PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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STRATIGRAPHIC AND TAXONOMIC REVISION OF THE FOSSIL VOLE REMAINS (RODENTIA, MICROTINAE) FROM THE LOWER PLEISTOCENE DEPOSITS OF EASTERN ENGLAND

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CONTENTS

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We review the fossil microtine rodent assemblages from the Lower Pleistocene deposits in eastern England, consisting mainly of marine sediments of the Norwich Crag and Cromer Forest-bed Formations. Material from 17 localities, including the 'Weybourne Crag' of the Norfolk Coast, the inland 'Norwich Crag', and the Crag of the north Suffolk coast has been studied.

The taxa *Mimomys pliocaenicus*, *M.rex*, *M.blanci*, *M.newtoni*, *M.reidi*, *M.pitymyoides*, *M.altenburgensis* and *Clethrionomys* are recognized. *Mimomys pitymyoides* and *M.altenburgensis* are described for the first time from Britain. The type material of *Mimomys reidi* and *M.newtoni* is redescribed, and we show that *M.newtoni* Major 1902 is a senior synonym of *M.hungaricus* (Kormos), thus resolving confusion that has existed in the literature. The prior name for the species described by M. A. C. Hinton (*Monograph of the voles and lemmings* (*Microtinae*) *living and extinct*. London: British Museum (Natural History) 1926) as *Mimomys newtoni* appears to be *Mimomys blanci* van der Meulen 1973.

No evidence has been found for mixing of faunas of different age at a single horizon or locality. Differences in crown height are demonstrated between samples of *Mimomys pliocaenicus* from different localities, and differences between localities in the presence and absence of various species are tabulated. This evidence combined with current interpretations of the stratigraphy leads us to recognize three faunal groups. Group 1 faunas contain *Mimomys pliocaenicus*, *M.reidi* (type level), *M.newtoni* (type level), *M.pitymyoides*, *M.blanci* and *Clethrionomys*. They come from coastal deposits previously termed 'Weybourne Crag' and currently considered to date from Pre-Pastonian *a* to Pastonian. The faunas are clearly later than group 2 faunas, which contain *Mimomys pliocaenicus*, *M.reidi*, *M.newtoni* (these three species less advanced than in group 1 faunas), *M.rex* and *M.altenburgensis* (these two species lacking in group 1 faunas). Group 2 faunas come from inland 'Norwich Crag' localities and crags in Suffolk yielding a Chillesford type pollen assemblage, which are currently considered to date from the Bramertonian stage. Group 3 faunas contain *Mimomys pliocaenicus*, *M.reidi* and *M.blanci* and are from coastal deposits at Covehithe and Easton Bavents associated with Baventian stage clays.

The evidence from the microtine rodents confirms the relative position of the Bramertonian and Pre-Pastonian *a* stages, but does not yet allow conclusions to be drawn on the relative age of group 3 faunas or the deposits in which they occur. The fauna of the Pastonian stage still requires clarification, since it is not possible to allocate unambiguously to this stage any of the material described here.

The British Lower Pleistocene assemblages are broadly similar to material from Tegelen, The Netherlands (Tiglian TC4-6) and to material from superimposed loess levels at Stranzendorf, Austria. The British assemblages are characterized by the presence of *Mimomys pliocaenicus* and the absence of species with unrooted teeth, indicating that they belong to the *Mimomys* superzone of the biostratigraphic system of A. J. van der Meulen (*Quaternaria* **17**, 1–144, 1973) corresponding to the Villanyian stage. On the basis of microtine evidence we suggest limits to the correlation of the Pre-Pastonian and Bramertonian stages with the Netherlands chronostratigraphy. These limits are earlier than suggested by other lines of evidence. Correlation of the Pre-Pastonian with part of the Eburonian and the Bramertonian with part of the Tiglian is thought to merit consideration.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

1. Introduction

This work reviews British Lower Pleistocene voles (Rodentia: Microtinae). The fossil material has been collected in the course of the last 150 years from exposed deposits, primarily representing inshore marine facies, in East Anglia. As a result of many studies in this area, the fauna, flora and lithostratigraphy have become increasingly well known. The stratigraphic sequence of the Lower Pleistocene of Britain is based on work in East Anglia (see West 1980*a*; Funnell *et al.* 1979; Mitchell *et al.* 1973).

A review of the voles is timely for a number of reasons. First, the British material is as yet only partly described (Hinton 1926; Sutcliffe & Kowalski 1976). Secondly, the taxonomy of the group itself is still problematic, and British material, including types of certain species, is central to the solution of some problems. Thirdly, rodents, and in particular voles, demonstrate rapid evolution during the Pleistocene, and this makes the group suitable for stratigraphic discrimination. Fourthly, stratigraphic conclusions based on voles can be compared with the results from other lines of biostratigraphic and lithostratigraphic investigation. Finally, comparisons between British and continental European stratigraphic systems can therefore be based on a greater range of criteria.

Apart from these general aspects, this paper also addresses a number of specific problems identified in a review of the literature. These include: the diagnosis and identification of the species *Mimomys reidi* Hinton; the taxonomy of the species *Mimomys newtoni* Major; the composition of the fossil vertebrate assemblages recovered from the locality East Runton; and differences between samples of *Mimomys pliocaenicus* Major from different localities.

This work is based on existing museum collections including some previously figured teeth, as well as on new collections of previously unstudied material. We have attempted to examine all available specimens from the Lower Pleistocene of eastern England.

2. Stratigraphy

The British Lower Pleistocene succession

With the exception of one or two cave deposits, the Lower Pleistocene of the British Isles is represented almost entirely by the 'Crags' of East Anglia (figure 1). The Crags comprise marine shelly sands and gravels, clays and silts, mainly representing inshore deposits. Freshwater horizons are known within the Pre-Pastonian and Pastonian successions (Funnell & West 1977; West 1980*a*).

The currently recognized stages of the Lower Pleistocene of Great Britain (table 1) are based, to a large extent, on the results of pollen analyses from boreholes through a deep part of the Crag basin at Ludham, Norfolk (West 1961, 1980*b*), together with analyses of the Foraminifera (Funnell 1961). Further evidence comes from a similar borehole at Stradbroke, Suffolk (Beck *et al.* 1972), and from many fossiliferous surface exposures in pits and cliff sections; in particular Easton Bavents, Suffolk (Funnell & West 1962), Bramerton, Norfolk (Funnell *et al.* 1979), and the earlier part of the Cromer Forest-bed Formation of the Norfolk and Suffolk coasts (West 1980*a*). The sequence shown in table 1 is, however, undoubtedly incomplete, as indicated by the number of recognized stratigraphical hiatuses. Many more climatic fluctuations are recorded in the much thicker Lower Pleistocene sequence in The Netherlands (see, for example, Zagwijn 1974). Marine mollusc assemblages provide important information on the depositional environments of the beds, and some data on climatic changes (see, for example, Norton 1977).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

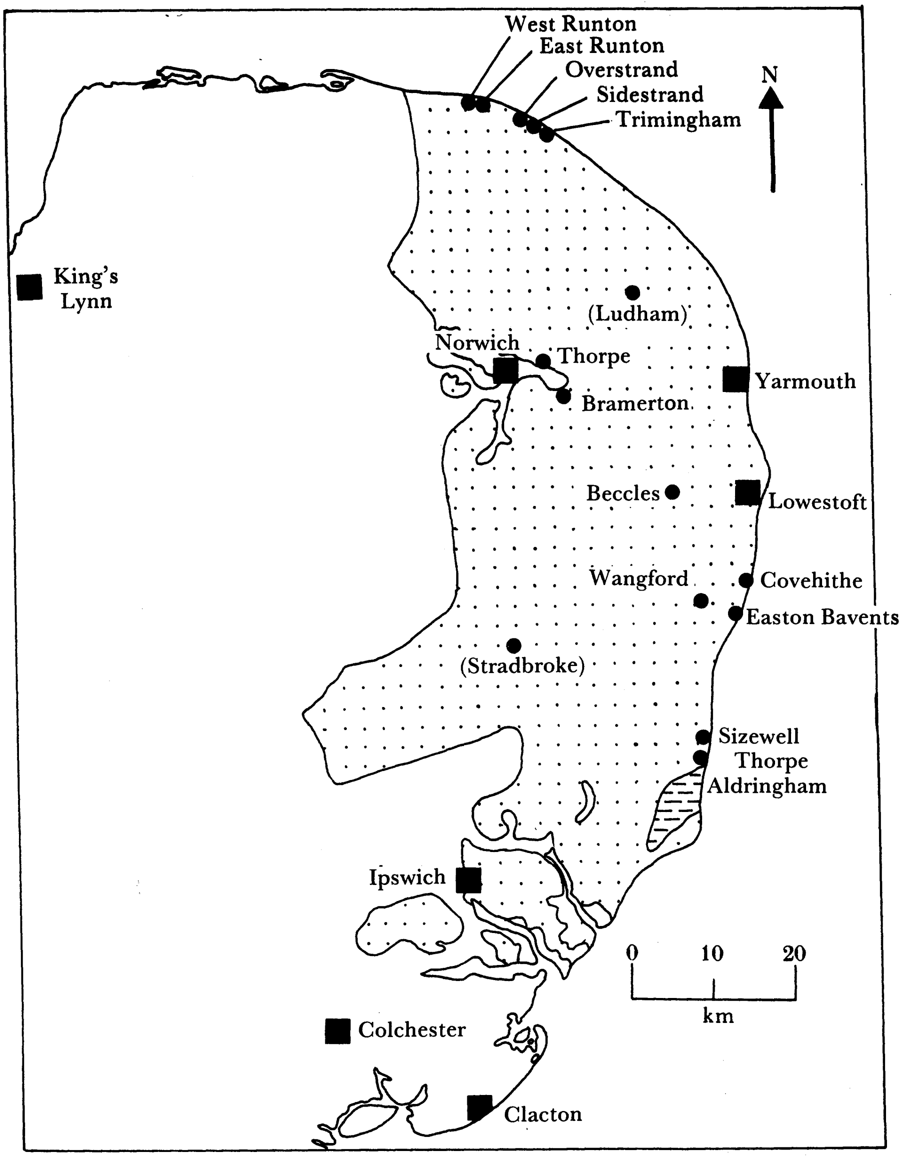

FIGURE 1. Location map of main sites with Lower Pleistocene vole material. The sites of the Ludham and the Stradbroke boreholes and the extent of the Lower Pleistocene Crags (stippled) and Pliocene Coralline Crag (dashed) are given.

Alternating periods of cool and temperate climatic conditions are recorded by both pollen and Foraminifera (Funnell & West 1977). There are difficulties in the interpretation of vegetational conditions from the pollen spectra, as at present not enough is known concerning pollen deposition and preservation in marine environments. Nevertheless, the general picture, of alternating phases of cool climate with oceanic health and temperate phases with mixed coniferous and deciduous forest is clear (West 1977, 1980*b*). The recent discovery of arctic assemblages of Foraminifera and Mollusca in marine clays at Covehithe, Suffolk, indicates that the Baventian stage records the earliest cold period of truly glacial intensity in the British Lower Pleistocene succession (West *et al.* 1980). The chalk below the Stone Bed and 'Crags' at West

Table 1. British Pleistocene stages

(Based on Mitchell *et al.* 1973; West 1977, 1980*a*, 1980*b*; West & Norton 1979.)

	stages	gaps in succession	time b.p. (base) ka	climate	Crags	CF-bF
Upper	Flandrian		10	t		
	Devensian		*ca.* 110	c, p, g		
	Ipswichian			t		
	Wolstonian			c, p, g		
Middle	Hoxnian			t		
	Anglian		? *ca.* 350	c, p, g		
	Cromerian			t		│
		×				│
	Beestonian	×		c, p, ?g		│
		×				│
Lower	Pastonian			t	WC	│
	Pre-Pastonian	×		c, ?p	WC	
	Bramertonian			t	NC	
	Baventian			c, p	NC	
	Antian			t	?	
		×				
	Thurnian			c		
	Ludhamian		? *ca.* 2000	t		
		×				
	Waltonian (Pre-Ludhamian)				RC	

Abbreviation: t, temperate; c, cold; p, evidence for permafrost; g, glacial deposits known; WC, Weybourne Crag; NC, Norwich Crag; RC, Red Crag; CF-bF, Cromer Forest-bed Formation.

Runton, Norfolk, is deeply shattered, resembling the Upper Pleistocene 'Coombe Rock' of southern England and suggesting permafrost conditions within or before the Pre-Pastonian stage (West 1980*a*).

3. Taphonomy and provenance of the fossil vole material

Fossil remains of marine vertebrates, including whales, seals and fishes, are recorded from many crag localities (Newton 1891). It is both fortunate and remarkable that non-marine mammals and other vertebrates are also recorded in some abundance from a number of crag sites, although at others they are scarce or absent (Newton 1891; Stuart 1974, 1982; Funnell *et al.* 1979). For the most part, the occurrence of fossils of non-marine vertebrates in marine sediments is likely to result from material washed into the sea by rivers and streams. At both West Runton, Norfolk (Norton, in West 1980*a*), and Bramerton, Norfolk (Funnell *et al.* 1979), there is a clear association of such material with shells of non-marine Mollusca, indicating a common transport by influxes of fresh water. The Lower Shell Bed of the Bramerton Common Pit was described as 'fluviomarine crag' because of the mixed origins of its molluscan fauna (Harmer 1914–1925).

Fossil voles have so far been obtained from deposits of presumed Antian age and younger (Norwich Crag Formation and Cromer Forest-bed Formation). They are unknown from the Pre-Ludhamian (Red Crag Formation) while Ludhamian and Thurnian deposits have not yet been proved in surface exposures.

It is difficult to assess accurately the importance of reworking of vole remains from older into younger deposits. The fossil teeth show a variety of states of preservation, ranging from fresh and unabraded to rounded and polished, probably reflecting different amounts of fluvial and marine transport. Many molars still retain evidence that they had once been incorporated in the pellets regurgitated by predatory birds, showing characteristic corrosion of the angles near the crown surface (Mayhew 1977). At some localities, limb bones and skull elements of voles are recovered (for example, mandibles at Bramerton). There is apparently, however, no correlation between any species and the state of preservation of the fossil material by which it is represented, which argues against any significant reworking having occurred. Moreover, the geographical distribution of the crags is such that deposits of widely different age are seldom found within the same area (except where there are deep basin-fills known only from boreholes) and not more than two stages or parts of stages are represented at any single crag vole site. It is therefore considered unlikely that vole material could have been reworked from deposits more than one stage earlier than those in which they are now found. The consistency of size distributions for particular taxa within localities strongly indicates that the West Runton, East Runton, and Bramerton Lower Shell Bed assemblages at least do not comprise mixtures of derived and contemporaneous fossils (see figures 2, 4 and 5).

Many of the sites that yielded fossil vole remains in the past are unfortunately now no longer available, so that it is impossible to determine accurately the precise stratigraphic context of the finds. In many cases only the locality is known, so that the age can only be estimated approximately. However, there are a number of crag localities that have also yielded pollen, together with marine mollusca and foraminifers, and these can be related to the standard Lower Pleistocene sequence. Because in the British Lower Pleistocene we are dealing in the main with remains of terrestrial animals transported into a marine depositional environment, little can be said regarding the palaeoecology of the vole taxa. The pollen data only provide evidence (assuming no reworking) of the broad association of a fauna with a regional vegetation of either temperate forest or oceanic heath (see above).

4. Localities yielding fossil vole material (see table 2)

(*a*) *Easton Bavents*; *Covehithe*

The cliff section at Easton Bavents, Suffolk (TM518787), north of Southwold, is subject to rapid erosion, and includes at least 2.8 m of Norwich Crag comprising sands with bands of marine shells and seams of silt overlain by over 2 m of laminated grey and blue clays (Funnell & West 1962).

Pollen analyses of the silt seams in the basal metre of crag indicate temperate forest with *Tsuga*, and the spectra are correlated with pollen assemblage biozone (p.a.b.) Lp3 (Antian stage) of the Ludham borehole (West 1961). The pollen spectra from the laminated clay largely comprise non-tree pollen, mostly Gramineae and Ericales, and resemble the Lp4b assemblages from the Ludham borehole. Easton Bavents has been designated the type section of the cold stage, namely, Baventian, represented by these spectra.

A single pollen sample from the crag, about 1 m below the contact with the overlying clay, records intermediate vegetational conditions and is placed in the first zone of the Baventian stage (Ludham zone Lp4a). Foraminifera from the Lp4a horizon suggest a climate intermediate between glacial and interglacial. The marine Mollusca (Norton & Beck 1972) record changes

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 2. Summary of localities, sites, deposits, dating, and collections studied

locality	site, level, deposits	dating and reference	collection	institution/number	fauna reference
Easton Bavents,	shelly sands underlying and	Baventian; Funnell &	A.J.S.	—	Stuart 1974, 1982
Suffolk	intercalated with clays	West 1962	P. Long	IM	
			P. Long	BMNH/M20278, 9	Cranbrook 1955*a*, *b*
		type locality	P. Long	IGS	Carreck 1966
			R. Markham	IM	
Covehithe, Suffolk	shelly sands underlying	Baventian; Long 1974;	P. Long	—	Stuart 1974, 1982
	clays (Covehithe Warren)	West *et al.* 1980	P. Long	IM	
			P. G. Cambridge	—	
Bramerton, Norfolk	(*a*) Bramerton Common Pit	Bramertonian,	Kennard	BMNH/M36156–8	
	shelly sands, silt	Funnell *et al.* 1979	Hinton–Johnson	BMNH/M35153–5	Hinton 1926
	('Norwich Crag')		?	BMNH/M36159, 60, 62	Stuart 1974, 1982
	(*b*) Blake's Pit	type locality	Reeve	NCM/524, 728, 747	Newton 1882
	shelly sands, silt		P. G. Cambridge	SM/X.7918–7933	Funnell *et al.* 1979
			Blake's Pit		
Sizewell, Suffolk	shelly sands at Rifle	? Bramertonian	P. Long	—	Stuart 1974;
	Range Pit and excavations for	Funnell *et al.* 1979;	P. G. Cambridge	—	Newton 1882
	power station	West & Norton 1974			
Thorpe, Aldringham,	pit near Shell Pit	? Bramertonian;	P. G. Cambridge	—	—
Suffolk	Cottages, basal shelly sands	Funnell *et al.* 1979;			
	with *Macoma calcarea*	West & Norton 1974			
Wangford, Suffolk	Icenian Crag	? Bramertonian;	P. G. Cambridge	—	—
		Funnell *et al.* 1979;			
		West & Norton 1974			
Thorpe, Norwich,	Asylum Pit, shelly sands	?? Bramertonian	Fitch	NCM/971*a*–*h*, 551	Stuart 1974
Norfolk					Major 1902
					Newton 1882
Sidestrand,	site SSB, sand with shells	Pre-Pastonian *a*;	A.J.S.	—	Stuart 1982
Norfolk	and silt-clay laminae	West 1980*a*			
	overlying chalk mass				
Overstrand,	shelly sand overlying	? Pre-Pastonian *a*;	P. G. Cambridge	—	—
Norfolk	chalk mass	West 1980*a*			
East Runton,	grey shelly sands	Pre-Pastonian?;	Kennard	BMNH/M35163–68	Hinton 1926;
Norfolk	('Weybourne Crag')	West 1980*a*	Savin	BMNH/M6967/Savin 430	Major 1902;
			Reid	IGS/GSM115486–501	Stuart 1974, 1982
	clay gravel	? Pre-Pastonian or	Reid	IGS/GSM115482–5	
		Pastonian;			
		West 1980*a*			
Trimingham,	Weybourne Crag	? Pre-Pastonian;	Reid	IGS/GSM98637	Hinton 1926;
Norfolk		West 1980*a*			Stuart 1974
West Runton,	WRC-P; shelly sand 100 m E	? Pre-Pastonian or	A.J.S. }		Stuart 1982
Norfolk	of gap	?? Pastonian;			
	WRC-X; shelly sand 90 m W	West 1980*a*	A.J.S. }	UMZC/WRC1–700	
	of gap				
	WRC-G; shelly sand 27 m E		A.J.S. }		
	of gap		D.F.M.		
Yarn Hill,	'Norwich Crag'	?	Kennard	BMNH/M35152	—
Suffolk					
Caistor-by-Norwich,	'Norwich Crag'	?	P. G. Cambridge	—	—
Norfolk					
Holton, Suffolk	'Norwich Crag'	?	Packman	BMNH/M35151	—
Beccles, Suffolk	'Norwich Crag'	?	P. G. Cambridge	—	—
Kyson, Suffolk	?	?	?	BMNH/M36568	Hinton 1926

from open coast littoral conditions in the base of the crag to sublittoral conditions towards the top.

Non-marine vertebrates occur sparsely in the crag (for faunal lists see Stuart 1974, 1982). Teeth of *Mimomys pliocaenicus* from the 'Upper Shell Bed', probably of early Baventian age, were described by Carreck (1966). Unfortunately, these could not be traced for the present study. The material described here consists of a few teeth collected by A. J. S. from crag exposed at the cliff base near the type locality in 1976, and is of late Antian or Early Baventian age, probably the latter.

Marine clays with shells, of Baventian p.a.b. Lp4b, are recorded from Covehithe (TM527816), Suffolk, about 3 km northwards along the coast from Easton Bavents (West *et al.* 1980). The sparse material from Covehithe, collected by P. and D. Long from Covehithe Warren, came from shelly sand immediately underlying the blue-grey Baventian clay (Unit A of Long (1974)). This dates from either late Antian or early Baventian.

(*b*) *Bramerton*

The pit at Bramerton Common, near Norwich, (TG295060) has long been regarded as the type section for the Norwich Crag (Reid 1890) and was first described by Taylor (1823). A later excavation known as Blake's Pit (TG298060) some 300 m away was first noted by Reeve in 1870. The stratigraphy, pollen, Foraminifera and marine Mollusca from these two localities have recently been described in detail by Funnell *et al.* (1979), who include a review of earlier work.

At both localities, sands with local shell seams and minor beds of silts and gravel rest on chalk at about 2–3 m O.D. The thickness of crag deposits varies from about 6 m at Blake's Pit to about 12 m at Bramerton Common. Pollen analyses from silts at Blake's Pit permit the recognition of an *Alnus–Quercus–Carpinus* p.a.b. covering the basal 4 m and a *Pinus*–Ericales–Gramineae p.a.b. for a single sample at about 5 m above the chalk. The earlier p.a.b., representing temperate forest, is assigned by these authors to a new stage named the Bramertonian with Blake's Pit as the type locality, whereas the later p.a.b., representing heath and herbaceous communities, and a sharp deterioration in climate, is correlated by them with the Pre-Pastonian *a* substage of the Norfolk coast. The foraminiferan and molluscan assemblages at Blake's Pit confirm the climatic sequence inferred from pollen evidence and allow fairly definite correlation with the Bramerton Common section. Here the lower 3–4 m appear to be of Bramertonian age, with a cooler phase beginning at about 4.5 m above the chalk.

The Mollusca indicate littoral or sublittoral conditions of deposition for most of the sequence, interrupted by periods with brackish sheltered tidal flat conditions and a 'fluviomarine' molluscan assemblage comprising marine, brackish and washed-in non-marine species. Significantly, this 'fluviomarine' facies corresponds to the Lower Shell Bed at both Blake's Pit and Bramerton Common, and to the Upper Shell Bed at the former site. All three horizons are known to have yielded non-marine vertebrates, including voles.

The vertebrate fauna from Bramerton was listed by Mayhew (in Funnell *et al.* 1979). Most of the material was found in the last century, notably by Reeve. Unfortunately it is not certain from which pit most of the specimens are derived. Recently, a very valuable collection of fossil voles has been collected from the Lower Shell Bed of Blake's Pit (that is, type Bramertonian) by Mr P. G. Cambridge. Older material labelled 'Lower Shell Bed' is also almost certainly of Bramertonian age, while material labelled 'Upper Shell Bed' is likely to date from the subsequent cool phase.

We consider the proposed correlation of the cool phase in the Bramerton sequence with the Pre-Pastonian stage (Funnell *et al.* 1979) to be unlikely, since the mollusc *Macoma balthica* which occurs abundantly in Pre-Pastonian sediments is absent from Bramerton. The evidence presented here from the vole faunas also suggests a considerable interval of time between the Bramertonian and the Pre-Pastonian stages.

(*c*) *Sizewell*; *Thorpe Aldringham*; *Wangford*

Pollen spectra from the Norwich Crag of both Sizewell (TM474632) and Thorpe Aldringham (TM465608), Suffolk, were correlated with the Chillesford pollen assemblage by West & Norton (1974). This assemblage is now correlated with the Bramertonian temperate stage (Funnell *et al.* 1979). Material from Thorpe Aldringham has been collected by Mr P. G. Cambridge from the basal shell layer (with *Macoma calcarea*) of the pit near Shell Pit Cottages noted by West & Norton (1974). At Sizewell, vole remains have been recovered from the old Rifle Range Pit, now obscured, and from later excavations in connnection with the power station (P. Long, personal communication). The pollen spectrum from Wangford (TM464779), Suffolk, was less confidently matched with the Chillesford pollen assemblage by West & Norton (1974), so the age of vole material from this site is less certain.

(*d*) *Thorpe Asylum Pit, Norwich*

Sutcliffe & Kowalski (1976, p. 96) discussed several possible options concerning the source of material collected in the last century by Mr R. Fitch, and labelled 'Thorpe'. Prestwich (1871) clearly states, however, that Fitch collected a large series of mammalian and molluscan remains from the pit near the Asylum at Thorpe, Norwich (TG276090). He stated that the pit 'exhibits the best known and most interesting section of the Norwich Crag' and includes a drawing of the section. This is summarized below.

deposits	thickness
(*c*) Ochreous and ferruginous sands and flint–shingle, with a layer of iron–sandstone full of casts of shells near base.	20 feet (6 m)
(*b*) Grey clay with a few large worn flints.	1–1.5 feet (0.3–0.45 m)
(*a*) White sands with seams of gravel and patches of shells, with a layer of flints at base.	5–12 feet (1.5–3.6 m)
Chalk	

Mammalian remains, including '*Arvicola*' (that is *Mimomys*) are stated to be common chiefly among or immediately upon the basement bed of worn flints. It is possible that some of the material was from higher horizons. The pit is unfortunately no longer accessible. Because the deposits have not recently been studied the stratigraphical position of the crag here is unknown. It is considered likely to be of Bramertonian or similar age on the basis of the mammalian fauna.

(*e*) *Sidestrand*; *Overstrand*

Large chalk masses with overlying Lower Pleistocene deposits have been thrust up and are now exposed in cliff section between Sidestrand (TG252410) and Overstrand (TG255405),

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Norfolk. This provides an opportunity to study deposits which elsewhere are confined to beneath the beach and the foreshore. At locality SSB, 2.5 m of sand with marine shells, occasional silty-clay laminae and seams of clay-conglomerate and gravel overlie the Stone Bed, which in turn rests on Chalk (West 1980*a*). Pollen spectra from silts within the crag at SSB show a high non-tree pollen content with Gramineae and *Empetrum*, and trees dominated by *Pinus* with smaller amounts of *Picea*, *Alnus* and *Betula*. These spectra are correlated by West to the Pre-Pastonian *a* substage (West 1980*a*). A park–tundra vegetation and a cold climate are indicated. Funnell (1970) reported that the Foraminifera at this site were indicative of semiglacial conditions, and Norton (1967) concluded from a study of an adjacent section (SSK) that the Molluscan fauna was impoverished, and indicated very shallow, tidal, conditions. Samples of small vertebrates were obtained by A.J.S. by sieving the basal 30 cm of crag at SSB. The specimens are considered to date from the Pre-Pastonian *a* substage.

The material identified here as from Overstrand was collected by Mr P. G. Cambridge from shelly sand overlying the most westerly chalk mass in the cliff between Sidestrand and Overstrand. This corresponds closely to the locality SSB described above, and is presumed to be of similar age.

(*f*) *East Runton, Norfolk*

Reid (1882, p. 15) recorded a typical section in the foreshore 0.25 mile (400 m) southeast of East Runton Gap, (TG203428) in which about 4 feet (1.2 m) of grey shelly crag with about 6 inches (15 cm) of unworn flints and clay (Stone Bed) at the base, together constituting the 'Weybourne Crag', were seen resting on chalk. The crag was succeeded by a bed of rolled clay pebbles, resting on an eroded surface, in turn overlain by a bed of laminated clay with wood and other plant material. Reid stated that the vole '*Arvicola intermedius* Newton' is very abundant in this bed 'and land and freshwater shells not uncommon'. The same sequence was observed by Reid to occur westwards along the coast as far as Wood Hill. Grey crag containing iron pyrites, overlain by clay–pebble conglomerate in a small basin structure was seen by A.J.S. in 1976 about 200 m west of East Runton Gap. This crag yielded sparse fragments of vole teeth and other vertebrate material.

West (1980*a*) describes a bed of iron-cemented gravels with marine shell fragments and containing clay conglomerate (bed *c*), at a lower level than bed *d*i (elsewhere containing Pastonian zone II pollen), stretching to about 50 m east of Woman Hithe Gap. He also states that a horizon of similar lithology, with many small basin structures a few metres across extends from 500 m east of Woman Hithe Gap eastwards as far as East Runton, and also to the west. It has an estimated thickness of 2–3 m and overlies up to 40 cm of grey or red shelly sands (bed *c*) which rest on the stone bed.

At ERA, 400 m east of East Runton Gap, West records freshwater muddy silt yielding a Pre-Pastonian *d* pollen spectrum. This is equated with the Lower Freshwater Bed of Reid (1882) who observed that it rested on crag and was overlain by laminated silts, probably equivalent to West's beds *d*i and *d*ii.

The age of the East Runton crag resting on the stone bed therefore appears to be Pre-Pastonian, while the clay conglomerate may be of Pre-Pastonian or Pastonian age. Vole teeth labelled 'shelly sands' (Savin collection, BMNH), and 'Weybourne Crag' (Reid collection, IGS) are probably therefore of Pre-Pastonian age. Material from the clay–pebble bed (Reid collection, IGS) is of either Pre-Pastonian or Pastonian age.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(*g*) *Trimingham*

A single vole tooth, the type of *Mimomys reidi* Hinton, is recorded from the 'Weybourne Crag' of Trimingham, Norfolk (TG281391). In the absence of more precise data on both the locality and the stratigraphic position of the find, the age cannot be determined. According to West (1980*a*) the crags of this part of the coast date from a period including the Pre-Pastonian and Pastonian stages.

(*h*) *West Runton*

Trenches dug for the construction of sea defences near West Runton Gap, Norfolk (TG186433) (Woman Hithe) in 1975–76 exposed up to 2 m of shelly sands ('Weybourne Crag') and tidal silts extending from about 2–4 m O.D. At about 40 m west of Woman Hithe these silts were seen to occupy a channel cut into the crag, whereas up to 20 m east of the gap, silts were seen to interdigitate with crag deposits (West 1980*a*, figure 8).

Pre-Pastonian *a* pollen spectra (*Pinus–Betula*–Gramineae–Ericales p.a.b.) were recorded from crag (bed *c*) at localities WRQ and WRE by West (1980*a*). The silts, bed *d*i, have yielded pollen characteristic of zone II of the Pastonian temperate stage (West 1980*a*).

Sparse vertebrate remains including vole teeth were collected by A. J. S. from the shelly sands in the trench at about 100 m east of Woman Hithe (sample WRC-P). A single tooth was found in crag exposed at the base of the cliff approximately 90 m west of Woman Hithe (WRC-X). The main vertebrate sample was taken from an excavation kindly dug by May–Gurney Ltd, through the auspices of the Nature Conservancy Council, in 1976 at a spot 10 m north of the concrete sea wall, and 27 m east of the concrete slipway at Woman Hithe (WRC-G). About 150 kg of crag from a thickness of 1 m, equivalent to approximately 1–2 m below datum in figure 8*c* of West (1980*a*) was processed to extract small vertebrate remains. The sample recovered by D. F. M. from West Runton came from crag excavated from a depth of approximately 1.5 m below the beach level near the main sample WRC-G.

Since the vertebrate samples were not taken in the immediate vicinity of pollen samples, no direct evidence of age in terms of pollen stages is available. They could be of Pastonian or Pre-Pastonian age.

(*i*) *Additional localities*

Sparse vole material is also recorded from several sites where the age of the crag is uncertain. These localities include Yarn Hill near Southwold, Suffolk (possibly Antian–Baventian), Caistor-by-Norwich, Norfolk (possibly Bramertonian), Holton, Norfolk (possibly Bramertonian or older), and Beccles, Suffolk. The records from Kyson, Woodbridge, Suffolk are enigmatic since this is thought to be a locality in Red Crag deposits, and the material is indistinguishable from that of *Mimomys pliocaenicus* from the younger crags.

5. History of research on the fossil material

Published research on British fossil voles began essentially with Owen (1846) who described specimens from the Cromer Forest-bed Formation as '*Arvicola*' intermediate in size between *A. amphibia* and *A. arvalis*. These specimens, and teeth from the 'fluviomarine crag' at Bramerton referred to *Arvicola amphibius*, were noted by Blackmore & Alston (1874). Newton

(1882) noticed that this fossil material included teeth that were rooted, and he therefore created a new species, *Arvicola* (*Evotomys*) *intermedius*. This species was said to differ from *A.amphibius* in having rooted cheek teeth and in being of smaller size (Newton 1891).

Major (1902) described and figured material from several British localities and from the Val d'Arno, drawing attention to the increasing frequency with geological age of the presence of an enamel islet on the wear surface of the lower first molar, and to size differences within material from a single locality. He introduced the generic name *Mimomys* for 'all those voles with rooted molars which are clearly different from *Evotomys*, *Phenacomys* and *Dolomys*', and concluded that the British Middle and Lower Pleistocene *Mimomys* material represented several species. He proposed the name *Mimomys newtoni* for 'a smaller, rooted form from the Norwich Crag and East Runton which has characters of its own', restricted the use of the name *Mimomys intermedius* (Newton) to specimens from East Runton and the Upper Freshwater Bed at West Runton, and used the name *Mimomys pliocaenicus* (Maj.) for 'the larger Crag form' from Thorpe, Bramerton, Ostend, East Runton and Kyson. The apparent presence of both *M.intermedius* and *M.pliocaenicus* in the deposits at East Runton was explained as being due to derivation of *M.pliocaenicus* from older deposits: 'this leads to the assumption that the Crag types have been washed into the East Runton deposit' (Major 1908).

Shortly after, Hinton (1910) published his preliminary results of a study of the British fossil vole material. The new species *Mimomys reidi* was created for a lower first molar from Trimingham, previously figured as *M.intermedius* by Newton (1882), and diagnosed as 'highly specialised as regards reduction of the third outer valley, but generalised with respect to persistent confluent dentinal spaces. Size small'. Hinton (1910) described two further species of *Mimomys*, *M.savini* and *M.majori* based on material from the Upper Freshwater Bed at West Runton. As a result of Hinton's conclusions, the use of the name *M.intermedius* (Newton) was restricted to those lower first molar morphotypes which were 'reduced so as to closely resemble the corresponding tooth of *Arvicola*'. Types of *M.intermedius*, *M.savini*, *M.majori* and *M.reidi* were designated by reference to figures in Newton (1882) and Major (1902).

The diagnoses and descriptions of these species were extended by the substantial review of Hinton (1926), who figured much of the then available British material of *Mimomys*, and took into account the then rather limited European literature on fossil voles. He recognized the following species: *M.intermedius*, *M.savini*, *M.majori*, *M.pliocaenicus*, *M.newtoni*, *M.reidi*, and *M.pusillus* (originally described by Méhely 1914). Since the work of Hinton, the British Lower Pleistocene vole material has attracted relatively little attention. Reports of new material contributing to locality records of individual species have been given by Cranbrook (1955*a*,*b*) and Carreck (1966). More recently, Sutcliffe & Kowalski (1976) reviewed the British Pleistocene rodents, recording the species *Mimomys pliocaenicus*, *Mimomys reidi*, and *Mimomys newtoni* from the Lower Pleistocene Norwich Crag and Weybourne Crag deposits. They pointed out that the material identified as *M.newtoni* in the BMNH collections from East Runton was heterogeneous, probably representing at least two species. In addition they noted that the type of *M.newtoni* lacked crown cement, an important point that had been overlooked by all previous workers.

In a discussion of the deposits at East Runton, Sutcliffe & Kowalski (1976) concluded that these had yielded remains of the vole species *M.savini* ('represented by a few specimens from the Shelly Crag'), *M.pliocaenicus* and *M.newtoni*, thus essentially echoing the conclusion reached by Major (1902, 1908) and repeated by Hinton (1926), that the faunal remains from East Runton represented a mixture of faunas of differing age.

Although Hinton's review of the voles and lemmings (1926) remains a standard work on the subject, subsequent research based on more abundant material in European collections, and progress in our understanding of ecological and evolutionary principles in relation to taxonomy have, inevitably, substantially modified some of the conclusions. For example, the 'species' *M.intermedius*, *M.savini* and *M.majori* are now regarded as based on extreme variants within a single species, the valid prior name of which is *M.savini* (Kretzoi 1965; Pasquier 1972). The species *M.petenyii* (Méhely) and *M.reidi* Hinton, thought by Hinton to be synonymous, are now regarded as separate species in different lines of descent (Janossy & van der Meulen 1975), and the diagnosis of *M.reidi* consequently requires revision.

Taking into account the advances in stratigraphic knowledge summarized by West (1980*a*), and Funnell *et al.* (1979), the following problem areas were identified through a review of the literature: the diagnosis of *M.reidi*, the taxonomy of material previously referred to *M.newtoni*, the composition of the assemblages from East Runton, and the differences between samples of *M.pliocaenicus* from localities of different age. In addition, examination of new collections of British Lower Pleistocene vole material in the light of current knowledge of European faunas indicated the presence of species previously unrecognized from Britain. It was therefore decided to examine all available material, including the older collections, to enable a thorough systematic and stratigraphic revision which would provide solutions to the problem areas listed above.

6. Systematic revision

(*a*) *Introduction*

The material brought together by earlier collectors such as Fitch, Savin, Reeve and Kennard is now, for the most part, in public collections which were studied in the following institutions: British Museum (Natural History) (BMNH); Institute of Geological Sciences (GSM); Norwich Castle Museum (NCM); Ipswich Museum (IM); Sedgwick Museum, Cambridge (SM) and the University Museum of Zoology, Cambridge (UMZC). In addition, the authors have been privileged to examine material in the private collections of Mr P. G. Cambridge (P.G.C.) and Dr P. E. Long (P.E.L.), and have themselves collected material mentioned here under the initials A.J.S. and D.F.M. While some of the specimens figured by previous authors could no longer be traced, and further material perhaps exists in private collections that have not been seen, the broad aim to review and figure the significant material is considered to have been achieved.

The study has been complicated by the nature of the material. Preservation ranges from poor to excellent. There are a number of localities, but each locality has yielded only a relatively small number of teeth, in some cases only a single tooth. This is not enough to provide specimens of all teeth of each species present at a particular locality. The identification of all teeth to species level, especially second and third molars, was therefore not possible. The relatively large sample from West Runton (Crag) collected by A.J.S. was particularly useful as a reference collection, as was some still undescribed material from the locality Bulcamp in the collections of D.F.M., P.E.L. and P.G.C.

The illustrations provided here are the first representations of the range of morphologies found in British Lower Pleistocene material which are adequate for comparison with recent work on continental European faunas. Their aim is to provide support for the identifications proposed here, and, perhaps more importantly, to provide a sound reference point for future work.

Measurements given here were taken with a travelling microscope and eyepiece micrometer

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

reading to 0.02 mm. Crown height and heights of enamel-free areas were measured by using the base of the enamel of the first labial reentrant fold as a reference point, as suggested by van de Weerd (1976).

As a result of this study, the following vole taxa have been recognized by the authors in British Lower Pleistocene material: *Mimomys pliocaenicus* Major, *Mimomys rex* Kormos, *Mimomys newtoni* Major (= *M. hungaricus* Kormos), *Mimomys reidi* Hinton, *Mimomys pitymyoides* Janossy & van der Meulen, *Mimomys blanci* van der Meulen, *Mimomys altenburgensis* Rabeder and *Clethrionomys* sp. These taxa are discussed in detail in the following sections.

(*b*) *Mimomys pliocaenicus* Major 1902

Figures 2–8, 18–26.

1874 *Arvicola amphibius* (L.): Blackmore & Alston: pp. 462–464 (*partim*).
1882 *Arvicola* (*Evotomys*) *intermedius*: Newton: plate 13 (*partim*).
1902 *Mimomys pliocaenicus*: Major: pp. 102–107, figures 13–15 (*partim*).
1910 *Mimomys pliocaenicus*: Hinton: p. 491.
1914 *Mimomys pliocaenicus*: Méhely: p. 186.
1926 *Mimomys pliocaenicus*: Hinton: p. 357 (*partim*).
1926 *Mimomys savini*: Hinton: p. 365 (*partim*).
1926 *Mimomys intermedius*: Hinton: p. 368 (*partim*).
1926 *Mimomys majori*: Hinton: p. 378 (*partim*).
1966 *Mimomys pliocaenicus*: Carreck: p. 491.
1976 *Mimomys pliocaenicus*: Sutcliffe & Kowalski: p. 95.
1976 *Mimomys newtoni*: Sutcliffe & Kowalski: p. 98 (*partim*).
1976 *Mimomys savini*: Sutcliffe & Kowalski: p. 98 (*partim*).
1976 *Mimomys pliocaenicus*: Freudenthal *et al.*: p. 15, figures 2 and 3.
1979 *Mimomys pliocaenicus*: Mayhew; in Funnell *et al.*: p. 531.

(i) *Diagnosis*

A large species of *Mimomys*, with abundant crown cement and with enamel thicker on the convex sides of the triangles. M_1 and M^3 with an enamel islet isolated before root formation and persisting for a relatively long period of wear. M^1–M^3 two or three rooted.

(ii) *Description*

The basic characters of this species were described by Hinton (1926). As a result of accumulation of new material it is possible to add to this, in particular by comparing the taxonomic characters in samples of *M. pliocaenicus* from different localities. The characters examined include the overall size of M_1, the number of roots in M^1 and M^3, and the relation between crown height and loss of the enamel islet in M_1. Before discussing the results of this study, however, it is necessary to review the taxonomic status of the larger *Mimomys* material from East Runton, to define the sample of *M. pliocaenicus* from this locality.

(iii) *Mimomys pliocaenicus from East Runton*

As recorded in the previous stratigraphic section, the Lower Pleistocene deposits at East Runton include shelly sands, termed 'Weybourne Crag' by earlier collectors, overlain in places by a 'clay conglomerate' ('clay pebbles') of later age. According to Hinton (1926, p. 358), the shelly sand at East Runton yielded remains not only of *M. pliocaenicus*, but also of *M. savini*, *M.intermedius* and *M.majori*. Sutcliffe & Kowalski (1976) recorded that *M.savini* (including *M.majori* and *M.intermedius*) was 'represented by a few specimens from the Shelly Crag', but raised the possibility that accidental mixing of material from different layers had occurred.

The material available from East Runton consists entirely of older collections which were also studied by Hinton (BMNH and GSM collections). After examining these collections and the diaries of the collectors there is, in our view, no evidence that any remains attributable to *Mimomys savini* have been recovered from the shelly sand or clay conglomerate layers in the foreshore at East Runton. The few specimens of *M.savini* labelled as having come from East Runton are from other deposits such as a 'gravel pan at the base of the cliff, ¼ mile S. of the gangway' (BMNH M69653) or the Upper Freshwater Bed at West Runton (specimen relabelled East Runton without explanation) which are known, or are presumed to be, of Cromerian age.

The remaining larger *Mimomys* material from East Runton, figured here on figures 24 and 25, appears to us to represent a single taxon. Although previous authors have referred specimens from this assemblage to a variety of taxa, including *M.newtoni* (*sensu* Hinton; Sutcliffe & Kowalski 1976, p. 98) and some of the teeth are labelled, in Hinton's handwriting, with a new name that was never published, this taxon is in our view an advanced form of *Mimomys pliocaenicus*.

Major (1908), who originally proposed the view that the East Runton deposits contained a mixture of remains of different geological age, used as evidence the supposed occurrence together of two beaver species, *Castor plicidens* and *Castor fiber*. These remains are now considered to belong to a single species, *Castor fiber*, the differences being due to ontogenetic age (Mayhew 1975). There is therefore no evidence for mixing of two faunas of different age in the shelly sands and clay conglomerate deposits of East Runton. The same species are present in these two types of deposit (see table 3). These species are also present in the shelly sands at West Runton.

(iv) *Size of* M_1 (figures 2–5, figure 8, table 4)

The sample from the crag at West Runton, taken by the authors from a restricted area and horizon is the most homogeneous in size. Teeth from the shelly crag and clay conglomerate at East Runton have a similar scatter but are of smaller average size ($t = 2.15$, $p < 0.05$).

Table 3. Vole species present in different collections from East Runton and West Runton (crag)

Species	East Runton					West Runton
	BMNH M35163–68 Kennard collection 'Weybourne Crag'	BMNH M6967 Savin collection 'Weybourne Crag 30 yards from cliff'	GSM 115482–85 Reid collection clay gravel W of gap'	GSM 115486–95 Reid collection 'Weybourne Crag grey shelly crag'	GSM 115496–501 Reid collection 'Weybourne Crag'	UMZC WRC 1–700 A.J.S. collection WRC-G, P, X 'Weybourne Crag'
Mimomys pliocaenicus	×	×	×	×	×	×
Mimomys reidi	.	.	×	×	?	×
Mimomys blanci	×	×	×	×	×	×
Mimomys newtoni	.	type	?	.	.	×
Mimomys pitymyoides	.	.	.	×	×	×

Samples from Thorpe and Bramerton have relatively large scatters, suggesting that both represent collections of material of different geological age. *M.pliocaenicus* from Tegelen is broadly similar in size to the British material. (length of M_1 3.20–3.45 mm (Janossy & van der Meulen 1975, figure 1).

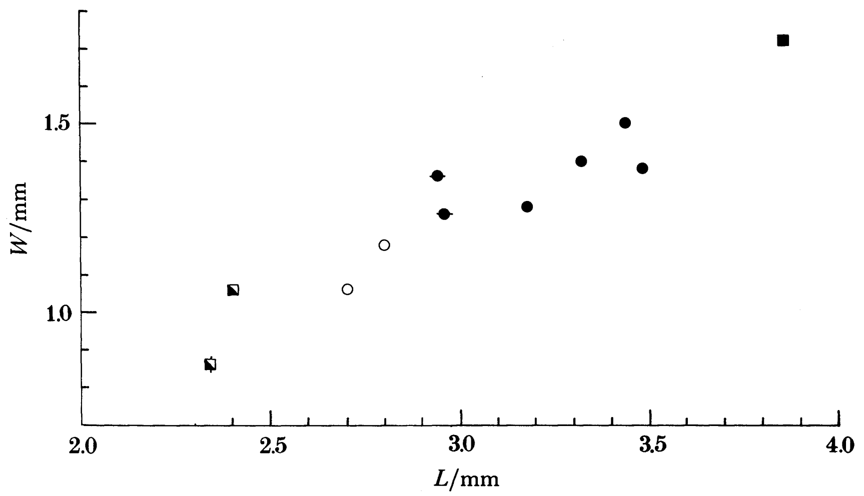

FIGURE 2. Scatter diagram of length (L) and width (W) of M_1 from Bramerton, Norfolk (Bramertonian). Key to figures 2–5: ●, *Mimomys pliocaenicus*; ▲, *Mimomys blanci*; ○, *Mimomys newtoni*; ■, *Mimomys rex*; □, *Mimomys reidi*; △, *Mimomys pitymyoides*; ◩, *Mimomys altenburgensis*. Lines through symbols indicate that the values were estimated.

TABLE 4. *MIMOMYS PLIOCAENICUS*: MEASUREMENTS OF M_1 WEAR SURFACE

	length/mm				width/mm			
locality	$\bar{x}$	range	s.d.	n	$\bar{x}$	range	s.d.	n
West Runton Crag	3.32	3.18–3.56	0.12	7	1.38	1.14–1.50	0.10	7
East Runton	3.14	2.94–3.36	0.18	6	1.34	1.22–1.42	0.08	5
Thorpe	3.26	2.88–3.64	0.26	7	1.41	1.18–1.66	0.19	7
Bramerton	3.21	2.94–3.48	0.24	6	1.36	1.26–1.50	0.09	6

(v) *Number of roots in* M^1 *and* M^3 (table 5)

Hinton (1926, pp. 359 and 362) stated that the M^1 of *M.pliocaenicus* was three-rooted, and the M^3 two-rooted. However, this does not mean that this description refers to molars from the same population, since the first molars were from Thorpe and Bramerton, the third molars were from East Runton, and these localities differ in age. Analysis of the available material indicates that the number of roots in M^1, M^2 and M^3 differs between localities, and that, in general, a higher number of roots is found in material from older localities. The information available is summarized in table 5.

While all upper first molars from the Norwich Crag localities of Bramerton and Thorpe are three-rooted, intermediate forms and specimens with only two roots are found in material from East Runton and West Runton. Upper third molars with three roots occur in material from Bramerton and Thorpe Aldringham. In addition it should be noted that some upper second molars from deposits of Bramertonian age have four roots.

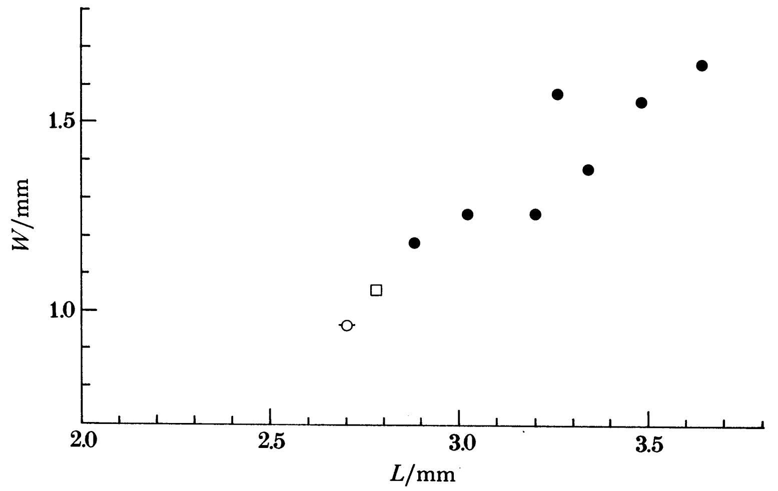

FIGURE 3. Scatter diagram of length (L) and width (W) of M_1 from Thorpe, Norwich. (For key to symbols see figure 2.)

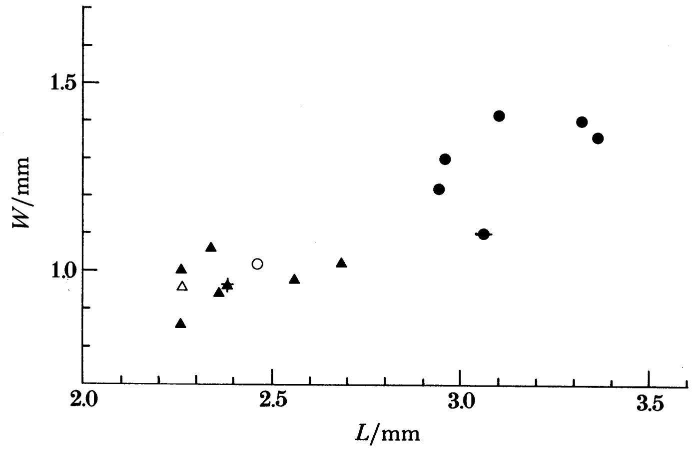

FIGURE 4. Scatter diagram of length (L) and width (W) of M_1 from East Runton, Norfolk (Pre-Pastonian, ? Pastonian). (For key to symbols see figure 2.)

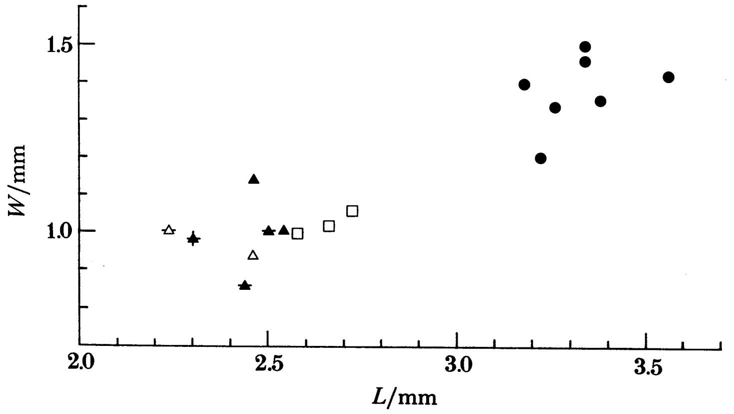

FIGURE 5. Scatter diagram of length (L) and width (W) of M_1 from West Runton, Norfolk. (For key to symbols see figure 2.)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(vi) *Crown height* (figures 6 and 7)

Differences in crown height between samples from the main localities were noticed. The differences are shown in figure 6. This indicates, for four localities, crown height (perpendicular distance from the wear surface to the base of the enamel of the first labial re-entrant) and enamel islet status (present, disappearing, lost) in lower first molars. The results suggest that the samples from Bramerton and Thorpe were derived from populations of similar crown height. However, the enamel islet disappears about 1 mm higher in the crown in the West Runton series than in the Bramerton series. The enamel islet is present only at an early stage of wear in the East Runton series. It can be concluded that we are dealing here with at least two stages in the evolution of hypsodonty in *Mimomys pliocaenicus*.

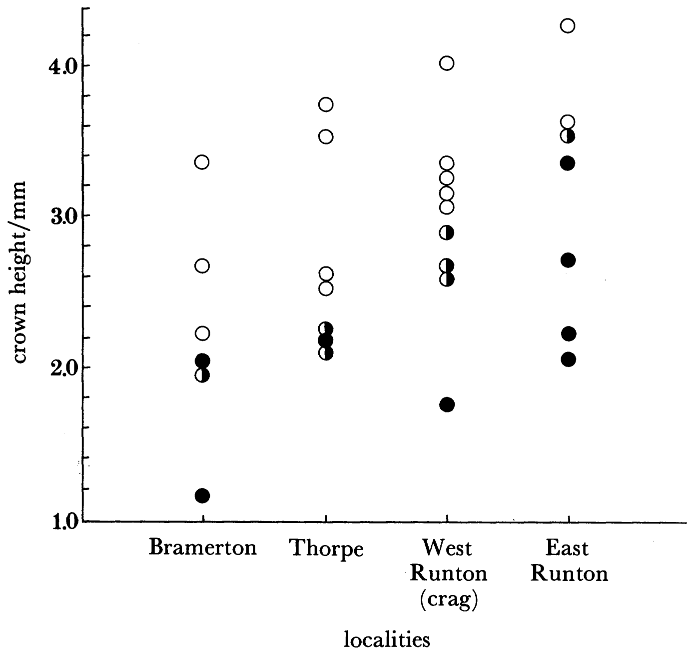

FIGURE 6. Relationship of crown height (measured according to van de Weerd (1976)) to disappearance of the enamel islet in lower first molars of *Mimomys pliocaenicus* from four British Lower Pleistocene localities ○, Enamel islet present; ◑, remains of islet visible as 'osteodentine' trace; ●, no islet. The islet disappears higher in the crown in teeth from West Runton (Crag) and East Runton (Pre-Pastonian–Pastonian) than in those from Bramerton and Thorpe (Bramertonian).

TABLE 5. *MIMOMYS PLIOCAENICUS*: NUMBER OF ROOTS IN M^1 AND M^3

	M^1			M^3		
locality	three roots	partly fused	two roots	three roots	partly fused	two roots
West Runton	1	1	1	—	—	3
East Runton	4	1	2	—	—	3
Sidestrand	—	—	—	—	—	1
Bramerton	4	—	—	3	—	—
Thorpe	9	—	—	—	—	—
Thorpe Aldringham	—	—	—	1	—	—
Easton Bavents	3	—	1	—	—	—
Covehithe	—	—	—	—	—	1

A further comparison of crown heights was suggested by Chaline (1974). In figure 7 the length of the wear surface of lower first molars is plotted against the height of the anterior enamel-free area, measured from the base of the enamel of the rear margin of the tooth. Compared with the method used for figure 6, this method has the disadvantage that hardly any suitably young teeth are well enough preserved to measure. Only two teeth, from East Runton and West Runton, were found to be suitable. This is insufficient, in view of individual variation, to provide information on the relative crown height between British localities. However, it does enable a broad comparison with material from some continental European localities. It appears that the British material is intermediate in crown height between *Mimomys polonicus* from the type locality, Rebielice Krolewski, Poland, and *Mimomys pliocaenicus* from Kadzielnia, Poland.

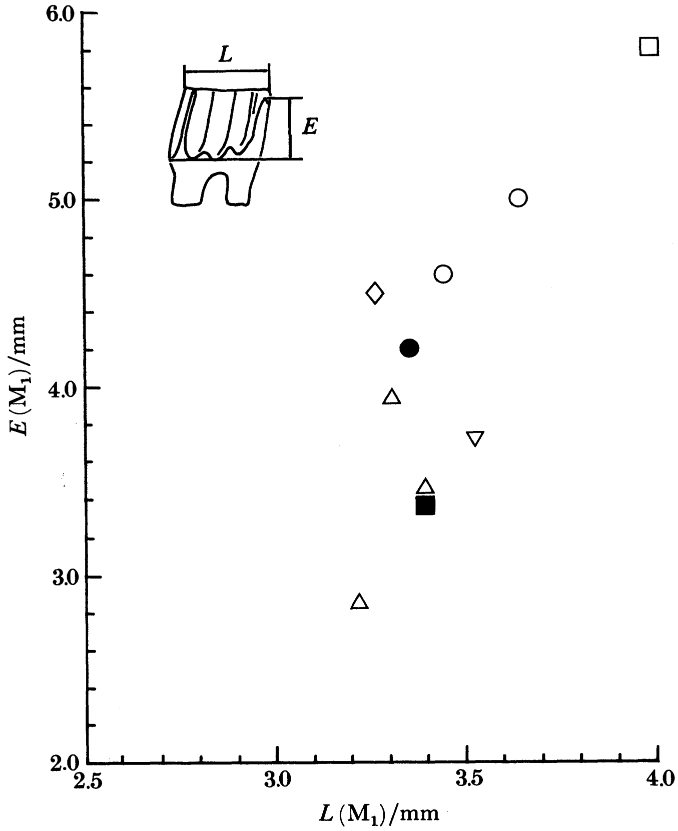

FIGURE 7. *Mimomys pliocaenicus*: comparison of length of wear surface (L, M_1) and anterior enamel-free area height (E, M_1) in M_1. ●, East Runton; ■, West Runton (Crag); ○, Kadzielnia, Poland; ◇, Beaune 1, France; ▽, Magny-les-Auxonne, France. For comparison, *Mimomys polonicus* from Rebielice Krolewski, Poland (△) and *Mimomys ostramosensis* from Kamyk, Poland (□). Data from Chaline (1974) and original.

(vii) *Discussion* (figure 8)

With the exception of a mandible from Bramerton (referred to *Mimomys rex*) all the material of large *Mimomys* from the British Lower Pleistocene deposits discussed here is referred to *M.pliocaenicus*. Within this group we have recognized differences in size and morphology between samples from different localities. These differences are particularly clear between localities of Bramertonian age (Bramerton, Thorpe) and later deposits (East Runton, West

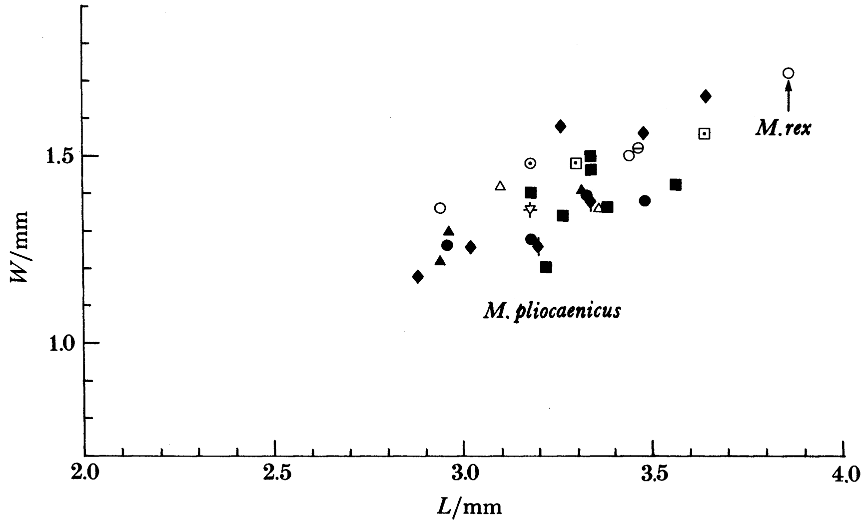

FIGURE 8. Scatter diagram of length (L) and width (W) of M_1 of *Mimomys pliocaenicus* and *Mimomys rex*. Key to figures 8–11. ▽, Easton Bavents; ⊙, Yarn Hill; ⊖, Holton; ⊡, Kyson; ◆, Thorpe, Norwich; ●, Bramerton lower shell bed, Blake's Pit and lower bed locality unspecified; ○, Bramerton, other specimens; ▼, Sidestrand SSB; ▽, Trimingham; ⦶, Overstrand; ▲, Easton Runton crag; △, East Runton clay pebble bed; ■, West Runton crag.

Runton), thus supporting the age differences inferred from other lines of evidence. This implies that the study of remains of *Mimomys pliocaenicus* can be expected to provide information of potential stratigraphic relevance. Suitable methods for comparing crown height have been indicated here, and further methods are described by Rabeder (1981).

Differences in heights of enamel-free areas between teeth of *M. pliocaenicus* from different levels within the same locality were noted by Mayhew (in Funnell *et al.* 1979; Bramerton Blake's Pit, Lower Shell Bed compared with Upper Shell Bed). The differences were small and require testing against larger samples.

(*c*) *Mimomys* (*Kislangia*) *rex* Kormos 1934

Figures 2, 8, 20.

1882 *Arvicola intermedius*: Newton: plate XIII, figure 12.
1902 *Mimomys pliocaenicus*: Major: p. 105, figure 14.
1926 *Mimomys pliocaenicus*: Hinton: figure 100/12.
1979 *Mimomys* (*Kislangia*) *rex*: Mayhew, in Funnell *et al.*: p. 531.

(i) *Material*

Fragmentary lower jaw with M_1, M_2, Upper Shell Bed, Blake's Pit, Bramerton. NCM 524.

(ii) *Diagnosis*

A large species of *Mimomys*. Molars with abundant crown cement and thin enamel. M_1 relatively wide with an acute, backwardly directed third labial salient, bearing an islet and *Mimomys*-ridge.

(iii) *Description*

M. rex is represented by a single mandible with M_1, and M_2 (NCM 524) from Bramerton ('upper bed'). M_1 has two large roots and abundant crown cement. It is wide, with asymmetrical triangles, T_1 and T_3 being much wider than T_2. There is no islet; the *Mimomys*-ridge is inconspicuous and runs to the base of the crown. The fourth lingual reentrant is filled with cement. M_2 has two substantial roots, abundant crown cement and is relatively wide. The triangles are essentially closed, T_1 and T_3 being larger than T_2.

Measurements: NCM 524, M_1: length, 3.90 mm; width, 1.78 mm. NCM 524, M_2: length, 2.46 mm; width, 1.64 mm.

(iv) *Discussion*

The Bramerton specimen agrees closely in morphology with material from Montagny-les-Beaune figured by Chaline & Michaux (1974) and referred by them to *M.rex*. It is also similar to material from Stranzendorf, Austria, described by Rabeder (1981) under the name *Kislangia regulus*. It appears to be more primitive in morphology than *Mimomys rex* from the type locality, Villany-3, Hungary. Since this is the only specimen available from English deposits it is referred to *M.rex* pending recovery of additional material that will allow more accurate comparisons.

(*d*) *Mimomys blanci* van der Meulen 1973

Figures 4, 5, 9, 15 and 16.

1902 *Mimomys newtoni?*: Major: p. 106, figure 23.
1926 *Mimomys newtoni*: Hinton: p. 375 (*partim*), figures 99/18, 99/19, 99/23 and 103.
1973 *Mimomys blanci*: van der Meulen: p. 39, plate V, figures 1–24.
1976 *Mimomys newtoni*: Sutcliffe & Kowalski: p. 97 (*partim*).

(i) *Diagnosis*

A small *Mimomys* species with abundant crown cement, and enamel thicker on the convex sides of the triangles. Hypsodont cheek teeth. M_1 lacking an enamel islet, M^3 with islet. A small fourth labial salient angle is present at the top of the crown of unrooted lower first molars.

(ii) *Description*

The taxon that we call *Mimomys blanci* is the most common small *Mimomys* species in the assemblages from 'Weybourne Crag' deposits such as those at East Runton, West Runton, and Sidestrand. It has previously been known under the name of *Mimomys newtoni* in much of the literature.

Teeth of *M.blanci* from East Runton are high crowned, with abundant cement even in juvenile stages. The M_1 has a fourth labial salient which is lost by the time the anterior enamel-free area reaches the wear surface (Hinton 1926, figure 103). Thereafter, the shape of the anterior loop of M_1 is simple, with one lingual and one labial re-entrant, generally not containing cement. In juvenile wear stages, the triangles are confluent, straight-sided, and acutely pointed lingually. In later stages of wear, the triangles become more or less closed and convex posteriorly. M_2 and M_3 have three dentine fields, the middle triangles being more or less confluent. M^1 and M^2 have well closed triangles, and abundant crown cement. M^3 has two dentine fields, and an enamel islet at an early stage of wear. There are two lingual and three labial reentrants.

Material of this species from West Runton (Crag), Sidestrand and Overstrand is similar in morphology and crown height to the East Runton sample. Measurements are given in table 6.

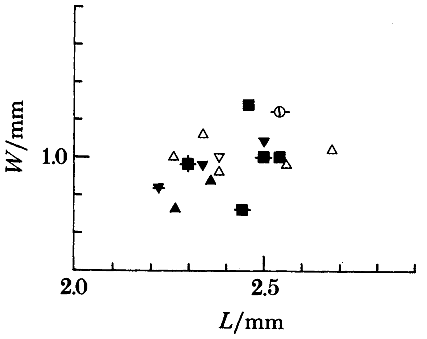

FIGURE 9. Scatter diagram of length (L) and width (W) of *Mimomys blanci* M_1. (For key to symbols see figure 8.)

TABLE 6. *MIMOMYS BLANCI*: MEASUREMENTS OF M_1 WEAR SURFACE

	length			width	
locality	mean	range	*n*	mean	range
East Runton	2.41	2.26–2.68	7	0.97	0.86–1.06
West Runton	2.45	2.30–2.54	5	1.00	0.86–1.14
Sidestrand–Overstrand	2.40	2.22–2.54	4	1.02	0.92–1.04
Easton Bavents	2.38	—	1	1.00	—
Monte Peglia (van der Meulen 1973)	2.49	2.22–2.70	113		

(iii) *Discussion*

Hinton's (1926) description of *Mimomys newtoni*, which has formed the basis for all subsequent work on this species, was based not on the type, but on referred material of a small *Mimomys* species with abundant crown cement and enamel thicker on the convex sides of the triangles. However, the type of *M.newtoni* lacks crown cement, has enamel thicker on the concave sides of the triangles, and represents a different taxon. Consequently, the name *M.newtoni* is, unfortunately, not available for the taxon described by that name by Hinton.

Van der Meulen (1973) described the species *Mimomys blanci* on the basis of remains from Monte Peglia, Italy (Lower Biharian). We are unable to find significant differences between this material and the taxon from British deposits formerly known as *M.newtoni*. The name *Mimomys blanci* van der Meulen appears to us to be the valid prior name for this species. *M.tornensis*, described from Osztramos-3, Hungary, by Janossy & van der Meulen (1975), is similar in morphology to the British material referred to *M.blanci*, but is rather larger.

Of the material considered under *M.newtoni* by Sutcliffe & Kowalski (1976), the major part is referred here to *M.blanci*, the type and the specimen from Bramerton (Hinton 1926, p. 376 footnote) are referred to *M.newtoni*, and the three specimens from East Runton (BMNH M6967: 19, 20, 23) are referred to *M.pliocaenicus*.

We do not find *M.blanci* in the assemblages from Bramerton and Thorpe (Norwich Crag). This confirms the observation of Hinton (1926, p. 376). The specimen from Bramerton mentioned in the footnote (Hinton 1926, p. 376) is referred here to *M.newtoni*. *Mimomys blanci* is common in Lower Pleistocene assemblages in Europe, for example Tegelen (Freudenthal *et al.* 1976) and Monte Peglia (van der Meulen 1973).

(*e*) *Mimomys* (*Borsodia*) *newtoni* Major 1902

Figures 2, 4, 10 and 12.

1902 *Mimomys newtoni*: Major: p. 103, figure 7: p. 105, figure 10.
1914 *Microtomys newtoni*: Méhely: p. 223, plate VIII, figures 1 and 3.
1926 *Mimomys* sp.: Hinton: figures 100/22, 100/21.
1926 *nec Mimomys newtoni*: Hinton: figures 99/19, 99/27, 99/18, 99/23.
1926 *Mimomys newtoni*: Hinton: p. 375 (*partim*, type only).
1926 *Mimomys newtoni*: Hinton: p. 376 (footnote).
1938 *Mimomys newtoni hungaricus*: Kormos: plate 2, figures 1–4, 6–9.
1956 *Mimomys hungaricus*: Kretzoi: pp. 162, 179, 184, 188, 203.
1975 *Mimomys* (*Borsodia*) *hungaricus*: Janossy & van der Meulen: p. 389.
1976 *Mimomys newtoni*: Sutcliffe & Kowalski: p. 97 (*partim*).
1976 *nec Mimomys newtoni*: Freudenthal *et al.*: p. 15, figures 5 and 7.
1979 *Mimomys* (*Borsodia*) *newtoni*: Mayhew, in Funnell *et al.*: p. 531.

(i) *Material*

Bramerton: M_1 BMNH M35155, M_1 SM X7920, M_2 SM X7929, M^2 BMNH M35154.
Thorpe: M^1 NCM 971c. M_1 NCM 971d.
East Runton: M_1 (type) BMNH 6967a, M^2 GSM 115500.
West Runton: M^1 UMZC WRC 561.

(ii) *Diagnosis*

A small species of *Mimomys*, with molars lacking crown cement. The dentine fields of the triangles are closed, and the enamel is thicker on the concave sides of the triangles, as in the genus *Microtus*. Molar teeth each with two roots. M_1 has a *Mimomys*-ridge when young, but no islet. M^3 with islet.

(iii) *Description*

Type: the type of *Mimomys newtoni* is a lower left first molar (BMNH M6967a) figured by Major (1902, figures 7 and 10) and coming from the shelly sand at East Runton (Hinton 1926, p. 376).

Major's figure 7 showed a substance filling the re-entrant folds, and this was taken by subsequent authors to indicate the presence of crown cement. Sutcliffe & Kowalski (1976) pointed out that this type tooth lacks crown cement, and this observation has been confirmed by the present authors. In addition, we have found that the enamel is thicker on the concave sides of the triangles (so-called *Microtus* differentiation).

The type tooth (refigured here, figure 12, parts 8*a*, *b*) is high crowned, with no trace of an enamel islet. Crown formation is complete, but no roots are present. The anterior loop is elongated, with deep lingual and labial reentrants. The fourth labial salient persists for about one third of the height of the crown. Seen in anterior view the tooth is strongly curved labially. The length of the wear surface is 2.46 mm; the width, 1.02 mm.

Other British material (figure 12): teeth lacking crown cement and with undifferentiated or *Microtus*-differentiated enamel, referred here to *M.newtoni*, have been recovered from East Runton, West Runton (shelly sand), Bramerton and Thorpe. Besides the type, the assemblage from East Runton includes an upper second molar (figure 12.9); the West Runton deposits have yielded an upper first molar (figure 12.10). The Bramerton material consists of two lower first molars (figure 12.13, 12.14), a lower second molar (figure 12.11) and an upper second molar (figure 12.7), and from Thorpe there is a lower first molar (figure 12.15) and an upper first molar (figure 12.12).

The localities mentioned fall into two age groupings. East and West Runton (?Pre-Pastonian), and Bramerton and Thorpe (Bramertonian). Differences between the material from the two stratigraphic levels include the position of the *Mimomys* ridge (fourth labial salient) on the lower first molar (compare figure 12.8, 12.13), the relative width of the upper second molar, and the contour of the sides of the triangles in the upper first molar. Measurements of material from Bramerton and Thorpe are given in table 7.

(iv) *Discussion*

Major (1902) described *Mimomys newtoni* as 'a smaller rooted form from the Norwich Crag and East Runton which has characters of its own'. The type (Major 1902, figure 7) was from East Runton. A second tooth from this locality, figured by Major (1902, figure 16) as *M.newtoni*? is referred here to *Mimomys blanci*.

Méhely (1914) figured two M_1 from Hungary (Beremend, Nagyharsanyhegy) which he referred to *M.newtoni*. The figured teeth show no cement, but the absence was said by Méhely (1914, p. 224) to be due to accidental removal during cleaning.

Hinton (1914) reviewed the genus *Mimomys*. His extensive description of *M.newtoni* was based

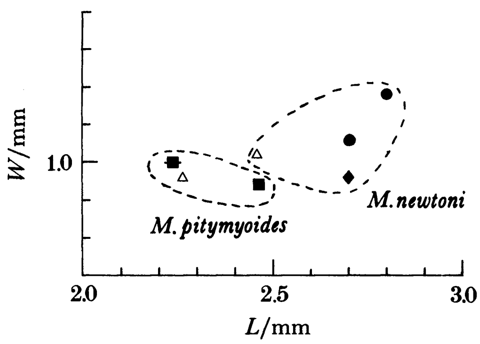

FIGURE 10. Scatter diagram of length (L) and width (W) of *Mimomys pitymyoides* and *Mimomys newtoni* M_1. (For key to symbols see figure 8.)

TABLE 7. *MIMOMYS NEWTONI*: MEASUREMENTS OF M_1 WEAR SURFACE

locality	length (mm)	width (mm)
Bramerton SM X.7920	2.80	1.18
Bramerton BMNH M35155	2.70	1.06
Thorpe NCM 971d	2.70	0.96

on material from several localities, but apparently did not consider the type tooth. '*M.newtoni*' *sensu* Hinton was a small-sized species of *Mimomys* with abundant crown cement, enamel thicker on the convex sides of the triangles, and no islet in M_1.

Kormos (1938) drew attention to abundant remains of a small sized *Mimomys* species from Hungary (Villany-3). Although Hinton had identified the Hungarian material as *M.newtoni* (Kormos 1938, p. 359), Kormos pointed out that, in contrast to *M.newtoni* from England, these specimens lacked crown cement. He suggested that the Hungarian material could be regarded as a separate subspecies, *M.newtoni hungaricus*.

Kretzoi (1956) treated the Hungarian material as a separate species, *M.hungaricus*. More recently, Janossy & van der Meulen (1975) found that specimens of *M.hungaricus* had *Microtus*-type enamel differentiation and therefore placed the species in a new subgenus, *Borsodia*.

According to our observations, the type of *Mimomys newtoni* from East Runton is rather similar to the material from Villany-3 previously called *Mimomys hungaricus*. We regard the name *Mimomys newtoni* Major 1902 as having priority over *M.hungaricus* (Kormos 1938). The prior name for the taxon formerly described by Hinton (1926) as *M.newtoni* appears to be *Mimomys blanci* van der Meulen 1973. The available British specimens agree well with material of *M.blanci* from the type locality, Monte Peglia, Italy.

According to Janossy & van der Meulen (1975), *Mimomys petenyi* Méhely from Beremend resembles *M.newtoni* (= *M.hungaricus*) but has less differentiated enamel. The M^1 has three roots, whereas the M^1 of *M.newtoni* from Villany-3 is two-rooted (Kormos 1938). Unfortunately, neither M^1 from British deposits has roots, so that it is not possible to decide on this basis whether *M.petenyi* is present. Provisionally, the British material mentioned here is all referred to *Mimomys newtoni* pending better characterization of *M.petenyi* on the basis of material from the type locality.

Recently, Rabeder (1981) has described material from Austria which resembles closely teeth from Bramertonian localities in England. He describes the material under the names *Borsodia parvisinuosa*, *Borsodia aequisinuosa*, *Borsodia altisinuosa* and *Borsodia hungarica*. The first three of these taxa are based on material from superimposed levels of a loess profile at Stranzendorf, and are said to represent three stages in the increase in crown height of a lineage. The resemblance to the English material described here is striking (compare figure 12.13 of this paper with text figure 45–2 and 45–3 of Rabeder 1981). However, very little material is available from Stranzendorf, and we prefer to await confirmation of the results of Rabeder by a study of larger samples before applying his nomenclature to English material.

(*f*) *Mimomys pitymyoides* Janossy & van der Meulen 1975

Figures 4, 10 and 12.

1960 *Mimomys* cf. *pusillus*: Kowalski: p. 12 (*partim*).
1975 *Mimomys pitymyoides*: Janossy & van der Meulen: p. 386.

(i) *Material*

East Runton: M^1 GSM 115492, M_1 GSM 115499, M_2 GSM 115482.

West Runton: M_1 DFM collection, M_1 UMZC WRC 321, M_1 UMZC WRC 565, M^2 UMZC WRC 36.

(ii) *Diagnosis*

A small species of *Mimomys*, distinguished by the confluency between triangles T2 and T3 in M_1 and M^2 (see Janossy & van der Meulen 1975).

(iii) *Description*

The following material of *M. pitymyoides* is available from British deposits: West Runton (crag), three M_1, one M^2; East Runton (shelly sand), one M_1, one M_2, one M^1.

The triangles of the molars have rather straight sides. The enamel thickness is uniform. Crown cement is sparse or lacking. The teeth are small compared with those of *M. reidi* from the same deposits. T_2 and T_3 of M_1 and M^2 are broadly confluent. The anterior loop of M_1 is long and narrow with a *Mimomys* ridge and narrow pointed salient angles. These teeth agree in size and morphology with *M.pitymyoides* from the type locality Osztramos-3, Hungary, described by Janossy & van der Meulen (1975).

TABLE 8. *MIMOMYS PITYMYOIDES*: MEASUREMENTS OF M_1 WEAR SURFACE

locality		length/mm	width/mm
West Runton D.F.M.	M_1	2.24	1.00
UMZC WRC 321	M_1	2.46	0.94
East Runton GSM 115499	M_1	2.26	0.96

(iv) *Discussion*

Mimomys pitymyoides is a distinctive species which has now been recognized in assemblages from Kadzielnia and Kamyk, Poland; Kolinany, Czechoslovakia; Sénèze, France, and Villany-5 and the type locality Osztramos-3, Hungary (Janossy & van der Meulen 1975). Rabeder (1981) records its presence in Austria (Deutsch Altenburg, Stranzendorf) under the names *M.stenokorys*, *M.jota* and *M.pitymyoides*. At Stranzendorf, different stages in the evolution of *M.pitymyoides* have been recorded from superimposed deposits. *M.pitymyoides* has not previously been recorded from Britain.

(*g*) *Mimomys altenburgensis* Rabeder 1981

Figures 2, 11, 13 and 14.

1979 *Mimomys reidi*: Mayhew, in Funnell *et al.*: p. 532 (*partim*).

(i) *Material*

Two M_1, one M_2, Lower Shell Bed, Blake's Pit, Bramerton. SM X.7918, 7919, 7924, Bramertonian. One M^1 Thorpe Asylum Pit, Norwich, Fitch collection. NCM 971c

(ii) *Description*

Size small. Enamel islet of M_1 present in at least top third of crown. Anterior loop relatively short and compressed. Little crown cement. Crown height medium, but posterior enamel-free areas of M_1 relatively low. Triangles partly confluent. *Mimomys* enamel differentiation. M^1 with low enamel-free areas. Triangles confluent.

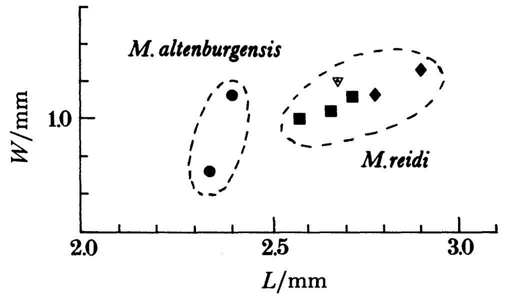

FIGURE 11. Scatter diagram of length (L) and width (W) of *Mimomys reidi* and *Mimomys altenburgensis* M_1. (For key to symbols see figure 8.)

TABLE 9. *MIMOMYS ALTENBURGENSIS*: MEASUREMENTS OF M_1, M^1

locality		length mm	width mm	E_a
Blake's Pit, Bramerton SM X.7919	M_1	2.34	0.86[a]	
Blake's Pit, Bramerton SM X.7918	M_1	2.40	1.06	2.94
Asylum Pit, Thorpe NCM971c	M^1	2.03	1.15	

[a] Estimated (tooth damaged).
E_a is height of anterior enamel-free area measured perpendicularly to the wear surface from the base of the enamel under the first lingual re-entrant.

(iii) *Discussion*

These teeth belong to a small species of *Mimomys*, distinct from *M.reidi*. Although no M_1 of *M.reidi* are present in the Bramerton assemblage, such teeth are found in other deposits of presumed Bramertonian age such as Thorpe and have been seen in still undescribed material from Bulcamp Pit, Norfolk.

There are very few indications in the literature of a species of this size and morphology. Chaline & Michaux (1974, plate 2, figure 14) illustrate an M_1, similar to those from Bramerton, as '*Mimomys reidi*'. Rabeder (1981) has described similar material as *Mimomys altenburgensis* and *Mimomys stranzendorfensis*. These two species are regarded by Rabeder (1981) as part of a lineage leading through *Mimomys stenokorys* and *Mimomys jota* to *M.pitymyoides*.

Comparison of the Bramerton material with the figures of the Austrian material indicates that it is intermediate between *M.altenburgensis* and *M.stranzendorfensis*, but closer to the former. Since *M.altenburgensis* is based on abundant material we regard it as well characterized, and think that it is appropriate to use this name for the British material.

Rabeder (1981) regards *M.altenburgensis* as ancestral to *M.pitymyoides*. In Britain, *M.altenburgensis* is recorded from the Bramertonian, and *M.pitymyoides* from the later 'Weybourne Crag' of East Runton and West Runton.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(h) *Mimomys reidi* Hinton 1910

figures 2–5, 11, 13 and 14.

1882 *Arvicola intermedius*: Newton: plate XIII, figure 8.
1910 *Mimomys reidi*: Hinton: p. 491.
1914 *nec Mimomys petenyi*: Méhely: p. 191.
1914 *Mimomys pusillus*: Méhely: p. 214 (*partim*).
1926 *Mimomys reidi*: Hinton: p. 363 (*partim*).
1926 *Mimomys newtoni*: Hinton: figure 99/27.
1926 *Mimomys* sp.: Hinton: figure 99/28.
1974 *Mimomys* cf. *reidi*: Chaline & Michaux: plate V, figures 6 and 23.
1976 *Mimomys reidi*: Sutcliffe & Kowalski: p. 97.
1976 *Mimomys reidi*: Freudenthal *et al.*: figure 4.
1979 *Mimomys reidi*: Mayhew, in Funnell *et al.*: p. 532 (*partim*).

(i) *Revised diagnosis*

A medium-sized species of *Mimomys* with enamel thicker on the convex sides of the triangles and small to moderate amounts of crown cement. Moderately high-crowned. M_1 with enamel islet which disappears (in the type) at an early stage of wear, persistent confluency of the triangles, and a *Mimomys* ridge typically persisting for at least half the height of the crown.

M_2 with T1 separated from the posterior lobe, T1 and T2 partly confluent, T2 separated from the anterior region and three dentine fields. M_3 with three dentine fields, T1 and T2 broadly confluent.

M^1 with two or three roots, dentine fields not completely separated, prominent and rounded second lingual salient with low enamel-free area. M^2 with two roots, T2 and T3 partly communicating. M^3 with two roots, enamel islet persisting until moderate stage of wear, anterior lobe and T2 poorly separated from posterior lobe.

(ii) *Description*

Type: *M.reidi* was described by Hinton (1910) on the basis of a single lower first molar from the 'Weybourne Crag' at Trimingham. No other specimens are known from this deposit.

The type tooth (refigured here, figure 13.6*a*,*b*) is a complete and well preserved specimen in which the enamel-free areas have not yet reached the wear surface. The crown is fully formed. There are two roots in formation. A small amount of cement is present in the reentrants. The dentine fields on the wear surface are confluent. Cleaning the surface has revealed the trace of an enamel islet in the dentine of the anterior loop. This confirms the opinion of Hinton that an enamel islet was present at an earlier stage of wear. The *Mimomys*-ridge extends about half the height of the crown. The triangles are acutely pointed, with undifferentiated enamel (juvenile features), towards the base the salients become less acutely pointed.

Other British material: a medium-sized *Mimomys* species with little crown cement and an islet in M_1 has been identified by the authors in assemblages from several Lower Pleistocene localities (see table 10), including East and West Runton, Bramerton, Thorpe, Easton Bavents and Covehithe. The material is not abundant, but appears to belong to a single lineage and here is referred to *M.reidi*.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

This material enables us to give a revised diagnosis of *M.reidi*. The upper first molar has a rather prominent rounded second lingual salient with a low enamel-free area. The number of roots in M^1 is not clear; two or three are possible.

The enamel-free areas of M^1 from West Runton (figure 14.5) are higher than those in M^1 from earlier localities (Thorpe, Bramerton, figure 14.4, 14.7, 14.10, 14.11). Lower first molars of *M.reidi* from British Lower Pleistocene localities, illustrated on figure 13, resemble the type in having an enamel islet and *Mimomys*-ridge or confluent dentine triangles, or both. Specimens from West Runton (figure 13.13, 13.14) are similar in size, morphology, and timing of disappearance of the enamel islet to the type from Trimingham, of approximately similar geological age.

Two M_1 from the older locality, Thorpe, illustrated as figure 13.9 13.12, are of relatively large size. The enamel islet extends lower in the crown than that of the type of *M.reidi*, which they otherwise resemble.

Table 10. *Mimomys reidi*: measurements of M_1

locality	length mm	width mm	E_a
Trimingham GSM 98637 (type)	2.68	1.10	2.70
East Runton GSM 115483	3.06[a]	1.10	—
West Runton Crag UMZC WRC 1	2.66	1.02	3.02
West Runton Crag UMZC WRC 169	2.72	1.06	
West Runton Crag UMZC WRC 381	2.58	1.00	
Thorpe NCM 971h	2.78[a]	1.06	
Thorpe NCM 971g	2.90	1.14	

[a] Estimated (tooth damaged).
E_a, height of anterior enamel-free area (see table 9).

(iii) *Discussion*

The recovery of additional material of *M.reidi* from deposits of broadly similar age, and geographical vicinity, to the type locality, such as those near West Runton, allows a more complete diagnosis of this species. Although second and third molars of *M.reidi* have been recognized in some of the assemblages, detailed description of these teeth should, in our view, await recovery of better material.

The differences observed between the samples of *M. reidi* from different localities in East Anglia are in accordance with the presumed stratigraphic relationships; the most advanced form comes from the youngest deposits.

The name *Mimomys reidi* has been used in the continental literature for a number of taxa. Much material previously referred to *M.reidi* is now recognized as *M.pitymyoides*. Confusion has existed between *M.reidi* and *M.pusillus* (Méhely 1914), mainly because of the previously limited description of *M.reidi*.

Following examination of material of *M.pusillus* from the type locality (Betfia-2) and the descriptions of van der Meulen (1973) and Méhely (1914), it seems that the species is characterized by high-crowned teeth, with relatively abundant cement, and a transient enamel islet in M_1, which also has a *Mimomys* ridge. Since none of these characters are primitive with respect to *M.reidi*, *M.pusillus* could be regarded as its descendant.

Material that in our opinion is referrable to *M.reidi* as diagnosed here has been described from Tegelen (Freudenthal *et al.* 1976) and Stranzendorf, Austria, (Rabeder 1981, '*M.hintoni*', '*M.* cf. *reidi*'). This species occurs only in Lower Pleistocene (Villanyian) assemblages in continental Europe.

(*i*) *Clethrionomys* Tilesius 1850

Figure 16.6.

A single upper third molar (PGC collection E1832), recovered by Mr P. G. Cambridge from shelly sand at Overstrand (Pre-Pastonian), is rooted, has crown cement, and lacks an enamel islet at this stage of wear. It most closely resembles teeth of the genus *Clethrionomys*, to which it is provisionally referred. This is the oldest record of the genus from Britain. It has been recorded from the Tegelen fauna (Tiglian C5) by Freudenthal *et al.* (1976).

7. Summary of taxa and stratigraphy (tables 11 and 12)

The following vole taxa have been identified from Lower Pleistocene deposits in East Anglia: *Mimomys pliocaenicus*, *Mimomys rex*, *Mimomys reidi*, *Mimomys blanci*, *Mimomys pitymyoides*, *Mimomys newtoni*, *Mimomys altenburgensis* and *Clethrionomys* sp. The records of species from the various localities are summarized in table 11.

M.pliocaenicus occurs at most localities; *M.rex* is known only by a single jaw from Bramerton. *M.reidi* occurs at nine localities, and *M.blanci* at five, where, however, it is generally the most abundant of the smaller species. *M.newtoni* and *M.pitymyoides* are relatively rare, occurring at low frequency in material from four and two localities, respectively. *M.altenburgensis* occurs at two localities, Bramerton and Thorpe.

The stratigraphic occurrence of various taxa is summarized in table 12. Three faunal groups are distinguished.

Group 1

Faunas from Norfolk coastal localities, mainly 'Weybourne Crag' with *Macoma balthica* (East Runton, West Runton, Trimingham, Overstrand, Sidestrand). The taxa recognized include *M.pliocaenicus*, *M.newtoni*, *M.reidi*, *M.blanci*, *M.pitymyoides* and *Clethrionomys* sp. The assemblages are derived mainly from sediments assigned to the Pre-Pastonian stage by West (1980*a*). There is no material from deposits that are undoubtedly of Pastonian age.

Group 2

Faunas from Norfolk and Suffolk localities ('Norwich Crag') without *Macoma balthica* (Bramerton, Thorpe (Norwich), Thorpe Aldringham, Sizewell). The taxa recognized include *M.pliocaenicus*, *M.newtoni*, *M.reidi*, *M.rex* and *Mimomys altenburgensis*. The assemblages are from deposits assigned mainly to the Bramertonian stage (Funnell *et al.* 1979).

Group 3

Faunas from Suffolk coastal localities ('Norwich Crag') without *Macoma balthica*, associated with the type Baventian deposits (Covehithe, Easton Bavents). The taxa recognized include

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

	taxa							
localities	*Clethrionomys* sp.	*Mimomys pliocaenicus*	*Mimomys rex*	*Mimomys reidi*	*Mimomys newtoni*	*Mimomys blanci*	*Mimomys pitymyoides*	*Mimomys altenburgensis*
East Runton	.	×	.	×	×	×	×	.
West Runton (Crag)	.	×	.	×	×	×	×	.
Overstrand	×	×	.	.	.	×	.	.
Sidestrand	.	×	.	.	.	×	.	.
Trimingham	.	.	.	×	.	.	.	.
Beccles	.	×	.	.	.	.	.	.
Bramerton	.	×	×	×	×	.	.	×
Caistor-by-Norwich	.	×	.	.	.	.	.	.
Covehithe	.	×	.	×	.	.	.	.
Easton Bavents	.	×	.	×	.	×	.	.
Holton	.	×	.	.	.	.	.	.
Sizewell	.	×	.	×	.	.	.	.
Thorpe (Norwich)	.	×	.	×	×	.	.	×
Thorpe Aldringham	.	×	.	×	.	.	.	.
Wangford	.	×	.	.	.	.	.	.
Yarn Hill	.	×	.	.	.	.	.	.
Kyson	.	×	.	.	.	.	.	.

Table 12. Summary of taxa and stratigraphy

		taxa							
fauna group	stages (see also table 1)	*Clethrionomys* sp.	*Mimomys pliocaenicus*	*Mimomys rex*	*Mimomys reidi*	*Mimomys newtoni*	*Mimomys blanci*	*Mimomys pitymyoides*	*Mimomys altenburgensis*
	(Cromerian)	—	— — —	—	— — —	— —	— —	— —	— —
	(Beestonian)	—	— — —	—	— — —	— —	— —	— —	— —
	(Pastonian)	—	— — —	—	— — —	— —	— —	— —	— —
1	Pastonian	—	ER — WR	—	ER WR —	ER WR	ER WR	ER WR	— —
	or Pre-Pastonian	—	— — —	—	Tm — —	— —	— —	— —	— —
	Pre-Pastonian *d*	—	— — —	—	— — —	— —	— —	— —	— —
	c	—	— — —	—	— — —	— —	— —	— —	— —
	b	—	— — —	—	— — —	— —	— —	— —	— —
	a	Ov	Sd — Ov	—	— — —	— —	Sd Ov	— —	— —
2	Bramertonian	—	Br Tp Sz	Br	Br Tp Sz	Br Tp	— —	— —	Br Tp
		—	TA — —	—	TA — —	— —	— —	— —	— —
	Lower Pleistocene	—	Bc CN Ho	—	— — —	— —	— —	— —	— —
	undivided	—	Wa Ky YH	—	— — —	— —	— —	— —	— —
3	Baventian	—	EB Cv —	—	EB Cv —	— —	EB —	— —	— —
	Antian	—	(EB) — (Cv)	—	(EB) — (Cv)	— —	(EB) —	— —	— —
	(Thurnian)	—	— — —	—	— — —	— —	— —	— —	— —
	(Ludhamian)	—	— — —	—	— — —	— —	— —	— —	— —

Bc, Beccles; Br, Bramerton; CN, Caistor-by-Norwich; Cv, Covehithe; EB, Easton Bavents; ER, East Runton; Ho, Holton; Ky, Kyson; Ov, Overstrand; Sd, Sidestrand; Sz, Sizewell; TA, Thorpe Aldringham; Tm, Trimingham; Tp, Thorpe (Norwich); Wa, Wangford; WR, West Runton; YH, Yarn Hill.

Rationale for stage allocations given in §4.

M. pliocaenicus, *M. reidi*, and *M. blanci*. The assemblages are derived from sediments dating from the Early Baventian, or the latest part of the previous temperate stage (?Antian) (West *et al.* 1980).

Group 1 faunas differ in the following respects from group 2 faunas: (i) *Mimomys pliocaenicus* and *M. reidi* are higher crowned (that is, have higher enamel-free areas) in group 1 faunas; (ii) *Mimomys pitymyoides* is absent in group 2 faunas; (iii) *Mimomys rex* is absent in group 1 faunas (although its presence in group 2 is based on a single specimen); (iv) *Mimomys altenburgensis* is absent in group 1 faunas; (v) *Mimomys blanci* is absent in group 2 faunas; (vi) *Mimomys newtoni* is more advanced (*Mimomys* ridge of M_1 lies more anteriorly).

Group 3 faunas are relatively poorly known. Since *M. blanci* is present, they resemble group 1 faunas rather than group 2.

8. Discussion

(*a*) *British stratigraphic sequence*

The current stratigraphic column for the British Pleistocene is given in table 1. Current views on the ages of the localities yielding the assemblages reviewed here are treated at length in §4 and summarized in tables 2 and 12.

The general conclusions of our study largely support previous stratigraphic interpretations. Thus we find two faunal groups corresponding to most 'Norwich Crag' localities without *Macoma balthica* (group 2) and coastal 'Weybourne Crag' localities with *Macoma balthica* (group 1). The conclusions based on microtine evolution indicate that group 1 faunas postdate group 2 faunas. This is in agreement with the conclusion that the Bramertonian is a separate stage which precedes the Pre-Pastonian stage.

The upper levels of the Bramerton type locality yielded pollen indicating cool conditions (*Pinus*–Ericales–Gramineae p.a.b.). It has been suggested that this time period might correspond to the Pre-Pastonian *a* substage described from coastal sediments (Funnell *et al.* 1979). However, the differences noted here between the vole faunas of these two groups of sediments suggest that they are unlikely to date from the same period. It is not clear how much time may have intervened.

The group 3 faunas (Covehithe, Easton Bavents) are at present too poor to allow direct comparison with other groups in terms of evolutionary differences. The presence of *M. blanci* (so far only a single tooth) tends to relate the fauna to group 1 rather than group 2. The implication of this is that the present stratigraphic assumptions may need review. Alternatively, the possibility of cyclical disappearance and reappearance of taxa in response to fluctuations of climate should be considered. Work currently under way in The Netherlands may be expected to throw light on this point. Further research on group 3 faunas from Britain is also indicated.

The faunas described here are much older than that of the type Cromerian from the Upper Freshwater Bed at West Runton described by Stuart (1975). In continental Europe, an intervening series of faunas containing the vole *Microtus* (*Allophaiomys*) is well documented (see, for example, van der Meulen 1973).

(*b*) *Comparison with continental European Lower Pleistocene localities and faunas*

(i) *The Netherlands*

The only fauna described from Holland comparable to those discussed here is that from Tegelen in the southern Netherlands, reviewed in a preliminary report by Freudenthal *et al.* (1976). The vole species *Mimomys pliocaenicus*, *M.reidi* and *M.blanci* ('*M.newtoni*') were identified. A more extensive review of the fauna is awaited. As far as can be judged from the material seen by the authors, the Tegelen fauna is broadly similar to those described here from English localities. The crown height of *M.pliocaenicus* corresponds to that of group 1 localities. The presence of *M. blanci* suggests correspondence with either group 1 or group 3 faunas. Van der Meulen & Zagwijn (1974) described teeth from a boring at Brielle. Here, *Microtus* (*Allophaiomys*) *pliocaenicus* was found. This is considered to represent a later fauna than groups 1–3 from Britain, which do not contain *Microtus*.

(ii) *Austria*

Rabeder (1981) described and figured material from several Lower Pleistocene localities in Austria. Two of these sites have yielded material from several superimposed levels. The English material corresponds closely to the material from Deutsch Altenburg 21–Stranzendorf A–D (faunal group 2) and Stranzendorf G to i (faunal group 1). *Mimomys blanci* was not, however, found in the Austrian faunas. Since the extreme similarity of the Austrian faunas to the British material is obscured by differences in terminology, a comparison is given below.

taxon	Bramerton (present work)	Stranzendorf D (Rabeder 1981)
1	*M.altenburgensis*	*M.stranzendorfensis*
2	*M.pliocaenicus*	*M.praepliocaenicus*
3	*M.rex*	*M.regulus*
4	*M.newtoni*	*M.parvisinuosa*
5	*M.reidi*	*M.hintoni*

The difference in terminology results from different views on the taxonomy of fossil species. We believe that the taxa may be synonymous as listed, but further work is required to clarify this.

(iii) *Hungary*

The fauna of the Osztramos-3 fissure filling (Janossy & van der Meulen 1975) resembles that of English faunal group 1 localities, but is probably from a later period, since a more advanced form of *M.newtoni* (= *M.hungaricus*) is present, and *M.pliocaenicus* is absent (replaced by its presumed descendant, *M.osztramosensis*).

Material from the locality Villany-3 (type locality of the Villanyian stage of Kretzoi (1941)) is not fully described and has not been examined in detail by the present authors. It has been concluded by other authors (for example, van der Meulen in Freudenthal *et al.* 1976) that the species present were similar to those found at Tegelen. The faunal list from Villany-3 includes *Mimomys pliocaenicus*, *M.reidi*, *M.newtoni*, *M.rex*, and *M.pitymyoides*. The locality Villany-5 has yielded a broadly similar fauna to Villany-3, which it overlays, except that the first representative of the genus *Microtus*, *M.*(*Allophaiomys*) *deucalion* is present (van der Meulen 1974).

The fauna of the locality Villany-8 has been discussed by Kretzoi (1956, 1965) and van der Meulen (1973). The latter author has designated this locality, in part, as the type for the Biharian stage, first recognized by Kretzoi (1956, 1965) on the basis of a number of sites. The fauna of Villany-8 consists primarily of voles with unrooted teeth such as *Microtus* and *Lagurus*. *Mimomys* is represented by *Mimomys savini*, considered to be a descendant of *Mimomys pliocaenicus*. Villany-8 is clearly later than the British localities reviewed here.

(iv) *Romania*

The locality Betfia-2 (Episcopia, Püspökfürdö) has provided mainly remains of unrooted vole species such as *Microtus* (*Allophaoimys*) *pliocaenicus* (type locality), as well as rooted species such as *Mimomys pusillus* (presumed type locality) (Kretzoi 1965; van der Meulen 1973). These species have not been recognized in the Lower Pleistocene faunas from England described here and are considered to have existed at a later time.

(v) *Italy*

A fauna of small mammals from a fissure filling at Monte Peglia, Italy, was described by van der Meulen (1973). The material includes the species *Mimomys savini*, *Mimomys blanci* (type locality), and unrooted voles such as *Microtus* (at least two species). It represents a later fauna than those from Britain described here.

(vi) *Poland*

A Lower Pleistocene fauna of small mammals from Kadzielnia, first described by Kowalski (1958) includes, according to latest studies, the species *Mimomys pliocaenicus*, *M.pitymyoides*, *M.blanci*, and *Microtus* (*Allophaiomys*) *pliocaenicus*. *Mimomys pliocaenicus* and *Mimomys pitymyoides* from Kadzielnia are somewhat higher crowned than material of these species from West and East Runton (see also figure 7). This suggests that English faunal groups 1–3 described here are somewhat earlier than Kadzielnia.

The fauna of Kamyk, described by Kowalski (1960), is considered to be younger than that from Kadzielnia (see also figure 7).

The locality of Rebielice Krolewskie yielded a fauna described by Kowalski (1960) and regarded as Late Pliocene or Early Pleistocene in age. This is the type locality of *Mimomys polonicus*, thought to be ancestral to *Mimomys pliocaenicus*. The locality is somewhat older than the English crag localities.

(vii) *Summary* (table 13)

In England, three faunal groups can be recognized in the microtine faunas from the Lower Pleistocene Icenian crag. Groups 1 and 2 are well defined and are represented by the localities East and West Runton (group 1) and Bramerton and Thorpe (group 2). The relative geological age of these localities compared with continental European localities on the basis of microtine faunas is given in table 13.

No remains of vole species with unrooted teeth (for example, *Microtus*) have been seen by the authors in the collections from the Norwich and Weybourne crag which form the subject of the present study. This implies that either such teeth have been selectively excluded or that we are dealing with deposits whose age predates that of the arrival in Europe of *Microtus*. The first alternative is considered less likely.

Table 13. Relative age of selected European localities on the basis of microtine remains

relative age	Great Britain		continental Europe
			Villany-8
			Monte Peglia
younger ↑			Betfia-2
		× × ×	Brielle, Osztramos-3, Kamyk
			Villany-5, Kadzielnia, Schambach
	East Runton		Tegelen, Villany-3
	West Runton (Crag)		Stranzendorf G–i
	Bramerton		Stranzendorf D–G
	Thorpe		
↓ older			Rebielice Krolewskie

× × ×, Approximate boundary of Villanyian and Biharian mammal stages.

Table 14. Limits to correlation of British and Netherlands stages on the basis of microtine remains

(For description see text.)

Netherlands sequence		British stages: Pre-Pastonian*	British stages: Bramertonian
	C		
Waalian	B		
	A		
Eburonian		I	
	6	I	
	5	I	
	4		I
Tiglian	C		I
	3		I
	2		I
	1		I
Tiglian	B		I
Tiglian	A		I
Praetiglian			

* These limits are provided by Pre-Pastonian material from Overstrand and Sidestrand. The limits for the Pastonian are not considered further here.

(*c*) *Relation to continental European stratigraphic systems*

(i) *Netherlands chronostratigraphy* (table 14)

The Netherlands local stratigraphic system for the Quaternary has been summarized by Zagwijn (1974). In the early Pleistocene three cool stages (Praetiglian, Eburonian, Menapian) and two warm stages (Tiglian, Waalian) are recognized. These stages include a number of substages representing further climatic oscillations.

The Tegelen small mammal fauna described by Freudenthal *et al.* (1976) is derived from channel deposits exposed in the type section of the Tiglian, located at a level defined by plant remains as zone TC 5, one of the two climatic optima within the Tiglian. Teeth of *Dicrostonyx torquatus* and *Microtus* (*Allophaiomys*) *pliocaenicus* have been described from Eburonian deposits at Brielle by van der Meulen & Zagwijn (1974). Finally, teeth referred to *Mimomys* cf. *polonicus* have been recovered from deposits at De Meern dating from the Praetiglian–Tiglian boundary (Suc & Zagwijn 1983).

On the basis of these records an outline of the limits to correlation of the Bramertonian and Pre-Pastonian with the stages of the Dutch sequence can be developed (table 14). This relies on the following lines of argument. Group 1 faunas from British 'Weybourne Crag' deposits (for example, Sidestrand, East Runton, West Runton) are unlikely to postdate the Brielle faunule because they lack *Microtus*. They are unlikely to predate the Tegelen fauna substantially, since they are very similar in the crown height of *Mimomys pliocaenicus* (personal observation). Group 2 faunas from British Norwich Crag deposits (for example, Bramerton, Thorpe) are unlikely to postdate the Tegelen fauna since the crown height of *Mimomys pliocaenicus* from these localities is less. The earliest possible date for such faunas in relation to the Dutch sequence can be defined as the Praetiglian–Tiglian boundary (*Mimomys* cf. *polonicus* reported).

Now the group 1 faunas are from deposits to which a Pre-Pastonian or Pastonian age has been assigned (see §4), and the group 2 faunas come from deposits that are from the type locality of the Bramertonian stage, or have been correlated with these here.

An additional piece of evidence defining the bottom limit of the Pre-Pastonian in terms of stages of the Dutch sequence comes from the mollusc, *Macoma balthica*. This is absent in the Dutch Lower Pleistocene which is marine up to and including Tiglian C 4c, but abundantly present in British sediments of Pre-Pastonian age (Spaink & Norton 1967; West 1980*a*).

The correlations suggested by the microtine evidence have lower limits rather older than has been suggested by other lines of evidence, such as pollen analysis. This aspect deserves further investigation.

(ii) *Small mammal biostratigraphy* (see also table 13)

The system originally developed by Kretzoi (1956, 1965) for Hungarian fissure deposits, and widely adopted in continental Europe, has been elaborated and redefined in biostratigraphic terms by van der Meulen (1973). Thus the chronostratigraphic stages Villanyian and Biharian of Kretzoi have been defined as the *Mimomys* superzone and the *Pliomys* superzone, respectively. Within these superzones, biozones (which may be assemblage zones, total range zones, or partial range zones) are recognized. The bases for biozonation of the Biharian were outlined by van der Meulen (1973); biozonation of the Villanyian has been elaborated by Rabeder (1981).

British faunal groups 1–3 recognized here fall within the *Mimomys* superzone (= Villanyian). This allocation can be made by the presence of *M.pliocaenicus* rather than *M.savini* which occurs in the *Pliomys* superzone. No species characteristic for the *Pliomys* superzone are present.

Rabeder (1981) recognizes six biozones in the *Mimomys* superzone, the four lower zones being based on the material from four superimposed levels at the locality Stranzendorf in Austria. The similarity of material from Stranzendorf to the British assemblages in faunal groups 1–3 has already been discussed in §8*b*. Faunal group 1 material can be placed in Rabeder's *Kislangia praerex* assemblage zone or *Mimomys jota* total range zone; faunal group 2 material appears to belong to the *Mimomys hintoni* assemblage zone of Rabeder, the basal zone of the Villanyian.

The fauna of the type Cromerian (Stuart 1975) is considered to fall in the *Pitymys arvalidens* partial range zone of the Biharian (van der Meulen 1973). On the assumption of contemporaneity of contained animal and plant fossils, the boundary between the Villanyian and Biharian may be placed in Britain between the Pre-Pastonian *a* substage and the Cromerian stage. In the Netherlands, this transition is placed within the Eburonian (van der Meulen & Zagwijn 1974).

9. Conclusions

This work reviews the fossil microtine material from British Lower Pleistocene deposits consisting of inshore marine sediments belonging to the Norwich Crag and Cromer Forest-bed Formations, also known as 'Icenian Crag'. The deposits include the 'Weybourne Crags' of the Norfolk coast, the classical inland exposures of 'Norwich Crag', and the Easton Bavents clay and crag of the north Suffolk coast. The material studied comes from 17 localities.

Eight microtine taxa are recognized, of which two, *Mimomys pitymyoides* and *M.altenburgensis* are described for the first time from Britain. *Clethrionomys* is recorded for the first time in the Lower Pleistocene of Britain. Reexamination of the type material of *Mimomys newtoni* has necessitated some changes in nomenclature. It is proposed that *M.newtoni* Major is a senior synonym of *M.hungaricus* (Kormos). The valid prior name for the species described by Hinton (1926) under the name '*M.newtoni*', and widely known under that name in the literature, appears to be *Mimomys blanci* van der Meulen 1973. A new description of the species *Mimomys reidi*, based on the type and referred material of similar geological age, is provided.

No evidence of *Mimomys savini* was found in the assemblages described here, whereas this species occurs abundantly in the later deposits of the Cromerian stage. This species does not occur with *Mimomys pliocaenicus* in deposits at East Runton, and there is no evidence for mixing of faunas of different age at this locality as proposed by Major (1908) and Hinton (1926).

Three faunal groups are recognized. Group 1 faunas are recovered from coastal deposits in Norfolk which have previously been termed 'Weybourne Crag'. These sediments are considered to date from either the Pre-Pastonian or Pastonian stages. Group 2 faunas are recovered from inland 'Norwich Crag' deposits in Norfolk and from crag deposits in Suffolk yielding a Chillesford-type pollen assemblage. These sediments are believed to date from the Bramertonian stage (Funnell *et al.* 1979). Group 3 faunas come from coastal exposures of crag at Covehithe and Easton Bavents associated with Baventian stage clays (Funnell & West 1962; West *et al.* 1980).

Group 1 faunas can be distinguished from group 2 faunas by certain characteristics, including the presence or absence of various taxa and differences in morphology thought to reflect evolutionary change within lineages. Group 3 faunas are poorly known, and cannot at present be distinguished from other faunas on the basis of a satisfactory number of characteristics. Separation is retained because, according to current stratigraphic interpretations, this group should represent the oldest assemblages from Britain.

Group 1 faunas contain *Mimomys pliocaenicus*, *M.reidi* (type level), *M.newtoni* (type level), *M.pitymyoides*, *M.blanci* and *Clethrionomys* sp. *M.blanci* is abundant.

Group 2 faunas contain *Mimomys pliocaenicus*, *M.reidi*, *M.newtoni* (these three species less advanced than in group 1 faunas), *M.rex* and *M.altenburgensis* (these two species lacking in group 1 faunas). *M.blanci* and *M.pitymyoides* are not found in group 2 faunas.

Group 3 faunas contain *Mimomys pliocaenicus*, *M.reidi* and *M.blanci*. Further collection may be expected to extend this list.

In general, these results confirm current stratigraphic interpretations. Group 1 faunas postdate group 2 faunas, supporting the relative position of Bramertonian and Pre-Pastonian stages. No firm conclusions can be drawn yet on the relative age of group 3 faunas.

The fauna of the Pastonian stage requires clarification. It is not possible to allocate unambiguously any of the material described here to this stage.

Comparison of these faunas with those from continental Europe indicates general similarity with the fauna from Tegelen, The Netherlands, although more detailed comparisons must await further description of the Tegelen material. The assemblages in faunal groups 1 and 2 closely resemble material from superimposed levels in the loess profile at Stranzendorf, Austria, described by Rabeder (1981).

The relationship of faunal groups 1–3 to current biostratigraphic systems is indicated primarily by the presence of *Mimomys pliocaenicus*, and the absence of voles with unrooted teeth such as *Microtus* (*Allophaiomys*) *pliocaenicus*. This demonstrates that the faunas belong to the *Mimomys* superzone of van der Meulen (1973), corresponding to the Villanyian stage. The zonation of the *Mimomys* superzone is currently a subject of discussion. It is considered probable that the British assemblages fall within the first four of the six biozones of the *Mimomys* superzone (Villanyian) proposed by Rabeder (1981).

On the basis of the microtine evidence upper and lower limits for the correlation of Bramertonian and Pre-Pastonian (*a*) stages with The Netherlands chronostratigraphy are proposed. These limits are earlier than have been suggested on the basis of other lines of evidence. Thus, correlation of the later part of the Pre-Pastonian with part of the Eburonian, and of Bramertonian with part of the Tiglian, is thought to merit consideration.

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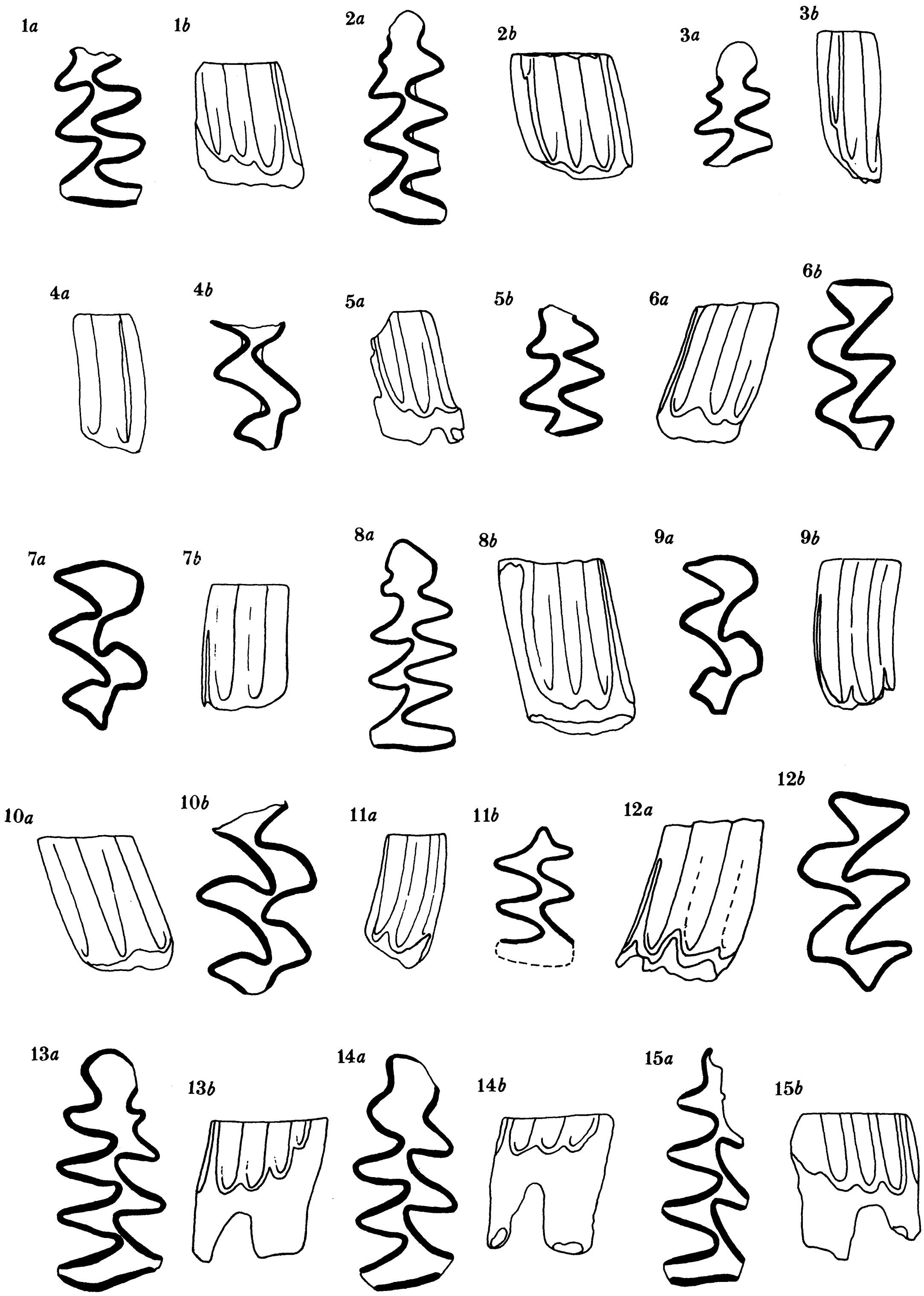

FIGURE 12. Parts 1–6: *Mimomys pitymyoides* Janossy and van der Meulen from East Runton and West Runton; parts 7–15: *Mimomys newtoni* Major from Bramerton, Thorpe, East Runton and West Runton.

Part 1*a*,*b*, M_1 West Runton, D.F.M. collection; part 2*a*,*b*, M_1 West Runton, UMZC WRC 321, A.J.S. collection; part 3*a*,*b*, M_1 West Runton, UMZC WRC 565, A.J.S. collection; part 4*a*,*b* M^2 West Runton, UMZC WRC 36, A.J.S. collection; part 5*a*,*b*, M_1 East Runton, 'Weybourne Crag', GSM 115499; part 6*a*,*b*, M^1 East Runton, 'shelly crag', GSM 115499; part 7*a*,*b*, M^2 Bramerton, BMNH M35154, Hinton collection; part 8*a*,*b*, M_1 type, East Runton 'shelly crag', BMNH M6967a, Savin collection, figd Major (1902) figure 7 and 10; part 9*a*,*b*, M^2 East Runton, 'Weybourne Crag', GSM 115500; part 10*a*,*b*, M^1 West Runton, UMZC WRC 561, A.J.S. collection; part 11*a*,*b*, M_2 Bramerton Blake's Pit, Lower Shell Bed, SM X.7929, P.G.C. collection; part 12*a*,*b*, M^1 Thorpe, NCM 971c, figd Hinton (1926) figure *100*, 21; part 13*a*,*b*, M_1 Bramerton Blake's Pit, Lower Shell Bed, SM X.7920, P.G.C. collection; part 14*a*,*b*, M_1 Bramerton, BMNH M35155 Johnson collection, mentioned Hinton (1926) footnote p. 376; part 15*a*,*b*, M_1 Thorpe, NCM 971d, figd Hinton (1926) figure *100*, 22.

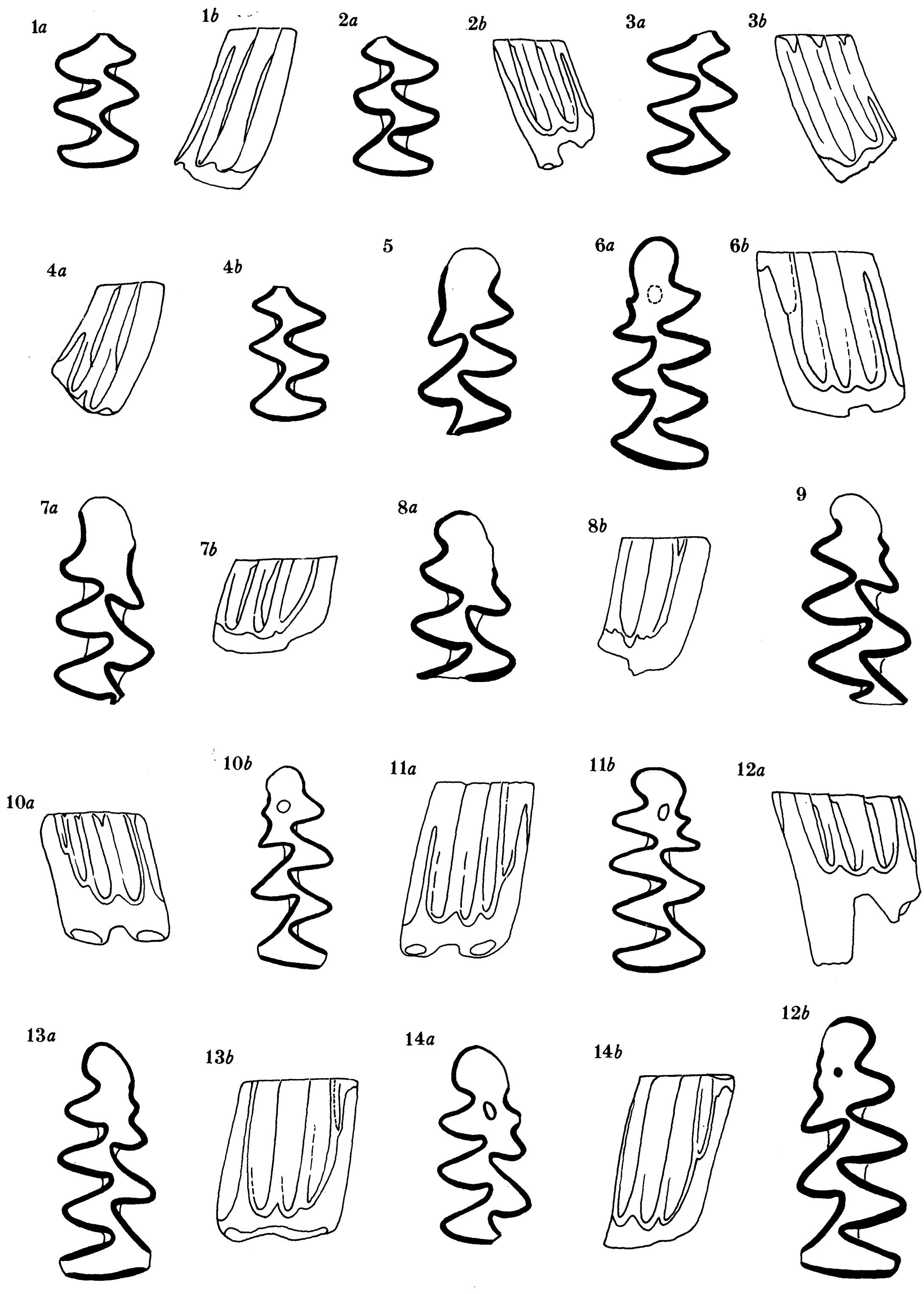

FIGURE 13. Lower molars of smaller *Mimomys* species from West Runton (crag), East Runton, Trimingham, Easton Bavents, Thorpe (Norwich), Bramerton, and Thorpe Aldringham. Parts 5–9, 12–14, *Mimomys reidi*; parts 3, 10 and 11, *Mimomys altenburgensis*.

Part *a,b*, M_2 West Runton, UMZC WRC 239, A.J.S. collection; part 2*a,b*, M_2 Thorpe Aldringham, P.G.C. collection; part 3*a,b*, M_2 Bramerton. Blake's Pit, Lower Shell Bed, SM X.7924, P.G.C. collection; part 4*a,b*, M_3 East Runton 'clay gravel', GSM 115482; part 5, M_1 Easton Bavents, IM; part 6*a,b*, M_1 type *Mimomys reidi* Hinton, Trimingham, GSM 48637; part 7*a,b*, M_1 East Runton 'clay gravel', GSM 115483, figd Hinton (1926) figure *99*, 27; part 8*a,b*, M_1 East Runton 'shelly sand', GSM 115491; part 9, M_1 Thorpe, NCM 971h Fitch collection, figd Hinton (1926) figure *99*, 28; part 10*a,b*, M_1 Bramerton. Blake's Pit, Lower Shell Bed, SM X.7919, P.G.C. collection; part 11*a,b*, M_1 Bramerton. Blake's Pit, Lower Shell Bed, SM X.7918, P.G.C. collection; part 12*a,b*, M_1 Thorpe, NCM 971g Fitch collection, figd Major (1902) figures 15 and 20; figd Hinton (1926) figure *100*, 7, 7a; part 13*a,b*, M_1 West Runton, UMZC WRC 169, A.J.S. collection; part 14*a,b*, M_1 West Runton, UMZC WRC 381, A.J.S. collection.

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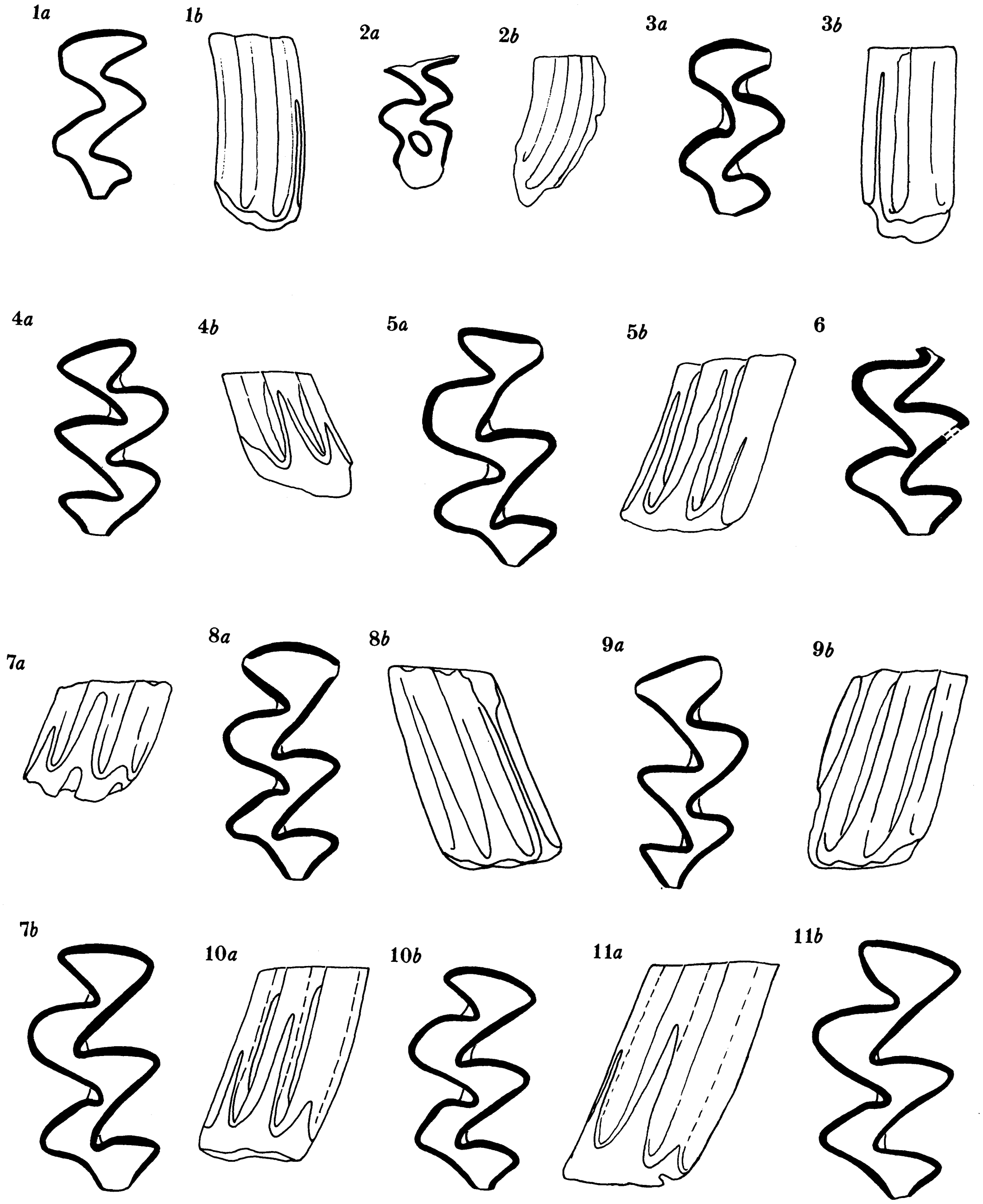

FIGURE 14. Parts 1–3, 5–11, *Mimomys reidi* Hinton from Sizewell, East Runton, West Runton, Bramerton and Easton Bavents; part 4, *Mimomys altenburgensis* Rabeder from Thorpe.

Part 1*a*,*b*, M^2 Sizewell, P.G.C. collection, G73831; part 2*a*,*b*, M^3 East Runton 'Weybourne Crag', GSM 115486; part 3*a*,*b*, M^2 East Runton 'Weybourne Crag', GSM 115488; part 4*a*,*b*, M^1 Thorpe, NCM 971c Fitch collection; part 5*a*,*b*, M^1 West Runton, UMZC WRC 112, A.J.S. collection; part 6, M^1 Easton Bavents, IM Long collection; part 7*a*,*b*, M^1 Bramerton Blake's pit Lower Shell Bed SM X.7930, P.G.C. collection; part 8*a*,*b*, M^1 East Runton 'Weybourne Crag', GSM 115492; part 9*a*,*b*, M^1 West Runton, UMZC WRC 33, A.J.S. collection; part 10*a*,*b*, M^1 Bramerton Blake's pit Lower Shell Bed, SM X.7927, P.G.C. collection; part 11, M^1 Bramerton, BMNH M35159 Kennard collection.

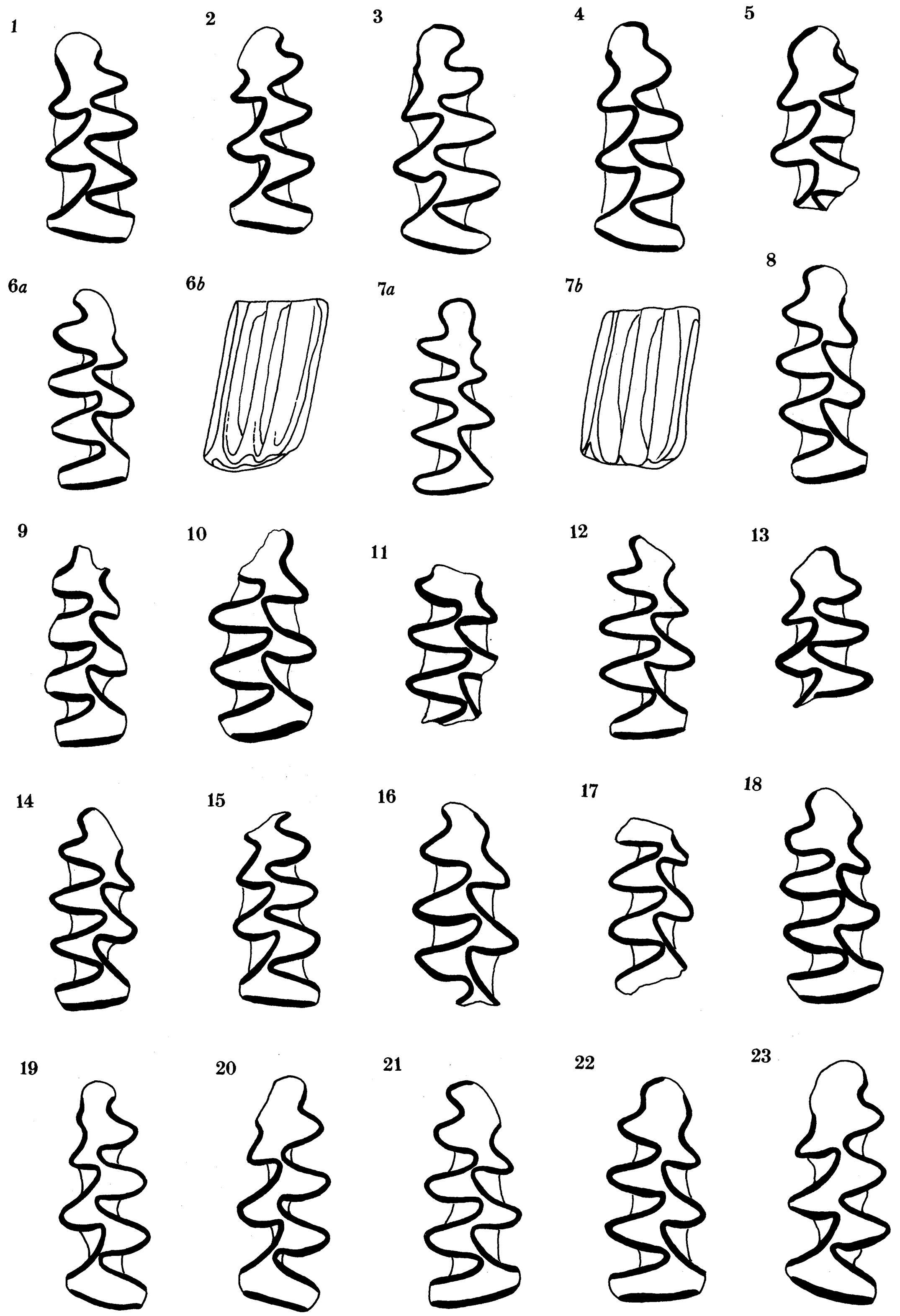

FIGURE 15. Part 1–22, *Mimomys blanci* van der Meulen M_1 from East Runton, Sidestrand, Overstrand, Easton Bavents and West Runton; part 23, *Mimomys reidi* M_1 from West Runton.

Part 1, East Runton 'clay gravel', GSM 115483; part 2, East Runton 'Weybourne Crag', GSM 115498; part 3, East Runton 'Weybourne beds', BMNH M6967 (15) Savin collection 430; part 4, East Runton 'clay gravel', GSM 115483, figd Hinton (1926) figure *99*, 19; part 5, East Runton, 'Weybourne Crag', BMNH M35165; part 6*a*,*b*, East Runton 'shelly crag', GSM 115500; part 7 *a*,*b*, East Runton 'clay gravel', GSM 115482, figd Hinton (1926) figure 103; part 8, East Runton 'shelly crag' BMNH M6967b Savin collection 464, figd Major (1902) figures 16 and 23; part 9, East Runton 'clay gravel', GSM 115482; part 10, Overstrand 'shelly sand', P. G. C. G1831; part 11–13, Sidestrand 'shelly sand', A. J. S. collection; part 14, Easton Bavents, A. J. S. collection; parts 15–17, 19–23, West Runton, UMZC WRC 222, 32, 603, 401, 601, 521, 492, 1; part 18, West Runton, D. F. M. collection.

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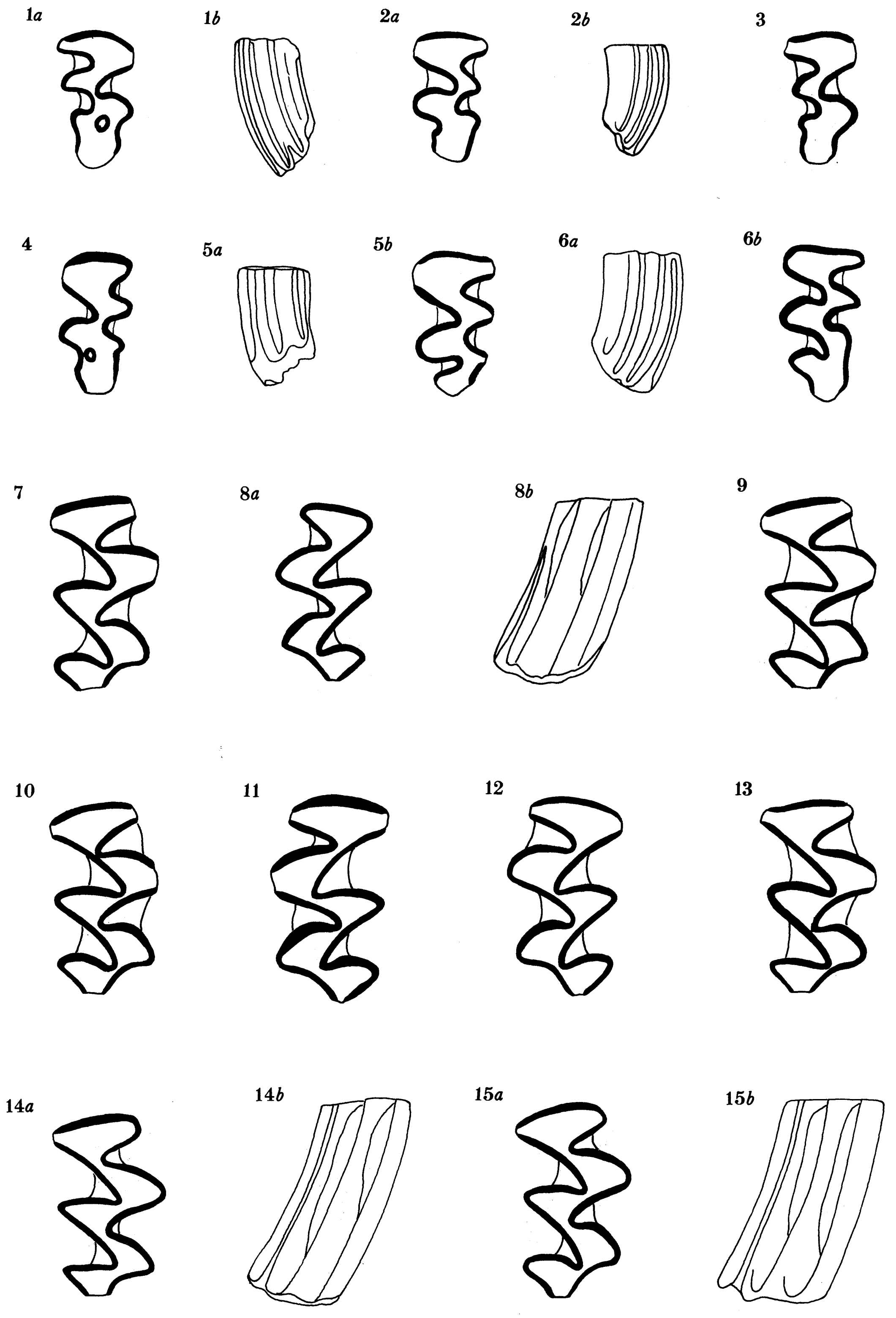

FIGURE 16. Parts 1–4, 7–15, *Mimomys blanci* van der Meulen from West Runton, Sidestrand and East Runton; figure 5*a*,*b* *Mimomys* sp. from Covehithe, figure 6 *Clethrionomys* sp. from Overstrand.

Parts 1*a*,*b*, 2*a*,*b*; 3, M³ West Runton, UMZC WRC 436, 463, 240; part 4, M³ Sidestrand, A.J.S. collection; part 5*a*,*b*, M³ Covehithe, IM; part 6*a*,*b*, M³ Overstrand, shelly sand, P.G.C. collection E1831; part 7, M¹ East Runton 'shelly crag', GSM 115492; part 8, M¹ East Runton 'shelly crag', GSM 115488; parts 9 and 10, M¹ East Runton 'shelly crag', GSM 115490; parts 11–15, M¹ West Runton, UMZC, WRC 354, 61, 354, 191, 119.

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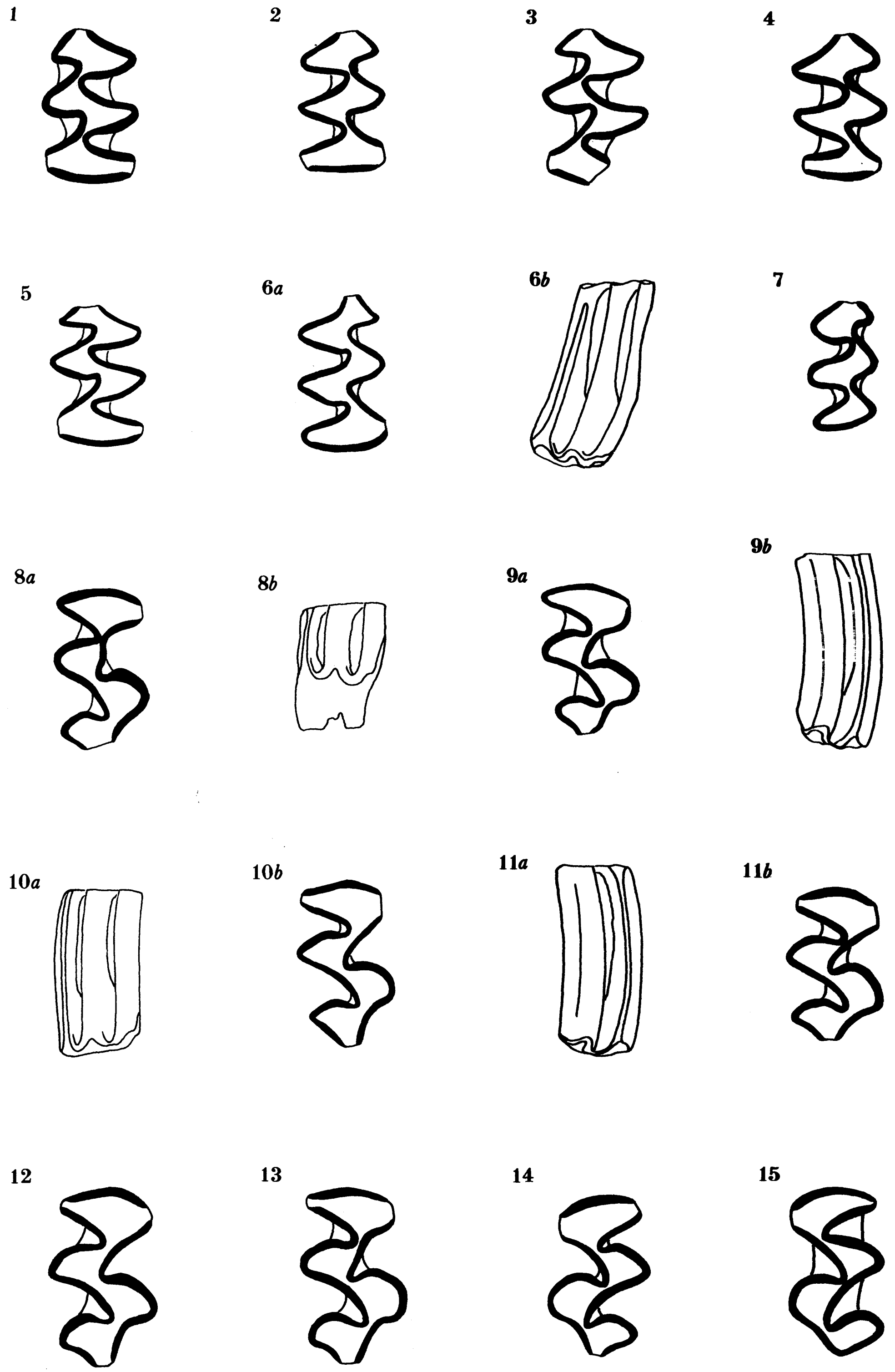

FIGURE 17. Parts 1–15, *Mimomys blanci* van der Meulen from East Runton and West Runton.

Part 1, M_2 East Runton 'clay gravel', GSM 115482; parts 2–6, M_2 West Runton, UMZC WRC 699, 434, 66, 196, 236, A.J.S. collection; part 7, M_3 West Runton, UMZC WRC 155, A.J.S. collection; parts 8–10, M^2 West Runton, UMZC WRC 114, 120, 113, A.J.S. collection; part 11 *a*,*b*, M^2 East Runton, BMNH 31568; parts 12–14, M^2 West Runton, UMZC WRC 64, 243, 435, A.J.S. collection; part 15, M^2 East Runton 'clay gravel', GSM 115482.

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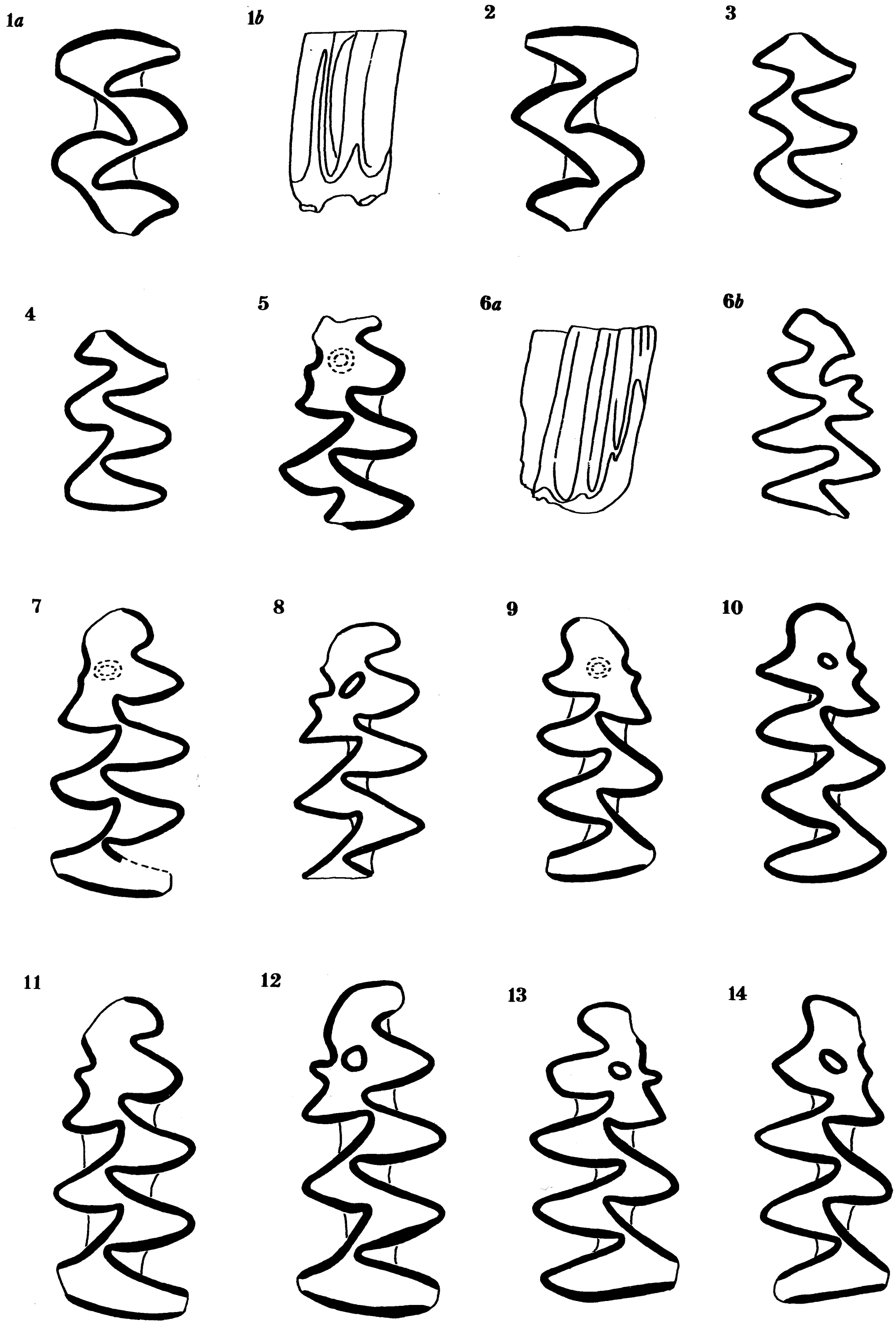

FIGURE 18. *Mimomys pliocaenicus* from Thorpe (Norwich).

Part 1*a*,*b*, M^2 NCM 971f Fitch collection; part 2, M^2 NCM 971f Fitch collection; part 3, M_3 NCM 971e Fitch collection; part 4, M_2 NCM 971c Fitch collection; part 5, M_1 NCM 971b Fitch collection; part 6*a*,*b*, M_1 NCM 971a Fitch collection, figd Major (1902) figure 29; Hinton (1926) figure *99*, 1, 1*a*; part 7, M_1 NCM 971b Fitch collection, figd Hinton (1926) figure *100*, 3, 3*a*; part 8, M_1 NCM 971d Fitch collection, figd Major (1902) figure 2; Hinton (1926) figure *99*, 4, 4a; part 9, M_1 NCM 551, figd Major (1902) figure 4. Hinton (1926) figure *100*, 10, 10a; part 10, M_1 NCM 971b Fitch collection, figd Hinton (1926) figure *100*, 8, 8a; part 11, M_1 NCM 971b Fitch collection, figd Hinton (1926) figure *100*, 2, 2a; part 12, M_1 NCM 551, figd Major (1902) figure 5; Newton (1882) plate XIII, figure 13; Hinton (1926) figure *100*, 1; part 13, M_1 NCM 971d Fitch collection, figd Major (1902) figure 3; Hinton (1926) figure *100*, 4, 4a; part 14, M_1 NCM 971b Fitch collection, figd Hinton (1926) figure *100*, 5, 5a.

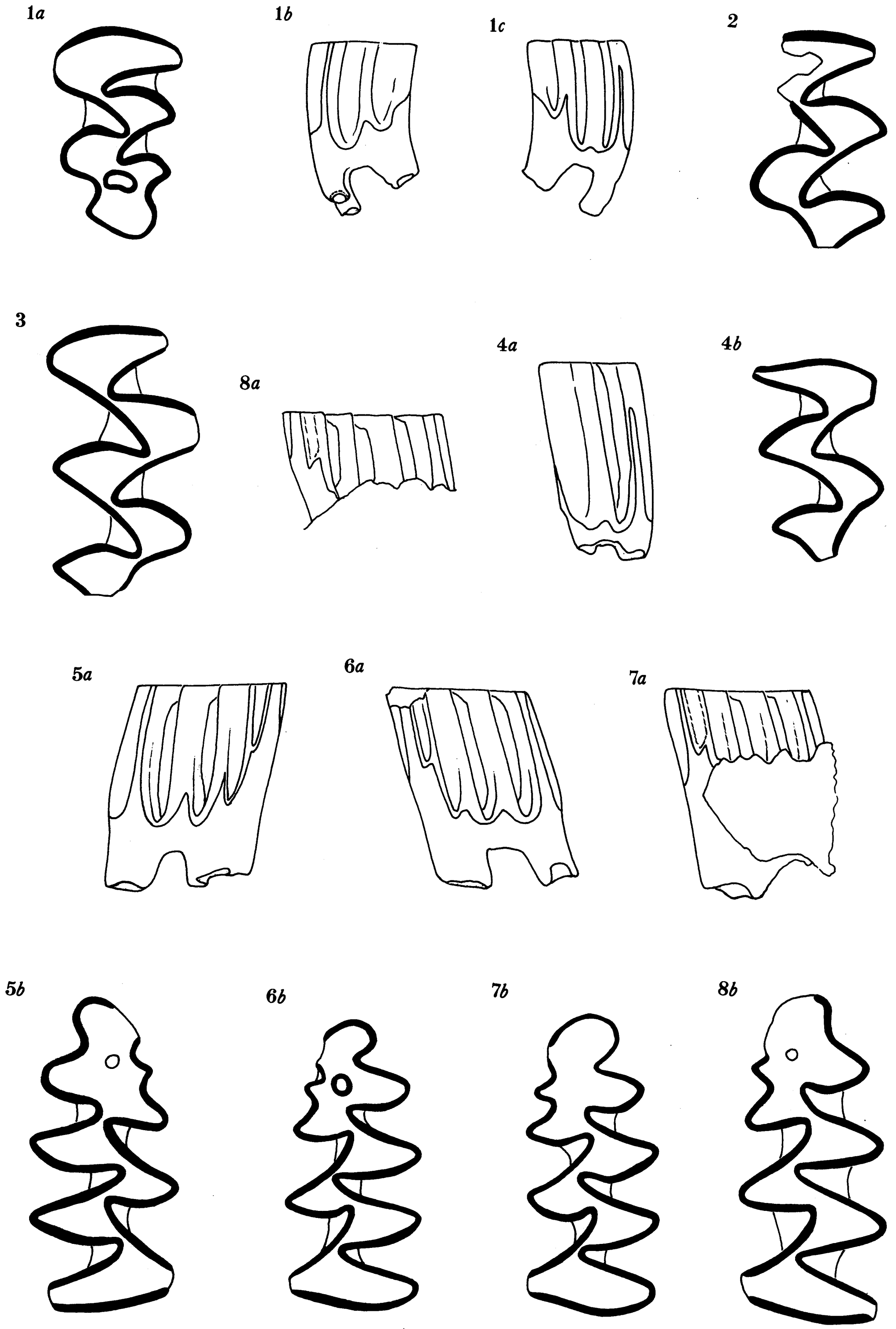

FIGURE 19. Parts 1–8, *Mimomys pliocaenicus* Major from Thorpe Aldringham, Kyson, Holton and Yarn Hill. Part 1*a,b,c*, M^3 Thorpe Aldringham, P.G.C. collection; part 2, M^2 Thorpe Aldringham, P.G.C. collection; part 3, M^1 Thorpe Aldringham, P.G.C. collection; part 4*a,b*, M^2 Thorpe Aldringham, P.G.C. collection; part 5*a,b*, M_1 Yarn Hill, BMNH M35152, figd Hinton (1926) figure *99*, 3; part 7*a,b*, M_1 Kyson, BMNH M36568a; part 8*a,b*, M_1 Kyson, BMNH M36568a.

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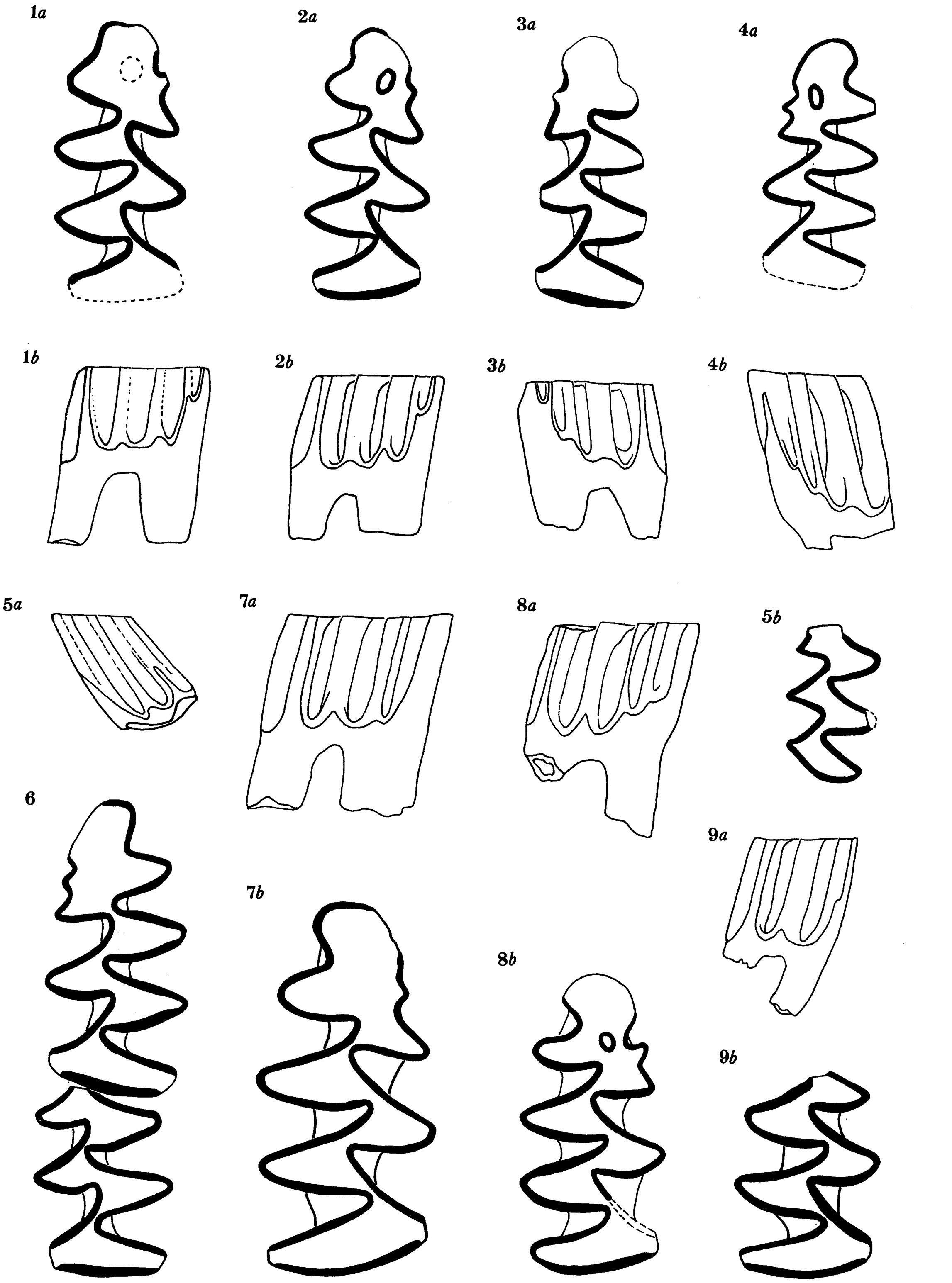

FIGURE 20. Parts 1–6, 8, *Mimomys pliocaenicus* Major, parts 7, 9, *Mimomys* (*Kislangia*) *rex* Kormos from Bramerton. *M. pliocaenicus*: part 1 *a,b*, M_1 Blake's pit Lower Shell Bed SM X.7932, P.G.C. collection; part 2 *a,b*, M_1 Blake's pit Lower Shell Bed, SM X.7931, P.G.C. collection; part 3*a,b*, M_1 'lower bed', NCM 747 Reeve collection figd Hinton (1926) figure *100*, 14; part 4*a,b*, M_1 BMNH M35158 Kennard collection, figd Hinton (1926) figure *100*, 9, 9a; part 5*a,b*, M_3 Blake's pit Lower Shell Bed, SM X.7925, P.G.C. collection; part 6, M_1, M_2 BMNH M35153 Johnson collection, ment. Hinton (1926) p. 363, footnote; part 8*a,b*, 'lower bed', NCM 747 Reeve collection, figd Hinton (1926) figure *100*, 6.

M. rex: part 7*a,b*, M_1 Blake's pit Upper Shell Bed, NCM 524 Reeve collection, figd Newton (1882) plate XIII, figure 12; Major (1902) figure 14; Hinton (1926) figure *100*, 12; part 9*a,b*, M_2 from same mandible as figure 7, figd Newton (1882) plate XIII, figure 12.

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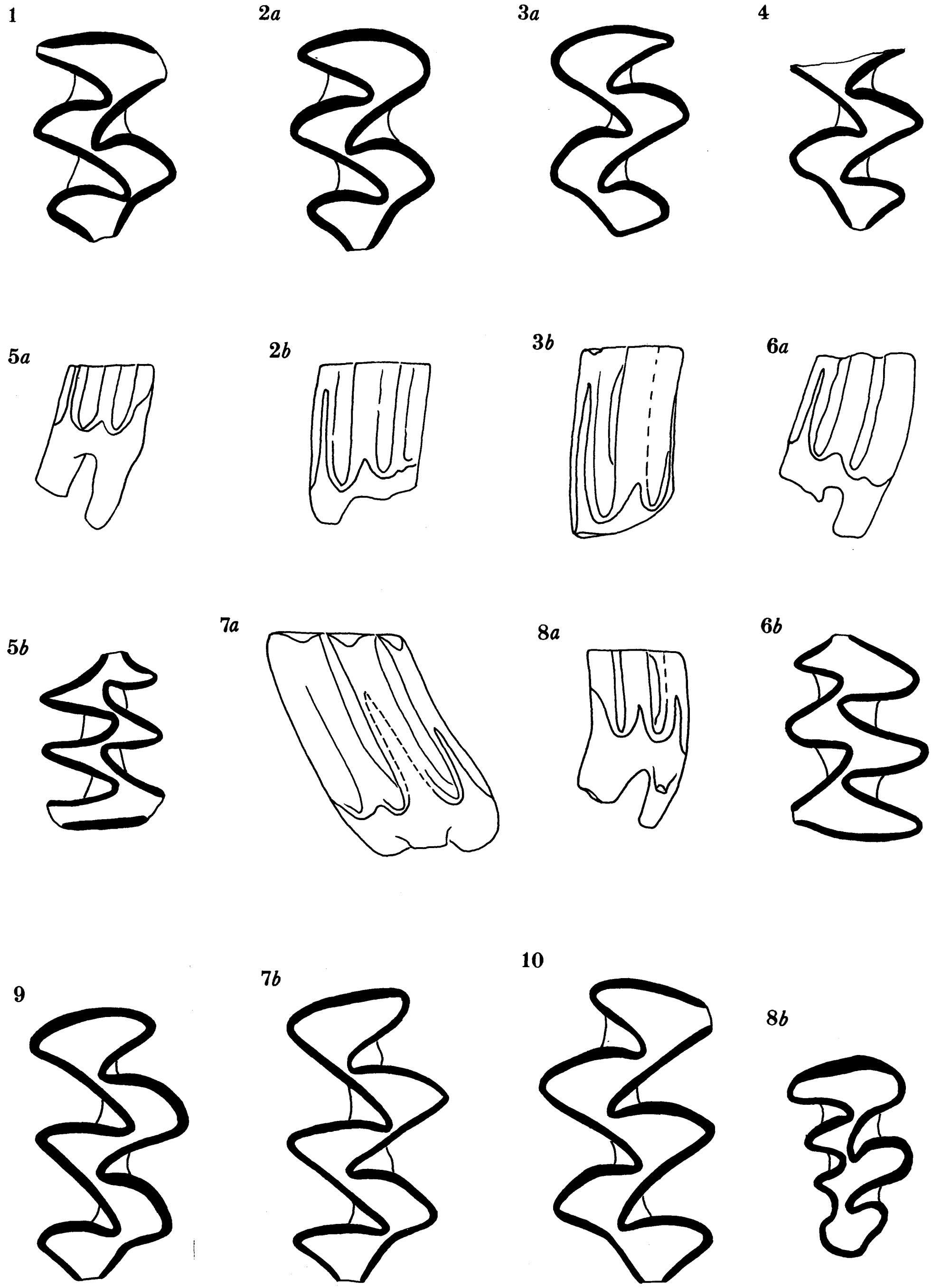

FIGURE 21. Parts 1–19, *Mimomys pliocaenicus* Major from Bramerton.

Part 1, M^2 Blake's pit, Lower Shell Bed SM X.7922, P.G.C. collection; part 2*a*,*b*, M^2 Blake's pit, Lower Shell Bed, SM X.7921, P.G.C. collection; part 3*a*,*b*, M^2 Blake's pit, Upper Shell Bed, SM X.7933 P.G.C. collection; part 4, M^2 ? Bramerton common, NCM 747; part 5*a*,*b*, M_2 BMNH M35160; part 6*a*,*b*, M_2 Blake's pit, Lower Shell Bed, SM X.7923, P.G.C. collection; part 7*a*,*b*, M^1 BMNH M35157 Kennard collection; part 8*a*,*b*, M^3 Blake's pit, Lower Shell Bed, SM X.7928, P.G.C. collection; part 9, M^1 BMNH M35156 Kennard collection; part 10, M^1 'lower bed', NCM 747, figd Hinton (1926) figure *100*, 15.

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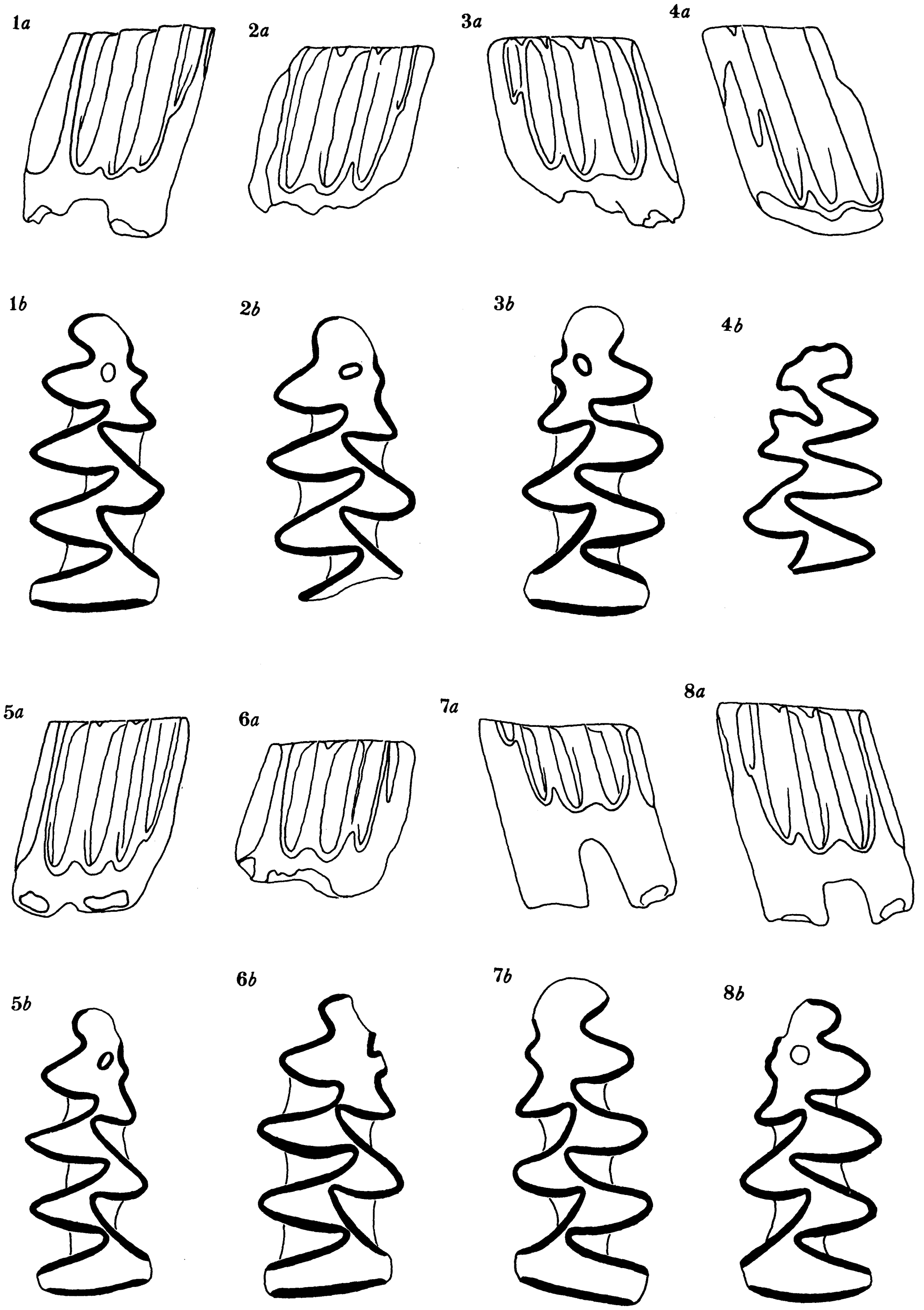

FIGURE 22. Parts 1–8, *Mimomys pliocaenicus* Major M_1 from West Runton (shelly crag). Parts 1–2, 5–8 UMZC WRC 151, 232, 351, 651, 402, 231; parts 3 and 4 D.F.M. collection.

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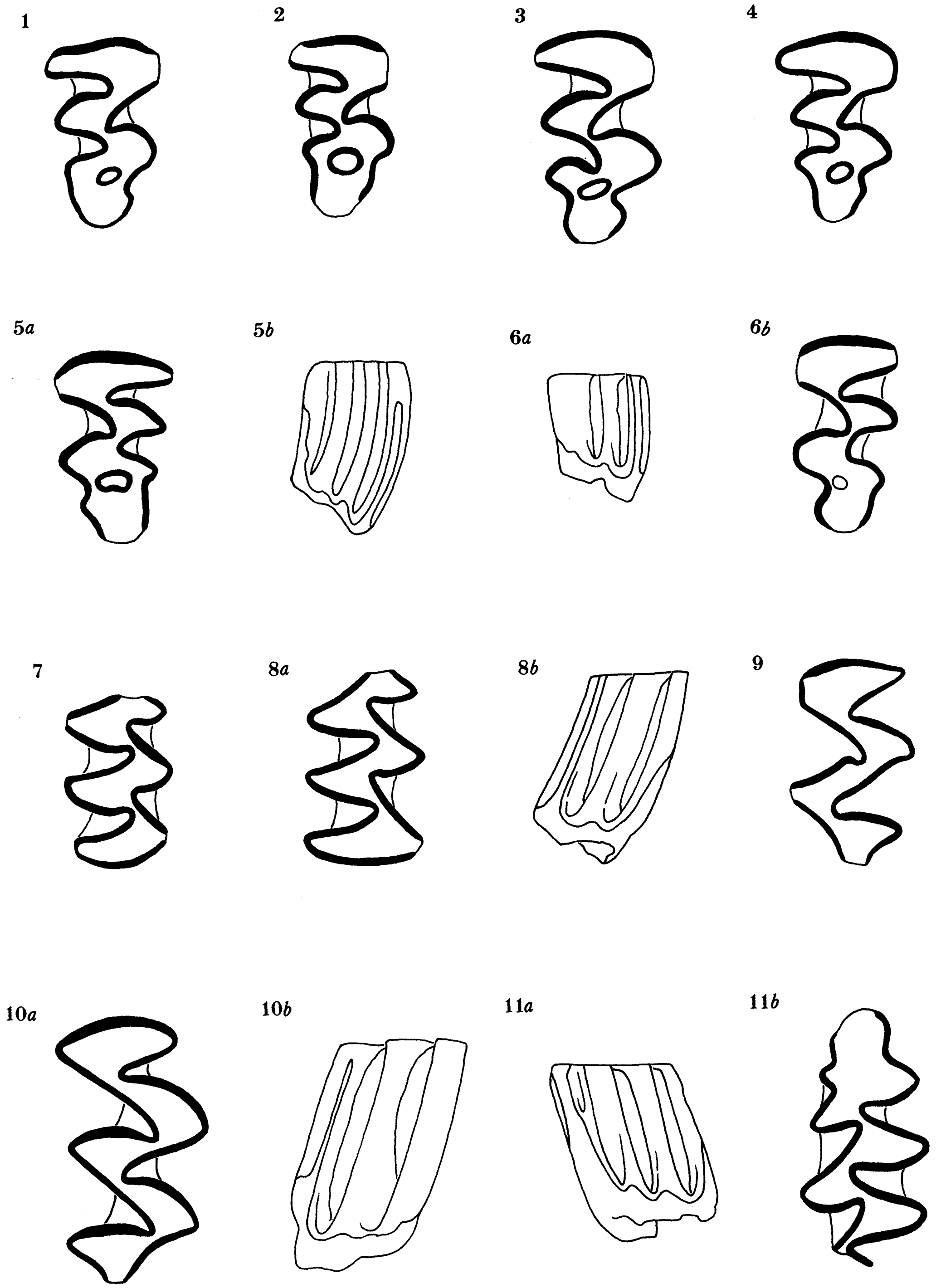

FIGURE 23. *Mimomys pliocaenicus* Major from West Runton (crag).
Parts 1–6, M^3 UMZC WRC 462, 404, 63, 193, 355, 461; part 7, M_3 UMZC WRC 234; part 8, M_2 UMZC WRC 62; part 9, M_2 UMZC WRC 353; part 10, M^1 UMZC WRC 111; part 11, M_1 UMZC WRC 433.

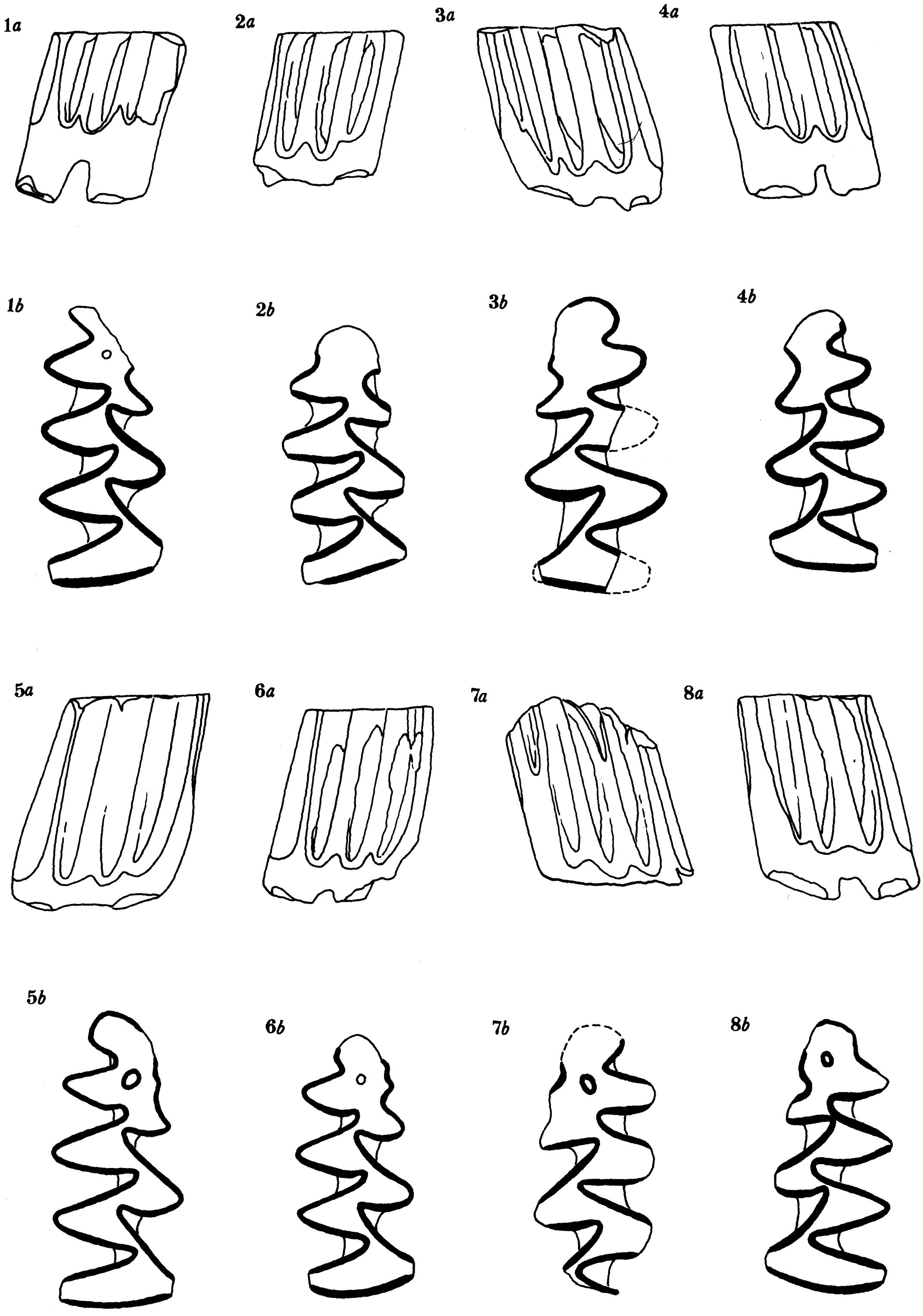

FIGURE 24. Part 1–8, *Mimomys pliocaenicus* Major M_1 from East Runton.

Part 1 *a,b*, 'Weybourne Crag', GSM 115497; parts 2, 4 and 6–8, shelly sand 30 yards from cliff N gangway', BMNH M6967 Savin collection 430; part 3*a,b*, 'shelly crag', GSM 115493; part 5*a,b*, 'Weybourne Crag', BMNH M35164 Kennard collection.

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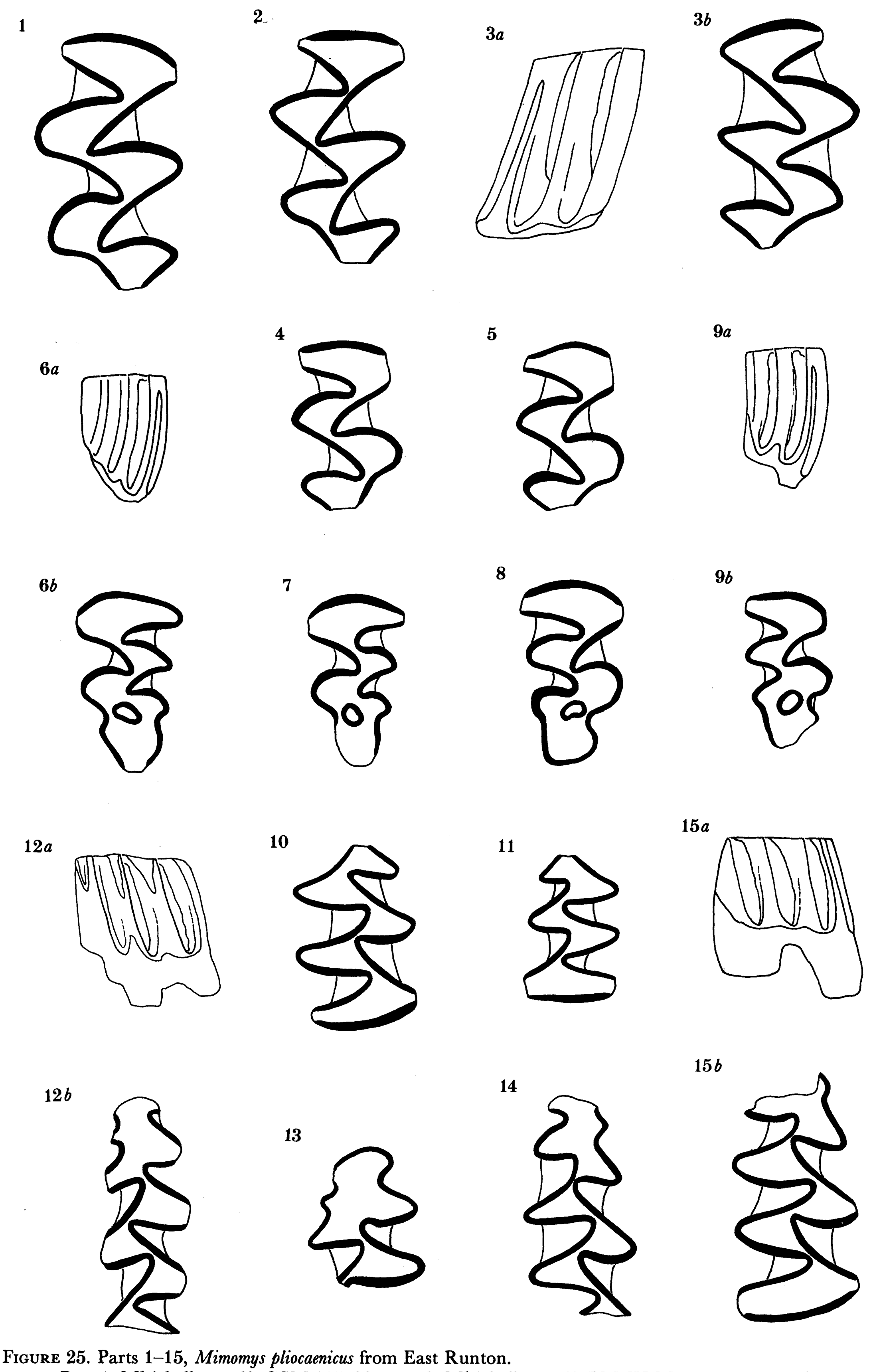

FIGURE 25. Parts 1–15, *Mimomys pliocaenicus* from East Runton.

Part 1, M^1 'shelly sand', GSM 115500; part 2, M^1 'shelly sand', BMNH M6967; part 3, M^1 'shelly sand', GSM 115486; part 4, M^2 'shelly sand', GSM 115486; part 5, M^2 'shelly sand', GSM 115487; part 6*a,b*, M^3 'Weybourne Crag', GSM 115499; part 7, M^3 'shelly sand', BMNH M6967; part 8, M^3 'Weybourne Crag', GSM 115500; part 9*a,b*, M^3 'shelly sand', BMNH M35153; parts 10 and 11, M_2 'Weybourne Crag', GSM 115498; parts 12*a,b*, M_1 'clay gravel', GSM 115483; part 13, M_1 'clay gravel', GSM 115482; part 14, M_1 'shelly sand', BMNH M6967j; part 15*a,b*, M_1 'shelly sand', GSM 115486.

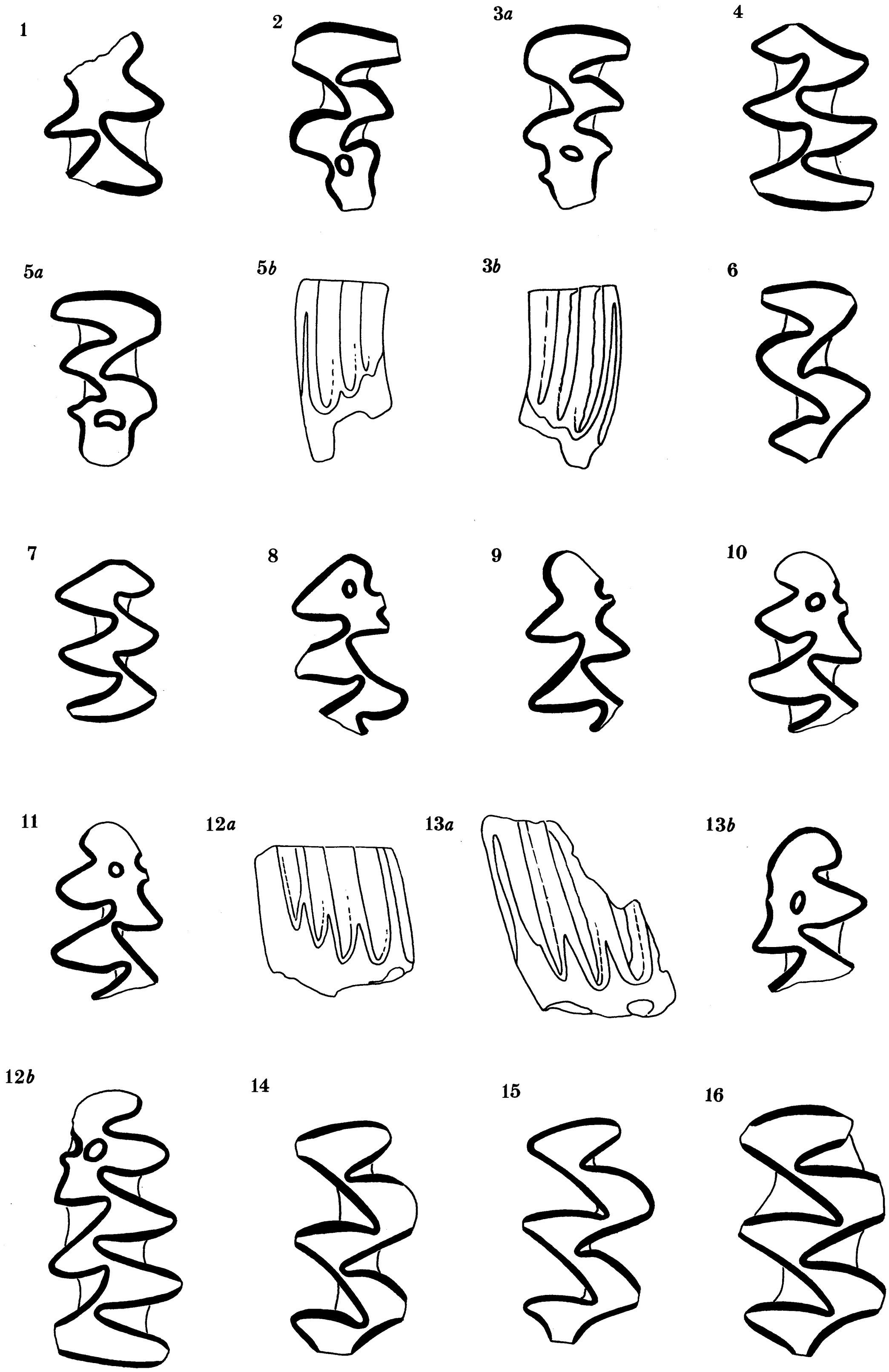

FIGURE 26. Parts 1–16, *Mimomys pliocaenicus* Major from Overstrand, Sidestrand, Easton Bavents and Covehithe. Part 1, M_1 Sidestrand, shelly sand, A.J.S. collection; part 2, M^3 Easton Bavents, IM Long collection; part 3*a*,*b*, M^3 Sidestrand, shelly sand, A.J.S. collection; part 4, M_2 Overstrand 'Weybourne Crag', P.G.C. collection, G1831E; part 5*a*,*b*, M^3 Easton Bavents, IM Long collection; part 6, M^2 Covehithe, IM Long collection; part 7, M_2 Covehithe, IM Long collection; part 8, M_1 Covehithe, IM Long collection; part 9, M_1 Easton Bavents, BMNH M20278; part 10, M_1 Covehithe, IM Long collection; part 11, M_1 Covehithe, IM Long collection; part 12*a*,*b*, M_1 Easton Bavents, A.J.S. collection; part 13*a*,*b*, M_1 Easton Bavents, IM Long collection; part 14, M^1 Easton Bavents, IM Long collection; part 15, M^1 Covehithe, IM Long collection; part 16, M^1 Easton Bavents, IM RADM collection.