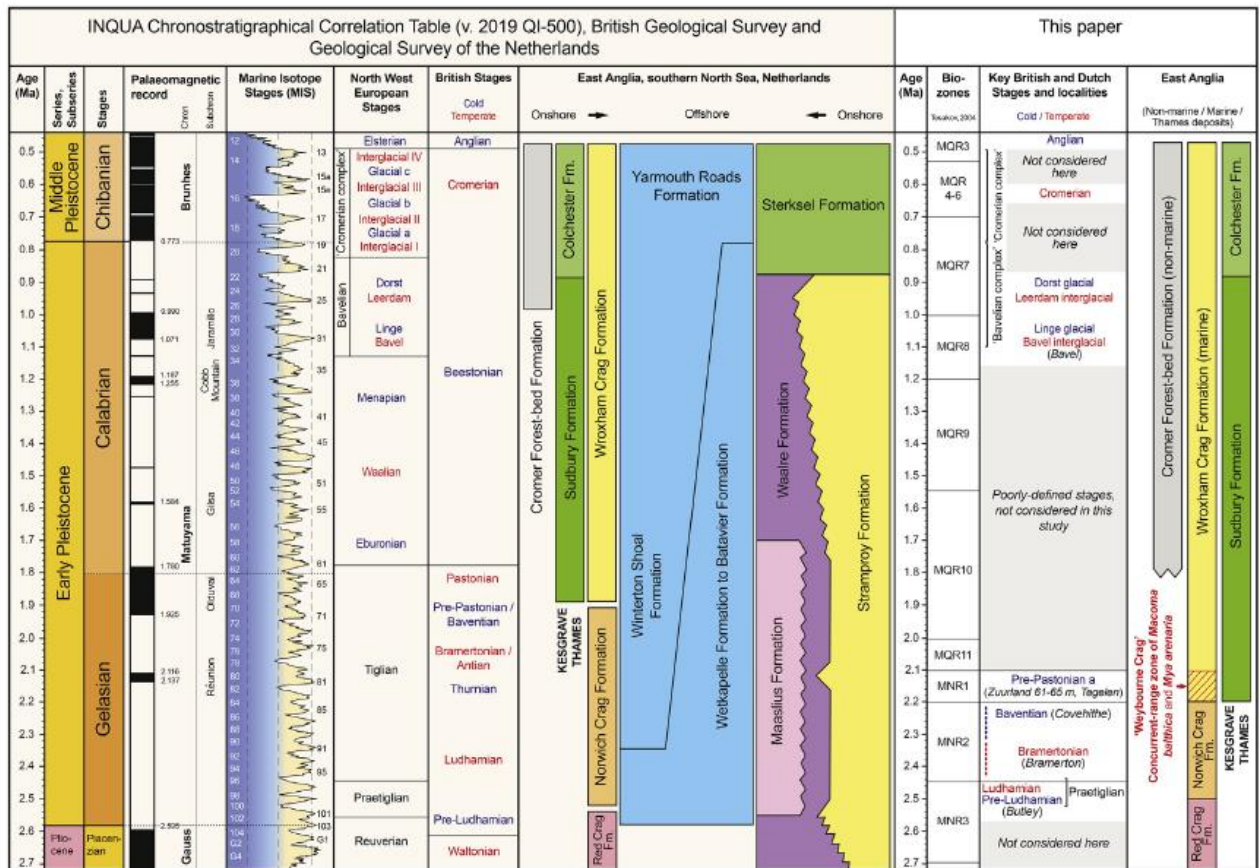


Fig. 18. Revision of the ages of sites and stages discussed in this paper shown alongside existing stratigraphical schemes for Early and early Middle Pleistocene sequences in the southern North Sea basin (Rijsdijk et al., 2005; Kuhlmann et al., 2006; Lee et al., 2015; Gibbard and Cohen, 2019). The Cromer Forest-bed Formation (CF-bF) as defined by West (1980) included all the pre-glacial sediments above the ‘Weybourne Crag’ (‘Pre-Pastonian a’) but in the most recent British Geological Survey scheme (Lee et al., 2015), the CF-bF is used in the more restricted way shown here on the left. Key British and Dutch stages tabulated on the right relate only to sites/stages mentioned in this paper. The ages attributed to the arvicolid biozones are taken from Tesakov (2004); the revised age of the Ludhamian and its inclusion within the Praetiglian is based on Meijer et al. (2006). The mammal assemblages from Bavel and the Cromerian cannot be securely tied to the East European Mammal zonation.

5.5. Age of the ‘Weybourne Crag’

While there is little doubt that the ‘Weybourne Crag’ does indeed correlate with a cold event(s) in the Late Tiglian, the belief that this occurred in MIS 68 during the Olduvai Event (~1.8 Ma) is at variance with the dates attached to arvicolid biozone MNR1 by Tesakov (2004), which imply a somewhat older age (2.2–2.1 Ma, approximately MIS 84-79). Using arvicolids (Supplementary Fig. 1, Fig. 18), this dating of the assemblage relies on current palaeomagnetic interpretations of Russian sequences. Here, the Ukrainian and Russian

localities of Kryzhanovka 4, Tizdar 1 and Tizdar 2 appear to demonstrate the arrival of *Allophaiomys* (biozone MQR11) before the start of the Olduvai Subchron (Pevsner et al., 1998; Maul et al., 2007). In North America, the arrival of *Allophaiomys* (= *Microtus* (*Allophaiomys*) sp.) is constrained to a period between 1.95 and 2.11 Ma, suggesting that early forms of *Microtus* had spread throughout both Eurasia and North America at this time (Martin, 2019). The arrival of *Allophaiomys* is thought to post-date the ‘Weybourne Crag’ assemblages (MNR1), meaning that they pre-date the Olduvai Subchron, and are probably ~2.1–2.2 Ma. Such a date might encounter objections in the form of evidence for persistence of *M. pliocaenicus* through or after the Olduvai Subchron. For example, *M. pliocaenicus* is said to be present at Dmanisi, Georgia, in ash layers above a basalt collectively dated at ~1.85–1.77 Ma with no unrooted voles present (Ferring et al., 2011). Reworking of the vole material cannot be excluded. In Russia and Ukraine, many workers consider arvicolid faunas of MN17 (including *M. pliocaenicus*) to occur in the Olduvai (e.g. Iosifova and Agadjanian, 2010) or even that *Allophaiomys* appears after the Olduvai (Krokhmal, 2010) but the basis for this interpretation is not clear.

If the dating of MNR1 between 2.1 and 2.2 Ma is correct, it follows that the normal palaeomagnetic polarity recorded at ‘Weybourne Crag’ sites such as Sidestrand (Hallam and Maher, 1994) must relate to a period of normal palaeomagnetic polarity pre-dating the Olduvai Subchron. It would also imply that the palaeomagnetic reversal recorded from the laminated clays above the ‘Weybourne Crag’ at Skelding Hill, assigned by West (1980) to the Pastonian, falls within the early part of the Matuyama Chron, assuming that there is no major hiatus between these units. We have shown that the Baventian appears to belong to a cold stage pre-dating the ‘Weybourne Crag’, which if correct, implies that its normal palaeomagnetic polarity (Thompson, 1991) pre-dates the Réunion Event. The revised age of the ‘Weybourne Crag’ has implications for the duration of the Norwich Crag Formation and the Tiglian Stage, which become shorter, and for the Kesgrave Thames formations, which are older than previously supposed (Fig. 18). It remains to be seen whether these correlations are supported by further work.

6. Conclusions

(a) The molluscs from the ‘Weybourne Crag’ are dominated by shallow-water marine species, including many characteristic of reduced salinities, together with a few implying deeper, subtidal habitats. The molluscan assemblages contain a range of species that now

inhabit low arctic/high boreal marine environments. *Macoma balthica* is the most abundant species.

(b) Non-marine molluscs occur at low frequency, but unlike the marine molluscan assemblages these include species, such as *Corbicula*, otherwise known only from temperate contexts. The extinct freshwater gastropods *Viviparus glacialis*, *Lithoglyphus jahni* and *Borysthenia goldfussiana* are stratigraphically significant records from the ‘Weybourne Crag’ (and from horizons in the southern North Sea correlated with it). The last two species also occur in later deposits but *V. glacialis* is unknown after the Tiglian.

(c) The co-occurrence of the marine bivalves *Macoma balthica* and *Mya arenaria* is biostratigraphically important as recognized by the definition here of the *Macoma balthica* – *Mya arenaria* Concurrent Range Zone (Appendix). This zone is known from ‘Weybourne Crag’ localities in Britain, from the Zuurland-2 borehole in The Netherlands, and from North Sea borehole BGS 52-02-472. The *Macoma balthica* – *Mya arenaria* Concurrent Range Zone occurs within the Late Tiglian.

(d) This conclusion is strongly supported by the assemblage of small mammals, which belongs to the *Borsodia newtoni* – *Mimomys pliocaenicus* biozone (MNR1). This assemblage has been recognized in the Zuurland-2 borehole (–61 m to –65 m) in the *Macoma balthica* – *Mya arenaria* Concurrent Range Zone, and at Tegelen, as well as sites in central Europe. The ‘Weybourne Crag’ mammal assemblage at Sidestrand is dominated by voles and includes two species (*Mimomys hordijki* and *Ungaromys dehmi*) previously unknown from the British Pleistocene. Significantly, the former was originally described from –61 m to –65 m in the Zuurland-2 borehole (Van Kolfschoten and Tesakov, 1998).

(e) The age of biozone MNR1 established at sites in Eastern Europe (2.1–2.2 Ma) indicates that the age of the ‘Weybourne Crag’ is older than previously supposed (~1.8 Ma). The previous conclusion was based on palaeomagnetic data and perhaps on incomplete knowledge of the stratigraphical ranges of certain taxa in relation to the magnetostratigraphy.

(f) Morphometric variation in arvicolid molars suggest that, although close in age, not all ‘Weybourne Crag’ sites are exactly contemporary.

(g) *Macoma balthica* is absent in the Baventian, which is considered to be a cold stage pre-dating the ‘Weybourne Crag’, a conclusion now supported by amino acid data on the shells of *Nucella lapillus*. The IcPD data for the Baventian at Covehithe plot close to those from Bramerton (Norwich Crag) but the proteins are more degraded than those from *Nucella* shells from the ‘Weybourne Crag’ sites studied here. This suggests that the Baventian and ‘Weybourne Crag’ belong to separate cold stages rather than belonging to different parts of a single stage.

(h) IcPD data from opercula of *Bithynia* from the Zuurland-2 borehole (−63 m to −65 m) show more degradation than samples from the type site of the Bavel interglacial and less degradation than those from the Norwich Crag at Thorpe Aldringham. IcPD data from the Tiglian type site at Tegelen plot in an intermediate position, but hint at a slightly older age than the samples from Zuurland-2 (−63 m to −65 m), which are similar to those from the ‘Weybourne Crag’ at its type locality.

(i) IcPD from shells of the marine gastropod *Nucella lapillus* from ‘Weybourne Crag’ sites (with *M. balthica*) is lower than those from the Norwich Crag and other Early Pleistocene sites (without *M. balthica*). The ‘Weybourne Crag’ therefore appears to be stratigraphically younger than the Norwich Crag rather than a facies of it.

(j) The ‘Weybourne Crag’ is one of a number of Early Pleistocene sea-level highstands from East Anglia associated with high boreal/low arctic conditions and ice-rafting in the southern North Sea (Larkin et al., 2011). This anomalous situation is the result of a lag in sea-level response to climate forcing (cf. Donders et al., 2018).

Authorship contributions

Richard C. Preece: Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing. **Tom Meijer:** Formal analysis, Writing - original draft. **Kirsty E.H. Penkman:** Formal analysis, Funding acquisition, Writing - original draft, Writing - review & editing. **Beatrice Demarchi:** Formal analysis, Writing - original draft. **David F. Mayhew:** Formal analysis, Writing - original draft. **Simon A. Parfitt:** Conceptualization, Formal analysis, Visualization, Writing - original draft, Writing - review & editing.

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Appendix.

The Concurrent Range Zone of *Macoma balthica* and *Mya arenaria* defined from the Pleistocene of the North Sea basin.

The zone, present in the southern part of the North Sea Basin, is characterized by the co-occurrence of the marine bivalves *Macoma balthica* and *Mya arenaria*, which have their FAD and LAD respectively in this zone. The extinct freshwater gastropod *Viviparus glacialis* occurs regularly and also has its LAD in this zone. Less frequent species, which are not restricted to this zone, include *Borysthenia goldfussiana*, *Lithoglyphus jahni*, *Boreoscala greenlandica*, *Ellobium pyramidale*, *Acila cobboldiae*, *Yoldia oblongoides*, *Macoma obliqua*,

and *Macoma praetenuis*. *Mya arenaria* was reintroduced to the North Sea from eastern North America about 1000 years ago but between ~2.1 Ma and the late Holocene it was absent.

The stratotype of this zone is defined in the Zuurland-2 borehole (registration number 37C554), The Netherlands (51° 53' 29" N, 4° 09' 39" E) at a depth of 62–66 m below ground surface (Fig. 5, Fig. 7). *Macoma balthica* occurs above 66 m, whereas *Mya arenaria* occurs below 62 m. Both species co-occur with *Viviparus glacialis* below 62 m.

The zone is recognizable at the following British sites at which *Viviparus glacialis* also occurs:

North Sea borehole BGS 52-02-472 (52° 03' 00" N, 2° 16' 61" E) at a depth of 8–10 m below seafloor; gravel dredged off the coast of Great Yarmouth (52° 30' N, 2° 00' E) at unknown depth below seafloor; Belaugh (52° 43' 15" N, 1° 22' 51" E), East Runton (52° 56' 15" N, 1° 16' 28" E), Rackheath (52° 40' 31" N, 1° 22' 12" E), Sidestrand (52° 54' 32" N, 1° 21' 56" E).

British sites where this zone occurs without *Viviparus glacialis* include: Crostwick (52° 41' 50" N, 1° 20' 24" E), Dobb's Plantation Pit near Wroxham (52° 41' 32" N, 1° 21' 37" E), Overstrand (52° 54' 56" N, 1° 21' 02" E), Sheringham (52° 56' 24" N, 1° 12' 47" E), Spixworth (52° 41' 22" N, 1° 19' 36" E), Swafeld (52° 50' 33" N, 1° 23' 43" E), Trimingham (52° 54' 04" N, 1° 23' 08" E), West Runton (52° 56' 28" N, 1° 15' 22" E), Beeston (52° 56' 40" N, 1° 13' 51" E) and Weybourne (52° 56' 55" N, 1° 08' 33" E).

Supplementary Data

Supplementary data files are appended after the references.

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Supplementary Data

Notes on species of interest

Molluscs

The following discussion is based on material recovered from the ‘Weybourne Crag’ at Sidestrand unless otherwise stated.

Notes on preservation

Poor preservation is not an infallible indication of derivation but it does give a general guide if an assessment is made of the whole assemblage. The distinction between ‘well preserved’ and ‘poorly preserved’ is somewhat arbitrary since different taxa show different modes of degradation. In *Littorina littorea*, for example, shells of living animals can already be poorly preserved, especially on exposed shores. In the *Spisula* present in this assemblage, the outer shell layer was almost completely leached, whereas this was not the case with other species such as *Yoldia oblongoides* (Fig. 6c-d), *Macra stultorum*, *Macoma balthica* and *Fabulina fabula*. Some specimens (e.g. *Mytilus* and *Acila*) are difficult to assign to either category. Poor preservation may be caused during transport and as the result of post-depositional leaching processes. Damage during transport may be penecontemporaneous or may result from the re-working of much older shells. Leaching can affect shells that have not been transported but it is not always easy to distinguish such damage from abrasion caused during transport. The distinction is important, however, because leached shells that have not been mechanically abraded are more likely to represent components of the original assemblage. Minute crystals of pyrite occur on the surface of many of the shells and these are likely to have caused most of the leaching, although imprints of sand grains suggests that pressure dissolution may also have been involved (Cadée and Wesselingh, 2005).

Marine species

Neptunea inversa Harmer, 1918

The taxonomy of this species (Fig. 7e) has been problematic. Reid (1890) recorded large sinistral whelks from the East Anglian crags as *Trophon antiqua* var *contraria* but most subsequent workers referred them to *Neptunea contraria*, a modern species originally described from Vigo, Spain. The crag shells were subsequently thought to differ from the modern species and were given the name *N. angulata* Harmer, 1914 but *N. inversa* Harmer, 1918 is the correct attribution for the shells from the Norwich and Weybourne crags (Vervoenen et al., 2014).

Nucella lapillus (Linnaeus, 1858)

Molecular phylogenetic and fossil evidence indicates that *N. lapillus* arose from a North Pacific ancestor and that the genus was an early participant in the trans-Arctic migration (Collins et al., 1996; Marko et al., 2014). This species is now abundant on rocky shores around the North Atlantic, where different shell morphologies reflect an ecophenotypic response to factors such as the degree of wave-exposure and predation pressure (Cambridge and Kitching, 1982; Crothers, 1985). Specimens from Sidestrand show slight angulation (Fig. 7d), also seen in *Nucella lapillus incrassatus* (J. Sowerby, 1823) from the Norwich and Red Crag formations. The fossil specimens of *N. lapillus* from the Yarmouth Roads Formation off Great Yarmouth do not show this angulation, perhaps indicating less intense wave-exposure.

Solariella obscura (Couthouy, 1838)

This arctic circumpolar species (Fig. 7a-c) today occurs south to the New England area, eastern and western Greenland, Iceland, between the Faroes and Shetland, Lofoten, and Norway, north to 64° N (Warén, 1993). Its normal depth range is 20-200 m (rarely 0-900 m) but it has occasionally been found intertidally.

Amauropsis islandica (Gmelin, 1791)

This is a circumpolar species (Fig. 7f) recorded locally only from the northern parts of the North Sea on sandy bottoms mostly in water-depths up to 80 m (Graham, 1988), although much deeper records are known (Peacock, 1993). It does not live in the intertidal zone. As a fossil this is an uncommon species that occurs in cold water assemblages in Quaternary deposits of the Southern Bight of the North Sea.

Boreoscala greenlandica (Perry, 1811)

The Greenland Wentletrap (Fig. 7l) has an arctic to high boreal distribution occurring to a maximum depth of 300 m where it feeds on sea anemones. It now lives in the North Atlantic from the Bay of Fundy, Gulf of St Lawrence and other sites in Canada to Greenland and along the entire Norwegian coast south to Oslofjorden (Bouchet and Warén, 1986). In the North Sea basin it is associated with Late Pliocene and Quaternary cold water assemblages (cf. Wesselingh et al., 2013).

Epitonium clathratulum (Kanmacher, 1897)

This species (Fig. 7i-k), a new record for the 'Weybourne Crag', ranges from the western Mediterranean to Norway and typically inhabits water 30-100 m in depth (Graham, 1988). In the British Isles there are records from the south west, western Ireland and Orkney, as well as from the southern North Sea (Graham, 1988).

Acila cobboldiae (Sowerby, 1817)

This extinct subtidal marine bivalve is readily recognizable by virtue of its taxodont hinge and characteristic zigzag sculpture (Fig. 6e-f). It is a component of cold water assemblages of boreal affinity (Moerdijk et al., 2010). This is a species of Pacific origin (Vermeij, 1991), which in the North Sea basin first appears in the Late Pliocene, persisting into the late Early Pleistocene. There are no secure British records after the 'Weybourne Crag'. Specimens from Sidestrand may have lived for at least 20 years as inferred from the growth banding on the shells ($n=5$).

Yoldia oblongoides (Wood, 1840)

This taxodont species (Fig. 6c-d) was recorded from several horizons within the crags by Reid (1890), who distinguished it from '*Leda myalis*' the index fossil of the '*Leda myalis* bed' that occurs above the 'Forest-bed'. These two species are similar to the extant *Yoldia myalis* (Couthouy, 1838), which has a circum-arctic and boreal distribution and lives at depths between 20 m and 165 m. However, Early Pleistocene specimens from the North Sea are larger with thicker shells and more pointed posteriors (rostrate) than modern *Y. myalis*, and it therefore seems safer to regard them provisionally as separate species, the Early Pleistocene fossils belonging to *Y. oblongoides* (P. Moerdijk, personal communication). Critical comparisons between the early Middle Pleistocene '*Leda myalis*' and modern specimens of *Y. myalis* have yet to be undertaken. *Y. oblongoides* is locally abundant in Early Pleistocene cold water assemblages in the southern part of the North Sea basin. Specimens from Sidestrand may have lived for at least 16 years according to the growth banding ($n=6$).

Macoma balthica (Linnaeus, 1758)

This euryhaline bivalve lives in thick mud, muddy sand and gravels in shallow water, principally from the upper regions of the intertidal zone to low water, although it has been recorded to depths of 45 m (Peacock, 1993). It occurs in the northern parts of both the Atlantic and Pacific, and also extends to the Subarctic both in North America and Europe. In the southern North Sea basin it first appears in the 'Weybourne Crag' in which it is often the most abundant species. Unlike most of the specimens of *M. balthica* that inhabit the North Sea today, the fossils from Sidestrand are smaller and have rather thick shells (Fig. 6h), although some thin-shelled forms (Fig. 6i) were also present. There is evidence that the smaller thicker shells lived longer (growth bands indicating minimum ages of 11-24 years; $n=18$) than the thinner-shelled forms, which appear to have grown for only 7-8 years ($n=2$). The significance of these differences is not clear but recent molecular analyses have revealed a complex phylogenetic structure of *M. balthica* populations in the North Atlantic, particularly in the North European marginal seas (the Baltic, White, Barents, and Pechora), suggesting that four independent trans-Arctic invasions from the Pacific gave rise to the current diversity in the North Atlantic (Nikula et al., 2007). Huber et al. (2015) have recently assigned this species to the genus *Limecola* Brown but the justification for doing so is not strong and we provisionally retain *balthica* within *Macoma*.

Macoma obliqua (Sowerby, 1817)

This marine bivalve (Fig. 6j-k) was formerly thought to be restricted to the Late Pliocene and Early Pleistocene until its discovery in the Eemian of the Netherlands (Meijer, 1993). It occurs commonly in the 'Weybourne Crag' but is far less common than the smaller *M. balthica*. It similarly occurs in the lower samples in the North Sea borehole BGS 52-02-472 (Fig. 10) and is present in the equivalent levels in the Zuurland-2 borehole (Fig. 9). Specimens from Sidestrand may have lived for about 75 years according to counts of the growth bands ($n=5$).

Mytilus cf. *trossulus* Gould, 1850

Many Early Pleistocene mytilid mussels from the North Sea region appear to have been misidentified as *Mytilus edulis*, and most of the better preserved specimens are clearly *M. trossulus*, which can be distinguished by colour and by differences in the shape and pattern of the interior (Vervoeven et al., 2000). *Mytilus trossulus* is another species that has spread eastwards from its original range in the North Pacific and Northwest Atlantic. In the North Atlantic, *M. trossulus* is found on the U.S. coast of Maine and northwards to Canada, as well as in scattered localities on North European coasts. In these regions it often coexists and hybridizes with *Mytilus edulis* (Väinölä and Strelkov, 2011). The identifications of the Sidestrand fossils (Fig. 6g) are only tentative because of poor preservation and because in the Plio-Pleistocene two additional species of *Mytilus* have been conflated with *M. edulis* (Vervoeven et al., 2000).

Ciliatocardium ciliatum (Fabricius)

This cockle inhabits sand and clay sediments to depths of >600 m (Ockelmann, 1958: 121). It has a modern arctic circum-polar range that extends south to the Faroes and Iceland but does not live in British waters. Two specimens of this species were found at Sidestrand, a new record for the 'Weybourne Crag'. It had previously been recorded (as either *Laevicardium* cf. *interruptum* or *Clinocardium ciliatum*) from the Baventian at Covehithe (Long, 1974; 2000).

Non-marine species

Lithoglyphus jahni Urbański, 1975

The freshwater genus *Lithoglyphus* has an essentially East European and SW Asian (Ponto-Caspian) distribution, where it is represented by several species. Until recently NW European fossils of this genus from the Early and Middle Pleistocene were assigned to *L. naticoides*, the species that still inhabits modern European rivers. During the Early and Middle Pleistocene *Lithoglyphus* extended much further west, *L. jahni* being recorded in deposits of the River Rhine of Tiglian and Bavelian age (Meijer, 1990; Gittenberger et al., 1998: figs 109-111). In Britain *L. jahni* (Fig. 8c-e) has previously been recorded from two ‘Weybourne Crag’ localities (East Runton and the North Walsham borehole) under the name *L. fuscus* (Reid, 1882, 1890, pl. 5, figs 9a-b; Harmer, 1914, pl. 1, fig. 16). In the Middle Pleistocene *L. jahni* was apparently not as widespread and has only been recorded from the ‘Holsteinian’ of Germany and Poland (Urbański, 1975).

Corbicula sp.

This freshwater bivalve is generally regarded as an ‘interglacial indicator’ species since it is unknown from cold stages in NW Europe (Meijer and Preece, 2000). Reid (1890) also recorded *Corbicula* from the ‘Weybourne Crag’, which he attributed to *C. fluminalis*. Our specimen (an immature shell) does have the finer ribbing present in this species (Fig. 8f-h) but the systematics of this genus are still not resolved (Meijer and Preece, 2000) and it seems best to leave the species attribution open. In the Zuurland-2 borehole *Corbicula* was frequent below 75 m and was recovered from 64-66 m (Fig. 9).

Pisidium clessini Neumayr, 1875

This species is characterized by its strong concentric ribbing, especially in the umbonal area, but this is less well developed on the specimen recovered from Sidestrand (Fig. 8i-j). This extinct freshwater bivalve occurs in fluvial deposits from the Lower Pleistocene until the late Middle Pleistocene of NW Europe. Reid (1890) recorded this species as *P. astartoides* from the Red and Norwich Craggs, as well as the Forest Bed. In Britain it is also known from the ‘Weybourne Crag’ at West Runton and from several later interglacials. In the Netherlands *P. clessini* occurs in all interglacials yielding fluvial molluscan assemblages, from the Tiglian to the late Middle Pleistocene (Meijer, 1990; 2003).

Mammal remains

Large mammals from Sidestrand and other ‘Weybourne Crag’ localities

A complete list of well-provenanced mammals from the ‘Weybourne Crag’ is given in Table 2. The remains of large vertebrates are found regularly along the stretch of the Norfolk coast near Sidestrand (Lister, 1993, 1996, 1998) but only the following identifiable remains have been recovered *in situ* from the ‘Weybourne Crag’.

Trogontherium

The beaver-like rodent *Trogontherium* is represented by two mandibles from RG and a maxilla from LG. These are important additions the Early Pleistocene record of *Trogontherium*, which in Britain is otherwise only known as *ex situ* finds from other sites at Sidestrand and nearby coastal localities (Mayhew, 1978).

Mayhew (1978) and Heinrich (1998) have argued that Pleistocene *Trogontherium* remains from Western Europe all belong to a single, probably geographically variable (Mayhew et al., 2008), species, *Trogontherium cuvieri*. The ecomorphology of *T. cuvieri* suggests that it was semi-

aquatic and inhabited slow-flowing rivers, lakes, fens, marshes and water-meadows, where it fed on succulent aquatic and waterside vegetation. Most occurrences are associated with temperate woodland (Mayhew, 1978) but *Trogontherium* also occurred during Middle Pleistocene interstadials at Hoxne, Suffolk (Ashton et al., 2008) and Schöningen, Germany (van Kolfschoten, 2012), and in association with conifer-dominated forest at the close of the Dutch Tiglian TC5 (Schreuder, 1929; van den Hoek Ostende and de Vos, 2006).

Eucladoceros tetraceros (Dawkins, 1878)

An incomplete antler of the comb-antlered deer *Eucladoceros tetraceros* (Fig. 12a) was excavated from the shelly sand at locality RG. The antler is shed and includes at least half of the beam with three largely intact tines; fresh damage suggests that other parts of the antler were recently lost to the sea. This specimen appears to represent the earliest known occurrence of this species, which is known principally from its type locality at Peyrolles, France (~1.46-1.47 Ma, according to Nomade et al., 2014a and b) and as *ex situ* finds from coastal sites in Norfolk.

At least two other species of comb-antlered deer are recognized in the ‘Weybourne Crag’/CF-bF of Norfolk, namely *E. ctenoides/tegulensis* (= *senezensis*) and *E. sedgwickii*. Lister (1993, 1996) highlighted intriguing patterns in the distribution and relative abundance of eucladocerine deer between these Norfolk sites. *Eucladoceros tetraceros* is well represented at Trimingham–Overstrand and East Runton (where it accounted for about half of the cervid antlers), but is absent at Mundesley and Bacton, where *E. sedgwicki* is the dominant eucladocerine. Extending these comparisons to the continent, Lister (1993, 1996, see also de Vos et al., 1995; Alcalde and van den Hoek Ostende, 2014) noted that at Tegelen, which has also yielded a large number of eucladocerine specimens (Spaan, 1992; de Vos et al., 1995), only one eucladocerine deer (*E. tegulensis*) is known. The factors behind these patterns of occurrence, whether taphonomic, ecological or chronological, remain unclear.

Eucladoceros cf. *sedgwicki* Falconer, 1868

A second species of *Eucladoceros* tentatively referred to *sedgwicki* is represented by a broad and flattened antler tine very different from that of *E. tetraceros*. It was found in the ‘Weybourne Crag’ overlying a Chalk raft at Sidestrand (J. Andrews coll.)

Ovibovini, ?*Pliotragus* or *Megalovis* sp.

This is represented by an upper molar (occlusal length 23.6 mm; crown height to top of mesostyle 29 mm), passing from early into middle wear (Fig. 12b-d). The tooth is hypsodont and does not have a basal pillar. The mesostyle is fairly prominent, the central fossettes are long from front to back, the vertical rib on the labial surface of the paracone is clear but not overly prominent, and there is a less noticeable rib on the metacone. Such characters suggest an ovibovine affiliation attributable to *Pliotragus* or *Megalovis* (A. Gentry, personal communication). The type species of *Pliotragus* is *Antilope ardea* Depéret, 1884 (p. 252, pl. 8, fig. 3) based on an upper tooth row from Côte d’Ardé, Étouaires, the Basle cast of which was figured by Duvernois and Guérin (1989, pl. 3 figs 4-5). The probable temporal range for the species in Western Europe is 3.1-1.8 Ma. Duvernois and Guérin, pl. 2 also figure a cast of a cranium from Senèze (just after 2.0 Ma). *Pliotragus* Kretzoi, 1941 is a replacement name for the preoccupied *Deperetia*, which Schaub (1923) had founded for *ardea*. Schaub also described and figured a skull from Senèze as *Megalovis latifrons* and Schaub (1944) showed it after restoration. It is unlikely that two ovibovine species occurred at Senèze, but if they were synonymised *Megalovis* would be senior to the more widely used *Pliotragus*.

There are bovids in the later Pliocene of Western Europe other than a gazelle, an ovibovine and *Leptobos*. *Procamptoceras* teeth are smaller than those of *Pliotragus* (Duvernois and Guerin 1989, table 3) and therefore too small to match the Sidestrand tooth. *Gazellospira* has teeth about the same size as the Sidestrand molar, but the labial ribs may be weaker and the hypsodonty less. A further possibility that should be considered for the Sidestrand molar is *Caprovis savinii* Newton, 1882 (page 49, pl. 10) based on a single right horn core in the Savin collection from Overstrand (NHMUK M6108). The biological affinity of this taxon is obscure and it is unknown on the continent, but de Wilde (2006) reported a number of horn-cores that he assigned to this species dredged from the Early Pleistocene Yarmouth Roads Formation in the North Sea.

A few other large mammals have been recovered from *in situ* ‘Weybourne Crag’ at other sites. Azzaroli (1953) mentioned a lower jaw of the elk *Cervalces gallicus* that was said to have been extracted from “shelly crag directly overlying the stone bed” at East Runton and West (1980: 27 and section fig. 11) found a left lower M2 of *Mammuthus meridionalis* in his section BN cemented between the Stone Bed and ‘Weybourne Crag’ at West Runton. The latter is now in Norwich Castle Museum (Accession number CRRMU : 1997.43). Material in private collections from Weybourne include other molars of *Mammuthus meridionalis* and antlers of *Eucladoceros* cf. *tetraceros* (Cruickshank collection, Reydon, Suffolk).

Small mammals from the ‘Weybourne Crag’ at Sidestrand

The R. Green collection from Sidestrand studied here contains remains of marine and freshwater fish, and small mammals, with about 250 arvicolid remains identifiable to species (Supplementary Table 3). The teeth are mineralized and in some cases rolled and polished (Fig. 13). Additional material seen from Sidestrand (Supplementary Table 3) included the specimens figured in Mayhew and Stuart (1986), and specimens from the Harrison collection (see Harrison et al., 1988a, b).

The arvicolids are assigned to *Mimomys pliocaenicus*, *M. reidi*, *M. hordijki*, *M. tigliensis*, *Pitymimomys pitymyoides*, *Borsodia newtoni*, *Clethrionomys kretzoi*, *Ungaromys dehmi*, *Lemmus kowalskii*. Several of these species are indicative of open and/or steppic environments. The taphonomy clearly indicates fluvial transport into a shallow marine environment, but the assemblage does not contain species indicating derivation from different biozones. Indeed, it is a typical assemblage found at other ‘Weybourne Crag’ sites in Britain (Table 2) and at localities in Europe assigned to arvicolid biozone MNR1 (=MN17, Middle Villafranchian). This attribution is based on the presence of *M. pliocaenicus* rather than the precursor *M. praepliocaenicus*, the presence of *M. hordijki*, the presence of *P. pitymyoides*, and the presence of *B. newtoni* rather than the precursor *B. praehungarica*. Supplementary figure 1 shows the context of the assemblage at Sidestrand, and some other British and Dutch localities, in relation to the Eastern European arvicolid biostratigraphy (Tesakov, 2004).

Notes on selected species

Mimomys (Mimomys) pliocaenicus Forsyth Major, 1902

This is the most abundant species in the assemblage at Sidestrand (19 m1, 15 m2, 13 m3, 23 M1, 11 M2, 14 M3). The teeth represent a large arvicolid species with clearly differentiated enamel, abundant crown cement and islands in m1 and M3. There is some variation in morphology of the anterior loop of m1, some specimens resembling those illustrated and assigned to the new species *Mimomys clairi* by Chaline (1984) in having a pointed backwardly directed T4 at a medium or advanced stage of wear. The M1 has 3 (n=8) or 2 (n=2) roots.). The height of the

enamel-free area in the upper third molar (M3) and the disappearance of enamel islets in the lower first molar (m1) in relation to crown height are shown in Fig. 14.

In the Early Pleistocene *Mimomys pliocaenicus* shows a progressive and marked increase in molar crown height. The names *Mimomys praepliocaenicus* and *M. pliocaenicus* have recently been applied to populations at the beginning and end of this evolutionary trend, differentiating Mammal biozone MNR2 and MNR1. Diagnostic measurements of molar teeth (Supplementary Tables 4-5) include the hypsodonty (HH) index (see Carls and Rabeder, 1988), the length of the hyposinulid (HSLD), the height of the enamel-free area in the upper third molar (M3) and the disappearance of enamel islets in the lower first molar (m1) in relation to crown height. At Sidestrand the hypsodonty (HH) index (2 teeth) was 5.11 and 5.22. A further two teeth of crown height >3.5 mm provided minimum HH index values of >6.13, >5.54. These HH values are clearly greater than in *M. praepliocaenicus* from the Norwich Crag at Easton Wood (mean 4.52, range 4.08-5.05, n 6, SD 0.34) (Mayhew, 2013; 2015). Hyposinulid (HSLD) values from the m1 from Sidestrand are compared with Norwich Crag localities and Tegelen in Supplementary Table 5.

Fig. 14a compares the timing of the disappearance of enamel islets in the lower first molar (m1) of *M. praepliocaenicus* and *M. pliocaenicus* at various localities. This shows a clear distinction between *M. praepliocaenicus* from Bramerton and Thorpe (near Norwich), both therefore belonging to biozone MNR2, and *M. pliocaenicus* from MNR1 ('Weybourne Crag' sites and Dutch localities). The data also show considerable variation between assemblages within MNR1, Sidestrand samples, for example, are significantly higher-crowned than those from the 'Weybourne Crag' at West Runton. This pattern is also reflected in the M3 with Sidestrand appearing to indicate a high-crowned, 'advanced' assemblage (Fig. 14b).

Mimomys (Tcharinomys) tigliensis Tesakov, 1998

The most frequent of the smaller species has very high crowned teeth and abundant crown cement and no enamel islet in m1. The name *M. blanci* was incorrectly applied to this taxon by Mayhew and Stuart (1986), and Tesakov (1998) proposed the new name *M. tigliensis* based on material from Tegelen, The Netherlands. The Sidestrand material (16m1, 3 m2, 4 m3, 11 M1, 8 M2, 3 M3) closely resembles the type material from Tegelen (collection NCB Naturalis, Leiden).

Mimomys tigliensis is relatively abundant in 'Weybourne crag' localities (biozone MNR1), and very rare in upper Norwich crag localities (biozone MNR2) (Mayhew, 2011). It currently appears to be absent from earlier Norwich crag localities, such as Bulcamp, Bramerton and Sizewell (Mayhew, 1990; Mayhew and Stuart 1986).

Mimomys (Pusillomimus) reidi Hinton, 1910

These teeth represent a medium-sized species of the subgenus *Pusillomimus* as redefined by Tesakov (2004) and are similar to the type of *M. reidi* from the 'Weybourne Crag' at Trimingham. The heights of the enamel free areas are similar to those of *M. reidi* from Tegelen described by Tesakov (1998). The Sidestrand material (11 m1, 4 m2, 1 m3, 8 M1, 3 M2, 5 M3) falls within the range of variation of the teeth of *M. reidi* previously described from the 'Weybourne Crag' by Mayhew and Stuart (1986).

Mimomys (Cromeromys) hordijki van Kolfschoten and Tesakov, 1998 (Fig. 13g-l)

The material consists of two fragmentary lower first molars and two upper first molars believed to belong to *M. hordijki*, but this dental element is so far undescribed in the literature. One m1 fragment preserves part of the prominent *Mimomys* ridge, with high mimosinulid, and the characteristically-shaped anterior loop (Fig. 13g-i). The m1s closely match the type and material

from the type locality (Hordijk coll.). *M. hordijki* was previously known only from two Dutch localities, its type locality at Zuurland (-60 m to -65 m), and from Maalbeek (van Kolfschoten and Tesakov, 1998; Tesakov and van Kolfschoten, 2011). This is the first record of *M. hordijki* from the UK, and the first report from outside of the Netherlands. A possible precursor of *M. hordijki* is *M. glendae*, described from Norwich Crag deposits at Easton Wood, Suffolk (Mayhew, 2013; 2015).

Mimomys sp. (large form)

A fragmentary anterior loop of a lower first molar and another m1 fragment represent a large arvicolid, larger than *Mimomys pliocaenicus*. The Sidestrand specimens resemble a large arvicolid from Bramerton described in Mayhew and Stuart (1986), which may represent an earlier part of the same clade. Both specimens are so large that it seems improbable they could come from coeval populations of *M. praepliocaenicus* or *M. pliocaenicus* (where the variability is now quite well quantified).

They resemble the genus *Kislangia* in large size and relatively thin enamel. However, the anterior part of the loop (LSA5) does not have the lingual extension or the cement filled LRA4 and the very abundant cement seen in *K. rex* from the type locality Villany-3. Arvicolids of exceptional size during the later Gelasian period have generally been referred to the genus *Kislangia* (Agusti et al., 1993, Mayhew, 2012), although there is unclarity about the position of some allocated species. This specimens are therefore identified here provisionally as *Mimomys* sp.? but may represent a new form or part of the *Kislangia* clade.

Pitymimomys pitymyoides (Jánossy and van der Meulen, 1975) (Fig. 13e)

Nine teeth are assigned to this taxon (3 m1, 2 m2, 1 M1, 1 M2, 2 M3). The M2 has the complete confluence of the triangles characteristic for *Pitymimomys*. The wear surface of the M3 is divided into two dentine fields in moderately worn teeth. *Pitymimomys* has been recognised as a component of many European Early Pleistocene faunas. Evolution in the lineage, indicated by increasing hypsodonty, was reviewed by Tesakov (2003, 2004). The material from Sidestrand belongs to the later part of the lineage. *P. pitymyoides* was previously recorded from other 'Weybourne Crag' localities (Mayhew and Stuart, 1986).

Borsodia newtoni (Forsyth Major, 1902)

A few teeth lacking crown cement belong to the genus *Borsodia* (Jánossy and van der Meulen, 1975). The teeth include 1 m1, 4 m2, 1 M1, 3 M2, 1 M3; measurements are as follows: M1: L 2.34 mm, W 1.45 mm, CH 1.58 mm; M2: L 1.86 mm, W 0.99 mm, PRS 3.03 mm, AS >3.57 mm, DS >3.16 mm.

These teeth are referred on the basis of the height of the enamel free areas of M2 to *B. newtoni* (see Tesakov, 2004 for values at different stages of evolution). The type of *Borsodia newtoni* was described from East Runton by Forsyth Major (1902) as *Mimomys newtoni*. The synonymy was clarified by Mayhew and Stuart (1986) who recorded the species also from the 'Weybourne Crag' at West Runton. Mayhew and Gibbard (1998) described it from crag overlying the Chalk at Weybourne. The species occurs in biozone MNR1, and later (Tesakov, 2004). *Borsodia* is a common component of assemblages from central and Eastern Europe associated with steppe environments (e.g. Villany-5, Hungary) repeatedly extending westwards as far as Britain.

Clethrionomys kretzoi (Kowalski, 1958)

The material consists of nine molars: 3 m1, 3 M1, 2 m2, 1 M2. The teeth are moderately hypsodont with poorly differentiated enamel and a small amount of crown cement. The m1 and M3

lack an enamel islet. They belong to an early representative of the clade of red-backed voles, *Clethrionomys kretzoi*.

Clethrionomys kretzoi is a rare component of UK arvicolid biozone MNR1 faunas, occurring for the first time in the "Weybourne Crag". It is recorded from an unpublished locality, Weybourne 2, and from Overstrand/Sidestrand (see here and also Mayhew and Stuart, 1986; Harrison et al. 1998a). It is unknown at present from the earlier MNR2 faunas of the Norwich Crag. It occurs widely in faunas from MNR1 across Europe, and is a common component in the assemblages from Tegelen, Netherlands, and Osztramos-3, Hungary, thought to represent forested environments (Tesakov, 1998; Jánossy, 1986).

Ungaromys dehmi Carls and Rabeder, 1988 (Fig. 13a-c)

The material consists of a single upper M1 (Measurements: L 2.09 mm, W 1.06 mm, CH 2.29 mm, PRS 0.36 mm, AS 1.52 mm, ASL 1.55 mm), having the thick enamel, confluent dentine triangles on the wear surface, and enamel free areas with a low protosinus characteristic of this species. It agrees in size and morphology with material from Tegelen. This small-sized arvicolid was first described from Schernfeld, Germany, and occurs at Early Pleistocene localities of biozone MNR1 through northern and central Europe, including Tegelen, The Netherlands (Tesakov, 1998) and Osztramos-3, Hungary (D.F. Mayhew, unpublished). Sidestrand is the first British record of *Ungaromys*.

Lemmus kowalskii Carls and Rabeder, 1988 (Fig. 13d and f)

This species was first recorded in Britain from Sidestrand (Harrison et al., 1989). It has since been found in earlier sediments at Easton Wood (Mayhew, 2013), as well as at a new 'Weybourne Crag' locality, Weybourne 2 (Mayhew, 2015). The Sidestrand material (1m1, 1M1, 1M3) closely resembles the type material described by Carls and Rabeder (1988). Measurements are as follows: m1: L 3.11 mm, W 1.28 mm; M3: L 2.45 mm, W 1.28 mm.

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Supplementary table 1. Mollusca from the Zuurland-2 borehole (-62 to -67 m). Key: (†) extinct; O – not living in the region.

sample depth (m.b.s.)	62-63			
	63-64			
	64-65			
Local mollusc zone	65-66			
Concurrent Range Zone	66-67			
	O	P		
	L-M			
Marine gastropods				
† <i>Ellobium pyramidale</i> (Sowerby, 1822)	x	x		
<i>Littorina littorea</i> Linnaeus, 1758	x	x	x	
<i>Littorina saxatilis</i> (Olivier, 1792)	x			
Marine bivalves				
<i>Barnea candida</i> (Linnaeus, 1758)	x	x	x	x
<i>Cerastoderma edule</i> (Linnaeus, 1758)	x	x		
<i>Cerastoderma</i> sp.	x	x		
<i>Hiatella arctica</i> (Linnaeus, 1767)	x			
<i>Macoma balthica</i> (Linnaeus, 1758)	x	x	x	
O <i>Macoma obliqua</i> (Sowerby, 1817)		x		
† <i>Macoma praetensis</i> (Leathes in Woodward, 1833)	x	x	x	
<i>Macomangulus tenuis</i> (da Costa, 1778)	x			
<i>Modiolus modiolus</i> (Linnaeus, 1758)		x	x	
<i>Mya arenaria</i> Linnaeus, 1758	x	x	x	x
O <i>Mytilus trossulus</i> Gould, 1850?	x	x	x	
<i>Ostrea edulis</i> Linnaeus, 1758			x	
<i>Scrobicularia plana</i> (Da Costa, 1778)	x	x	x	
Non-marine gastropods				
<i>Aegopinella</i> sp.	x	x		
<i>Anisus leucostoma</i> (Millet, 1813)	x	x		
<i>Anisus vortex</i> (Linnaeus, 1758)	x	x		
<i>Arianta arbustorum</i> (Linnaeus, 1758)	x	x		
<i>Bathymphalus contortus</i> (Linnaeus, 1758)	x	x		
O <i>Bithymia troschelii</i> Paasch, 1842 - opercula	x	x	x	
O <i>Bithymia troschelii</i> Paasch, 1842 - shells	x			
† <i>Borysthenia goldfussiana</i> (Wüst, 1901)	x	x		
<i>Carychium</i> sp.	x	x	x	
<i>Clausilia</i> sp.	x		x	x
<i>Cochlicopa lubrica</i> (Müller, 1774)	x	x		
<i>Cochlicopa</i> sp.	x		x	x
O <i>Columella columella</i> (Martens, 1830)	x	x	x	
<i>Discus rotundatus</i> (Müller, 1774)		x		
O <i>Discus ruderatus</i> (Férussac, 1821)	x			
<i>Galba truncatula</i> (Müller, 1774)	x			
O <i>Granaria frumentum</i> (Draparnaud, 1801)	x			
O <i>Granaria</i> sp.	x			
O <i>Gyraulus acronicus</i> (Férussac, 1807)	x			
<i>Gyraulus cristatus</i> (Linnaeus, 1758)	x	x		
<i>Gyraulus laevis</i> (Alder, 1838)	x	x		
<i>Gyraulus riparius</i> (Westerlund, 1865)	x	x		
O <i>Gyraulus rossmaessleri</i> (Auerwald, 1852)	x	x		
† <i>Helicigona</i> sp.	x			
<i>Limacidae</i> sp.	x	x	x	x
† <i>Lithoglyphus jahni</i> Urbanski, 1975	x	x		
<i>Lymnaeidae</i> sp.			x	
<i>Lymnaea stagnalis</i> (Linnaeus, 1758)	x	x		
<i>Marstoniopsis insubrica</i> (Küster, 1853)	x			
<i>Milacidae</i> sp.	x			
<i>Nesovitrea hammonis</i> (Ström, 1765)	x			
<i>Onghiscola glabra</i> (Müller, 1774)	x	x		
<i>Oxytoma elegans</i> (Risso, 1826)	x	x		
<i>Planorbis cornutus</i> (Linnaeus, 1758)	x	x		x
<i>Planorbis</i> sp.	x	x	x	x
<i>Planorbis carinatus</i> (Müller, 1774)	x	x		
<i>Planorbis planorbis</i> (Linnaeus, 1758)	x	x		
<i>Papilla muscorum</i> (Linnaeus, 1758)	x	x	x	x
<i>Radix peregrina</i> ovata	x	x		
<i>Segmentina nitida</i> (Müller, 1774)	x	x	x	x
<i>Stagnicola palustris</i> s.l.	x	x		
O <i>Succinella oblonga elongata</i> (Sandberger, 1875)	x	x		
† <i>Tournoisina belensis</i> (Delafield & Depéret, 1893)	x			
<i>Trochulus hispidus</i> (Linnaeus, 1758)	x	x		
<i>Vallonia costata</i> (Müller, 1774)	x	x		
<i>Vallonia pulchella</i> (Müller, 1774)	x	x	x	x
O <i>Vallonia tenuilabris</i> (A. Braun, 1843)	x			
<i>Valvata cristata</i> Müller, 1774	x	x		
<i>Valvata macrostoma</i> Mösch, 1864	x	x		
<i>Valvata piscinalis</i> (Müller, 1774)	x	x	x	
<i>Vertigo antivertigo</i> (Draparnaud, 1801)	x			
<i>Vertigo</i> sp.			x	
<i>Vertigo pygmaea</i> (Draparnaud, 1801)	x	x		
<i>Vertigo substriata</i> (Jeffreys, 1833)	x			
<i>Vitreu crystallina</i> (Müller, 1774)	x	x	x	
<i>Vitrinobrachium breve</i> (Férussac, 1821)	x	x	x	x
† <i>Viviparus glacialis</i> (Wood, 1872)	x	x	x	x
<i>Zonitoides nitidus</i> (Müller, 1774)	x			
Non-marine bivalves				
? <i>Corbicula</i> sp.	x	x	x	x
<i>Pisidium amicum</i> (Müller, 1774)	x			
† <i>Pisidium clessini</i> Neumayr, 1875	x			
<i>Pisidium casertanum</i> (Poli, 1791)	x			
<i>Pisidium henslowianum</i> (Sheppard, 1823)	x			
O <i>Pisidium lilljeborgi</i> Clessin, 1886	x			
O <i>Pisidium obtusale lapponicum</i> (Clessin, 1873)	x			
<i>Pisidium</i> sp.	x	x	x	x
O <i>Pisidium stewarti</i> Preston, 1909	x			
<i>Pisidium subtruncatum</i> Malm, 1855	x			
<i>Pisidium supinum</i> Schmidt, 1851	x			
<i>Sphaeriidae</i> sp.	x			
<i>Sphaerium corneum</i> (Linnaeus, 1758)	x			
<i>Unionidae</i> sp.	x	x		

Supplementary table 2. Details of the sites shown on Figure 11.

Serial number	Site code	Site name	Country	Exposure/borehole	Latitude	Longitude	orendance level	Top depth	Bottom depth	M. balteux / V. glacialis
0	-	Beeston	UK	E	52° 56' 40"	1° 13' 51"	-	-	-	B
1	-	Belagh	UK	E	52° 43' 15"	1° 22' 51"	-	-	-	BG
2	-	Bramerton	UK	E	52° 36' 11"	1° 23' 18"	-	-	-	-
3	-	Coltishall	UK	E	52° 43' 55"	1° 21' 36"	-	-	-	G
4	-	Covehithe	UK	E	52° 22' 38"	1° 42' 41"	-	-	-	-
5	-	Dobb's Plantation Pit	UK	E	52° 41' 32"	1° 21' 37"	-	-	-	B
6	-	East Runton	UK	E	52° 56' 15"	1° 16' 28"	-	-	-	G
7	-	Easton Wood	UK	E	52° 21' 40"	1° 42' 00"	-	-	-	-
8	-	Horstead	UK	E	52° 43' 32"	1° 21' 10"	-	-	-	G
9	-	Ormesby	UK	B	52° 40' 01"	1° 42' 56"	-	-	-	-
10	-	Overstrand	UK	E	52° 54' 56"	1° 21' 02"	-	-	-	B
11	-	Rackheath	UK	E	52° 40' 31"	1° 22' 12"	-	-	-	BG
12	-	Sidestrand	UK	E	52° 54' 32"	1° 21' 56"	-	-	-	BG
13	-	Stewell Broom Covert	UK	B	52° 12' 40"	1° 36' 21"	-	-	-	-
14	-	Swaffield borehole	UK	B	52° 50' 33"	1° 23' 43"	30,00	-	-	B
15	-	Trimingham	UK	E	52° 54' 04"	1° 23' 08"	-	-	-	B
16	-	Weybourne	UK	E	52° 56' 55"	1° 08' 33"	-	-	-	BG
17	43D10-1	Anna Wilhelminapolder	NL	B	51° 39' 30"	4° 17' 15"	2,00	47,30	47,60	G
18	40B0059	Arnhem, Kleefse Waard B2	NL	B	51° 58' 12"	5° 56' 16"	13,70	84,20	85,00	G
19	38H0178	Asperen	NL	B	51° 52' 35"	5° 05' 37"	0,98	89,00	91,00	G
19	38H0178	Asperen	NL	B	51° 52' 35"	5° 05' 37"	0,98	105,00	106,00	G
19	38H0178	Asperen	NL	B	51° 52' 35"	5° 05' 37"	0,98	107,00	108,00	G
20	37H0055	Barendrecht	NL	B	51° 51' 30"	4° 32' 00"	-0,95	84,00	87,50	G
20	37H0055	Barendrecht	NL	B	51° 51' 30"	4° 32' 00"	-0,95	88,50	91,00	G
21	44A0155	Biesbosch III, Van Elzelingenweg	NL	B	51° 45' 23"	4° 43' 26"	-0,80	66,30	70,00	G
22	37D0134	Brielle	NL	B	51° 54' 25"	4° 10' 47"	1,12	61,00	113,00	G
23	39A0187	Cohen	NL	B	51° 55' 39"	5° 11' 14"	3,80	135,00	136,00	G
24	43B0041	Den Bommel pb 47	NL	B	51° 42' 96"	4° 17' 33"	-0,38	44,00	55,00	G
25	43A0046	Dirksland	NL	B	51° 44' 39"	4° 05' 26"	0,51	65,00	66,00	G
25	43A0046	Dirksland	NL	B	51° 44' 39"	4° 05' 26"	0,51	119,00	120,00	G
25	43A0046	Dirksland	NL	B	51° 44' 39"	4° 05' 26"	0,51	121,00	122,00	G
26	44C0033	Dongen	NL	B	51° 37' 27"	4° 55' 36"	3,50	71,00	81,00	G
27	38C0445	Dordrecht I	NL	B	51° 48' 41"	4° 42' 39"	0,00	72,60	74,10	G
28	44A0156	Dordrecht X, Prinsenheuvel	NL	B	51° 45' 13"	4° 39' 98"	0,90	65,00	79,50	G
28	44A0156	Dordrecht X, Prinsenheuvel	NL	B	51° 45' 13"	4° 39' 98"	0,90	79,50	82,00	G
28	44A0156	Dordrecht X, Prinsenheuvel	NL	B	51° 45' 13"	4° 39' 98"	0,90	107,30	108,20	G
29	44B0061	Dordrecht XI, Hardenhoek	NL	B	51° 47' 30"	4° 47' 11"	0,65	65,50	79,50	G
29	44B0061	Dordrecht XI, Hardenhoek	NL	B	51° 47' 30"	4° 47' 11"	0,65	80,80	86,50	G
29	44B0061	Dordrecht XI, Hardenhoek	NL	B	51° 47' 30"	4° 47' 11"	0,65	86,50	95,00	G
29	44B0001	Dordrecht XIV, Dubbeldam 1	NL	B	51° 47' 49"	4° 44' 11"	0,68	72,40	86,40	G
30	44B0002	Dordrecht XV, Bildersteeg 2	NL	B	51° 47' 50"	4° 44' 14"	0,68	60,40	61,80	G
30	44B0002	Dordrecht XV, Bildersteeg 2	NL	B	51° 47' 50"	4° 44' 14"	0,68	61,80	67,00	G
30	44B0002	Dordrecht XV, Bildersteeg 2	NL	B	51° 47' 50"	4° 44' 14"	0,68	72,40	86,40	G
31	44B0003	Dordrecht XVI, Bildersteeg 3	NL	B	51° 47' 54"	4° 44' 10"	0,40	61,00	65,25	G
32	44B0004	Dordrecht XVII, Bildersteeg 4	NL	B	51° 47' 51"	4° 44' 09"	0,95	56,90	65,40	G
33	38C0184	Dordrecht-Gasfabriek	NL	B	51° 49' 07"	4° 40' 30"	3,36	46,90	48,40	G
34	38D0093	Dordrecht-Wingarden VII	NL	B	51° 50' 40"	4° 45' 47"	-1,50	91,50	92,75	G
34	38D0093	Dordrecht-Wingarden VII	NL	B	51° 50' 40"	4° 45' 47"	-1,50	100,50	109,20	G
35	42F0023	Drieischor	NL	B	51° 41' 47"	4° 00' 37"	-0,50	114,00	115,00	G
36	40E0156	Duiven	NL	B	51° 57' 21"	6° 03' 07"	9,40	68,70	70,10	G
37	51D0024	Eindhoven	NL	B	51° 28' 04"	5° 25' 43"	19,28	148,00	162,00	G
38	51F0039	Gemert HB-50 FB-45	NL	B	51° 33' 33"	5° 41' 47"	16,60	17,60	27,70	G
38	51F0039	Gemert HB-50 FB-45	NL	B	51° 33' 33"	5° 41' 47"	16,60	32,00	33,00	G
39	51F0069	Gemert S255	NL	B	51° 33' 32"	5° 41' 29"	16,00	30,00	-	G
40	38G0001	Gorkum Vischmarkt	NL	B	51° 49' 37"	4° 58' 31"	3,54	74,00	-	G
41	45C0017	Haaren	NL	B	51° 36' 95"	5° 15' 03"	7,30	142,40	148,50	G
41	45C0017	Haaren	NL	B	51° 36' 95"	5° 15' 03"	7,30	157,75	158,60	G
42	45C0113	Haaren P2	NL	B	51° 36' 35"	5° 14' 10"	6,38	133,00	139,00	G
42	45C0113	Haaren P2	NL	B	51° 36' 35"	5° 14' 10"	6,38	146,00	149,00	G
43	26F0001	Harderwijk II	NL	B	52° 24' 05"	5° 39' 06"	-5,00	248,00	253,00	G
43	38C0385	Hendrik Ido Ambacht	NL	B	51° 51' 22"	4° 38' 52"	0,40	73,00	101,00	G
44	14E0110	Hippolytshoef	NL	B	52° 54' 10"	4° 57' 42"	0,50	312,00	313,00	G
46	38E0012	Jaarsveld, Bor.A	NL	B	51° 58' 38"	5° 01' 20"	0,99	100,87	102,01	G
47	38H0148	Leerdam	NL	B	51° 53' 43"	5° 06' 06"	0,10	98,70	101,00	G
48	39E0036	Lienden	NL	B	51° 55' 40"	5° 30' 10"	6,00	51,00	53,70	G
49	45F0312	Loosbroek	NL	B	51° 42' 21"	5° 29' 35"	6,40	143,60	146,60	G
50	30H0147	Moerkapelle	NL	B	52° 02' 32"	4° 55' 01"	-4,50	119,50	121,50	G
51	30F0470	Noordwijk	NL	B	52° 13' 53"	4° 27' 34"	0,40	173,75	174,75	G
52	11B0078	Oldhoorn	NL	B	53° 03' 22"	5° 55' 23"	-0,59	236,00	237,00	G
53	42D0097	Oosterschelde, Roompot 4	NL	B	51° 37' 12"	3° 41' 37"	6,00	68,00	69,00	G
54	-	Ouddorp	NL	B	51° 48' 53"	3° 56' 14"	2,00	66,00	67,00	G
55	38B0142	Oudewater, no.1	NL	B	52° 00' 95"	4° 52' 30"	-1,10	150,00	157,50	G
56	44E0010	Raamsdonkveer B3	NL	B	51° 43' 18"	4° 53' 44"	1,00	85,50	98,50	G
57	45B0007	Rosmalen	NL	B	51° 43' 17"	5° 24' 51"	7,00	107,00	116,00	G
58	19E0085	Scharwoude	NL	B	52° 37' 21"	5° 00' 45"	-2,20	333,00	334,00	G
59	42G0022	Schelphoek A48	NL	B	51° 41' 10"	3° 49' 33"	3,11	52,00	54,00	G
60	38I0098	Schoonrewoerd	NL	B	51° 55' 17"	5° 07' 00"	1,00	90,50	93,80	G
60	38I0098	Schoonrewoerd	NL	B	51° 55' 17"	5° 07' 00"	1,00	99,80	109,10	G
61	44A0145	's-Gravendeel	NL	B	51° 46' 27"	4° 37' 20"	-0,60	49,50	69,20	G
61	44A0145	's-Gravendeel	NL	B	51° 46' 27"	4° 37' 20"	-0,60	69,20	70,40	G
61	44A0145	's-Gravendeel	NL	B	51° 46' 27"	4° 37' 20"	-0,60	75,40	81,60	G
62	38D0107	Streefkerk I	NL	B	51° 54' 42"	4° 49' 37"	-1,18	107,20	111,30	G
63	38E0121	Tienhoven	NL	B	51° 56' 09"	4° 56' 07"	-0,90	106,00	107,00	G
63	38E0121	Tienhoven	NL	B	51° 56' 09"	4° 56' 07"	-0,90	114,00	115,00	G
63	38E0121	Tienhoven	NL	B	51° 56' 09"	4° 56' 07"	-0,90	128,00	130,00	G
64	31H0172	Utrecht, Vreburg	NL	B	52° 05' 32"	5° 06' 49"	-3,73	150,00	-	G
65	30G0189	Wassenaar, Bor. I.	NL	B	52° 06' 36"	4° 19' 55"	-1,90	77,90	80,50	G
65	30G0189	Wassenaar, Bor. I.	NL	B	52° 06' 36"	4° 19' 55"	-1,90	80,50	82,37	G
66	05A0084	West Terschelling	NL	B	53° 22' 17"	5° 13' 09"	5,00	283,20	284,20	G
66	05A0084	West Terschelling	NL	B	53° 22' 17"	5° 13' 09"	5,00	290,80	292,20	G
66	05A0084	West Terschelling	NL	B	53° 22' 17"	5° 13' 09"	5,00	296,20	297,20	G
66	05A0084	West Terschelling	NL	B	53° 22' 17"	5° 13' 09"	5,00	300,20	301,20	G
66	05A0084	West Terschelling	NL	B	53° 22' 17"	5° 13' 09"	5,00	318,20	319,20	G
66	05A0084	West Terschelling	NL	B	53° 22' 17"	5° 13' 09"	5,00	321,20	322,20	G
66	05A0084	West Terschelling	NL	B	53° 22' 17"	5° 13' 09"	5,00	375,70	376,70	G
66	05A0084	West Terschelling	NL	B	53° 22' 17"	5° 13' 09"	5,00	390,20	391,20	G
67	31G0038	Woerden	NL	B	52° 05' 17"	4° 53' 04"	-4,50	136,00	142,00	G
68	32C0354	Zeist	NL	B	52° 05' 43"	5° 14' 48"	9,00	118,50	119,50	G
68	37C0554	Zuurland-2	NL	B	51° 53' 29"	4° 09' 39"	-0,40	62,00	64,00	BG
68	37C0554	Zuurland-2	NL	B	51° 53' 29"	4° 09' 39"	-0,40	76,00	77,00	G
68	37C0554	Zuurland-2	NL	B	51° 53' 29"	4° 09' 39"	-0,40	89,00	103,00	G
69	107-0002	-	NS	B	53° 36' 33"	4° 12' 24"	30,00	271,20	281,20	G
69	107-0002	-	NS	B	53° 36' 33"	4° 12' 24"	30,00	291,20	301,20	G
69	107-0002	-	NS	B	53° 36' 33"	4° 12' 24"	30,00	291,20	301,20	G
69	107-0002	-	NS	B	53° 36' 33"	4° 12' 24"	30,00	311,20	321,20	G
69	107-0002	-	NS	B	53° 36' 33"	4° 12' 24"	30,00	396,20	411,20	G
71	52-02-472	-	NS	B	52° 03' 00"	2° 16' 61"	-52,00	55,00	62,00	BG
70	-	Off coast of Great Yarmouth	NS	E	52° 30'	2° 00'	-25,00	-	-	BG
72	58E-	Maalbeek	NL	E	51° 18' 42"	6° 08' 52"	-	-	-	G
73	58E-	Tegelen, Pit Russel Tiglia Egypte	NL	E	51° 20' 45"	6° 10' 23"	-	-	-	G

Supplementary table 3. Mammal remains recovered *in situ* from the ‘Weybourne Crag’ at Sidestrand. Most of the previously published material was sieved from sediments overlying the Chalk raft at several locations at the eastern end of the sea defences (Fig. 2), as well as from localities on the foreshore (see Mayhew and Stuart, 1986; Harrison et al., 1988a and b; Harrison and Parfitt, 2009 for details). Unprovenanced remains of large vertebrates (especially deer and elephant) have also been recovered from the foreshore and some of these are likely to have come from the ‘Weybourne Crag’ (see Lister, 1993, 1996, 1998).

			Sidestrand #	
			NISP	Locality
	Sidestrand- Overstrand *	Sidestrand (HZM colln.) **		
Soricomorpha				
<i>Sorex (Drepanosorex) praeearaneus</i> Kormos, 1934		+	4	RG, LG
Soricidae gen. et sp. undet. (large form)			1	LG
<i>Galemys kormosi</i> (Schreuder, 1940)		+		
<i>Desmana thermalis</i> Kormos, 1913		+		
<i>Talpa</i> sp.		+	1	RG
Carnivora				
<i>Mustela praenivalis</i> Kormos, 1934		+		
Artiodactyla				
<i>Eucladoceros tetraceros</i> (Dawkins, 1878)			1	RG
Cervidae gen. et sp. indet.		+		
Ovibovine (<i>Megalovis/Pliotragus</i> or <i>Caprovius savinii</i> Newton, 1882)			1	RG
Rodentia				
<i>Trogontherium</i> sp.			3	RG, LG
<i>Ungaromys dehmi</i> Carls and Rabeder, 1988			1	LG
<i>Clethrionomys kretzoi</i> (Kowalski, 1958)	+	+	9	RG, LG
<i>Mimomys pliocaenicus</i> Forsyth Major, 1902	+	+	95	RG, LG
<i>Mimomys hordijki</i> van Kolfschoten and Tesakov, 1998			2 (2 cf.)	RG, LG
<i>Mimomys reidi</i> Hinton, 1910	+	+	32	RG, LG
<i>Mimomys tigliensis</i> Tesakov, 1998	+	+	45	RG/LG
<i>Mimomys</i> sp. (large form)			2	RG, LG
<i>Pitymimomys pitymyoides</i> (Jánossy and van der Meulen, 1975)		+	9	RG, LG
<i>Borsodia newtoni</i> (Forsyth Major, 1902)		+	10	RG, LG
<i>Lemmus kowalskii</i> Carls and Rabeder, 1988		+	3	RG, LG

* Mayhew and Stuart (1986), nomenclature updated

** Harrison *et al.*, 1998a, b, and Mayhew, pers. obs. HZM – Harrison Zoological Museum, Sevenoaks, UK

This paper

NISP = number of identified specimens

Supplementary table 4. Measurements (mm) of *Mimomys pliocaenicus* m1 from Sidestrand.

measurement	N	Mean	Min	Max	SD
L	12	3.27	3.05	3.53	0.13
W	12	1.44	1.34	1.61	0.08
ASD	2	3.34	3.04	3.63	
HSD	2	3.79	3.78	3.80	
HSLD	5	3.36	3.18	3.60	0.17

L = length at wear surface, W = width at wear surface, ASD = anterosinuid, HSD = hyposinuid, HSLD = hyposinulid.

Supplementary table 5. Hyposinulid (HSLD) height of m1 of large *Mimomys* (data from Tesakov, 1998; Mayhew, 2013 and 2015).

HSLD	Species	Biozone	N	Mean	Min	Max	SD
Sidestrand, UK	<i>M. pliocaenicus</i>	MNR1	5	3.36	3.18	3.60	0.17
Tegelen, NL	<i>M. pliocaenicus</i>	MNR1	6	3.16	3.00	3.43	0.18
Easton Wood, UK	<i>M. praepliocaenicus</i>	MNR2	18	2.73	2.26	3.34	0.34
Sizewell Broom Covert, UK	<i>M. praepliocaenicus</i>	MNR2	16	2.50	1.88	3.03	0.34

Supplementary table 6. Amino acid data from opercula of *Bithynia troschelii* from the Zuurland-2 borehole (-63 m to -65 m) and from *Nucella lapillus* shells from the various sites under discussion. Error terms represent one standard deviation about the mean for the duplicate analyses for an individual sample. Each sample was bleached (b), with the free amino acid fraction signified by 'F' and the total hydrolysable fraction by 'H*'.

Site	NEaar no.	Sample name	Asx D/L		Glx D/L		Ser D/L		Ala D/L		Val D/L		species	material	n
			x	σ	x	σ	x	σ	x	σ	x	σ			
Zuurland 63-65 cm, NITG 398, Netherlands															
	9993bF	NL2u63Bto-1	0.926	0.000	0.828	0.017	ND	ND	0.948	0.010	0.789	0.014	<i>Bithynia tentaculata</i>	operculum	1
	9994bF	NL2u63Bto-2	0.924	0.004	0.804	0.091	ND	ND	0.954	0.024	0.778	0.007	<i>Bithynia tentaculata</i>	operculum	1
	9995bF	NL2u63Bto-3	0.929	0.005	0.803	0.010	ND	ND	0.945	0.006	0.797	0.003	<i>Bithynia tentaculata</i>	operculum	1
	9996bF	NL2u63Bto-4	0.933	0.000	0.805	0.087	ND	ND	0.943	0.001	0.771	0.004	<i>Bithynia tentaculata</i>	operculum	1
	9993bH*	NL2u63Bto-1	0.846	0.003	0.756	0.047	ND	ND	0.891	0.002	0.666	0.018	<i>Bithynia tentaculata</i>	operculum	1
	9994bH*	NL2u63Bto-2	0.878	0.007	0.736	0.018	ND	ND	0.898	0.006	0.629	0.016	<i>Bithynia tentaculata</i>	operculum	1
	9995bH*	NL2u63Bto-3	0.879	0.003	0.748	0.014	ND	ND	0.900	0.005	0.678	0.008	<i>Bithynia tentaculata</i>	operculum	1
	9996bH*	NL2u63Bto-4	0.869	0.004	0.742	0.007	ND	ND	0.886	0.011	0.646	0.019	<i>Bithynia tentaculata</i>	operculum	1
Mya bed overlying WRFB, West Runton															
	4795bF	WrNi1bF	0.857	0.013	0.442	0.003	1.109	0.010	0.680	0.013	0.411	0.003	<i>Nucella lapillus</i>	shell	1
	4768bF	WrNi2bF	0.844	0.005	0.432	0.004	0.962	0.017	0.684	0.002	0.426	0.007	<i>Nucella lapillus</i>	shell	1
	4795bH*	WrNi1bH*	0.734	0.001	0.330	0.001	0.588	0.028	0.563	0.007	0.302	0.001	<i>Nucella lapillus</i>	shell	1
	4768bH*	WrNi2bH*	0.695	0.001	0.298	0.001	0.537	0.042	0.480	0.012	0.279	0.002	<i>Nucella lapillus</i>	shell	1
Weybourne Crag', East Runton, ER05c, 2005, SP coll. 2005															
	11038bF	ERNi1.1bF	0.887	0.001	0.687	0.013	0.945	0.060	0.903	0.003	0.684	0.000	<i>Nucella lapillus</i>	shell	1
	11039bF	ERNi1.2bF	0.886	0.004	0.677	0.001	ND	ND	0.904	0.008	0.691	0.001	<i>Nucella lapillus</i>	shell	1
	11040bF	ERNi2.1bF	0.879	0.000	0.597	0.012	0.710	0.052	0.875	0.002	0.675	0.001	<i>Nucella lapillus</i>	shell	1
	11041bF	ERNi2.2bF	0.877	0.001	0.614	0.014	0.665	0.079	0.882	0.000	0.680	0.001	<i>Nucella lapillus</i>	shell	1
	11038bH*	ERNi1.1bH*	0.819	0.002	0.602	0.004	0.338	0.034	0.826	0.003	0.576	0.001	<i>Nucella lapillus</i>	shell	1
	11039bH*	ERNi1.2bH*	0.821	0.005	0.605	0.001	0.304	0.096	0.830	0.001	0.578	0.002	<i>Nucella lapillus</i>	shell	1
	11040bH*	ERNi2.1bH*	0.826	0.000	0.553	0.002	0.342	0.021	0.810	0.002	0.564	0.002	<i>Nucella lapillus</i>	shell	1
	11041bH*	ERNi2.2bH*	0.823	0.001	0.558	0.002	0.357	0.090	0.805	0.005	0.567	0.004	<i>Nucella lapillus</i>	shell	1
Weybourne Crag', Weybourne Hope, Coll S. Parfitt 13/03/2002															
	10528bF	WecLap1bF	0.889	0.002	0.619	0.014	0.491	0.071	0.885	0.000	0.680	0.003	<i>Nucella lapillus</i>	shell	1
	10528bH+	WecLap1bH*	0.822	0.004	0.556	0.005	0.259	0.029	0.805	0.001	0.571	0.002	<i>Nucella lapillus</i>	shell	1
Weybourne Crag', Coll P Moerdijk, Off shore Great Yarmouth, 8 shells, 2006-2007															
	10543bF	WecLap2bF	0.890	0.000	0.640	0.026	ND	ND	0.901	0.004	0.725	0.005	<i>Nucella lapillus</i>	shell	1
	10544bF	WecLap3bF	0.882	0.002	0.599	0.010	0.000	0.000	0.896	0.000	0.717	0.006	<i>Nucella lapillus</i>	shell	1
	10545bF	WecLap4bF	0.869	0.002	0.579	0.000	0.528	0.202	0.870	0.000	0.700	0.007	<i>Nucella lapillus</i>	shell	1
	10543bH+	WecLap2bH*	0.828	0.001	0.598	0.002	0.228	0.017	0.811	0.000	0.600	0.000	<i>Nucella lapillus</i>	shell	1
	10544bH+	WecLap3bH*	0.825	0.001	0.569	0.003	0.115	0.162	0.795	0.004	0.599	0.004	<i>Nucella lapillus</i>	shell	1
	10545bH+	WecLap4bH*	0.818	0.002	0.554	0.000	0.266	0.010	0.764	0.004	0.574	0.005	<i>Nucella lapillus</i>	shell	1
Weybourne Crag', Sidestrاند															
	4764bF	SiCNi1bF	0.903	0.002	0.621	0.010	0.949	0.007	0.886	0.001	0.724	0.001	<i>Nucella lapillus</i>	shell	1
	4765bF	SiCNi2bF	0.899	0.012	0.613	0.009	0.949	0.059	0.890	0.010	0.713	0.002	<i>Nucella lapillus</i>	shell	1
	4764bH*	SiCNi1bH*	0.818	0.005	0.514	0.003	0.138	0.007	0.784	0.000	0.566	0.001	<i>Nucella lapillus</i>	shell	1
	4765bH*	SiCNi2bH*	0.840	0.009	0.579	0.004	0.309	0.072	0.819	0.002	0.611	0.006	<i>Nucella lapillus</i>	shell	1
Bavention, Covehithe, Luc E sample Red loamy sand 24/11/14															
	10446bF	CovNi1-1bF	0.891	0.002	0.669	0.010	0.000	0.000	0.911	0.003	0.766	0.002	<i>Nucella lapillus</i>	shell	1
	10447bF	CovNi1-2bF	0.900	0.001	0.695	0.021	0.320	0.453	0.914	0.004	0.775	0.000	<i>Nucella lapillus</i>	shell	1
	10448bF	CovNi1-3bF	0.889	0.002	0.666	0.006	ND	ND	0.898	0.002	0.755	0.005	<i>Nucella lapillus</i>	shell	1
	10446bH*	CovNi1-1bH*	0.853	0.000	0.636	0.002	0.000	0.000	0.851	0.001	0.675	0.002	<i>Nucella lapillus</i>	shell	1
	10447bH*	CovNi1-2bH*	0.857	0.002	0.641	0.004	0.396	0.113	0.866	0.000	0.682	0.003	<i>Nucella lapillus</i>	shell	1
	10448bH*	CovNi1-3bH*	0.850	0.002	0.627	0.002	0.324	0.102	0.848	0.000	0.672	0.004	<i>Nucella lapillus</i>	shell	1
Bramertonian (Norwich Crag), Bramerton, Blakes Pit															
	4780bF	BraNi2bF	0.918	0.000	0.699	0.000	0.792	0.029	0.922	0.006	0.795	0.011	<i>Nucella lapillus</i>	shell	1
	4805bF	BraNi1bF	0.922	0.000	0.704	0.009	0.999	0.035	0.923	0.001	0.793	0.001	<i>Nucella lapillus</i>	shell	1
	4780bH*	BraNi2bH*	0.865	0.001	0.671	0.005	0.287	0.002	0.848	0.005	0.697	0.001	<i>Nucella lapillus</i>	shell	1
	4805bH*	BraNi1bH*	0.865	0.000	0.669	0.001	0.261	0.008	0.876	0.015	0.692	0.000	<i>Nucella lapillus</i>	shell	1
Red Crag, Neutral Farm, Butley (base of unit), SAP, QRA 2004															
	11034bF	RCNi1.1bF	0.922	0.002	0.791	0.023	ND	ND	0.938	0.001	0.879	0.004	<i>Nucella lapillus</i>	shell	1
	11035bF	RCNi1.2bF	0.925	0.002	0.787	0.003	ND	ND	0.941	0.008	0.883	0.001	<i>Nucella lapillus</i>	shell	1
	11036bF	RCNi2.1bF	0.920	0.004	0.802	0.025	ND	ND	0.942	0.002	0.882	0.003	<i>Nucella lapillus</i>	shell	1
	11037bF	RCNi2.2bF	0.920	0.000	0.815	0.005	ND	ND	0.946	0.000	0.879	0.000	<i>Nucella lapillus</i>	shell	1
	11034bH*	RCNi1.1bH*	0.888	0.000	0.822	0.016	0.000	0.000	0.913	0.006	0.823	0.007	<i>Nucella lapillus</i>	shell	1
	11035bH*	RCNi1.2bH*	0.886	0.005	0.825	0.001	0.000	0.000	0.914	0.001	0.814	0.000	<i>Nucella lapillus</i>	shell	1
	11036bH*	RCNi2.1bH*	0.878	0.004	0.822	0.004	0.000	0.000	0.914	0.003	0.809	0.005	<i>Nucella lapillus</i>	shell	1
	11037bH*	RCNi2.2bH*	0.876	0.003	0.809	0.003	0.000	0.000	0.914	0.004	0.803	0.000	<i>Nucella lapillus</i>	shell	1

Supplementary Figure 1. The position of Sidestrand and other British and Dutch localities in relation to the East European arvicolid biostratigraphy (Tesakov, 2004); figure adapted from Mayhew (2015). The Concurrent-range zone of *Macoma balthica* and *Mya arenaria* is shown. The stratigraphical position of sites within square brackets is inferred from evidence other than arvicolid biostratigraphy. The palaeomagnetic record and marine isotope stage data are taken from Cohen and Gibbard (2019).

