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Systematic status of Kennard's shrew (*Sorex kennardi* HINTON, 1911, Insectivora: Soricidae): a study based on British and Polish material

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Abstract. A species of fossil shrew intermediate in size between *Sorex araneus* LINNAEUS, 1758 and *Sorex minutus* LINNAEUS, 1766 recently discovered in Obłazowa Caves (Site Obłazowa 2) dated at 33 430 ± 1230 y. b. p. is here identified as *Sorex kennardi* HINTON, 1911. This taxon was described from Ponder's End, Middlesex, U.K., an undated Late Pleistocene site. It remains little known in Britain, but a previously unrecorded specimen from Conningbrook, Kent dated at 34-38 000 y. b. p. is described here. The holotype is redescribed and compared in detail with the material from Obłazowa. The taxonomic relationships of *Sorex kennardi* are discussed and previous continental European references to it reviewed. The Lower and Middle Pleistocene *Sorex runtonensis* HINTON, 1911 is postulated as an ancestral form. *Sorex 'kennardi' hundsheimensis* RABEDER, 1972 (Type Locality Hundsheim, Austria, Middle/Late Biharian) is considered to be a different taxon, doubtfully related to *S. kennardi*. The most salient feature of the *runtonensis-kennardi* lineage is the tall narrow coronoid process of the mandible, appearing disproportionately delicate in relation to the size of the teeth. The two species are considered to be conspecific and the name *Sorex runtonensis* has priority.

Key words: Insectivora, Soricidae, Late Pleistocene, Vistulian, Devensian, taxonomy, Poland, U.K.

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I. INTRODUCTION

Remains of two species of shrew were recently excavated at Obłazowa caves, near Nowa Biała, Poland during joint studies of the Institute of Systematics and Evolution of Animals, Kraków and the Harrison Zoological Museum, Sevenoaks. A larger and rather less common species is indistinguishable from the extant *Sorex araneus* LINNAEUS, 1758. A smaller and more delicately built species, more abundant at this site has been referred tentatively to *Sorex kennardi* HINTON, 1911 by NADACHOWSKI et al. (1993). The fissure contained a rich Mid-Vistulian (late Pleistocene) vertebrate fauna dated 33 430 ± 1230 y. b. p. from a mandibular ramus of *Vulpes vulpes* (LINNAEUS,

1758) (Oxford Research Laboratory for Archaeology Ox A 3696 OBF). The soricid remains were mostly recovered from cave earth in a fissure deposit designated as Obłazowa 2.

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II. HISTORICAL REVIEW

In his description of the British fossil shrews HINTON (1911) described and figured (p. 533, Pl.25, Fig. 11 and Text Fig. 11a) a new species which he named *Sorex kennardi* after its discoverer, A. S. KENNARD. The holotype (BM M37004) consists of the anterior cranium with P4-M3 of both sides *in situ* and alveoli of the incisors and five unicuspids on each side. Both mandibular rami were associated, with the dentition and processes intact (Plate 1). It was found in the Third Terrace drift of the Lea Valley at Ponder's End , Middlesex, a Late Glacial site which has not been precisely dated. *S.kennardi* has remained a little known species in Britain since its discovery. During researches conducted by the Harrison Zoological Museum recently at Conningbrook, near Kennington, Kent, some rare shrew remains were recovered from the Mid-Devensian sands and gravels of the River Stour by screen-washing. This site has been dated at 34-38 000 y. b. p. and is thus nearly contemporaneous with Obłazowa 2. The material, previously unreported, consists of a right posterior ramus with coronoid, condyle and m1-m3 *in situ* (HZM.3.13623). It has been compared with the holotype and is considered similar in all respects. It is figured here in comparison with Recent *Sorex araneus* and *Sorex minutus* to illustrate general features of size and morphology (Fig. 1) and shape of the condyle (Fig. 2).

On the continent of Europe HELLER (1932) studied shrew remains of Late Pleistocene age from Raumgrotte in the Hersbrucker Jura and referred them to *Sorex kennardi* and later (HELLER 1959) identified it in the older Villafranchian fauna from Erpfingen. BRUNNER (1956) identified it from the Kleinen Teufelshöhle, Pottenstein. More recently RABEDER (1972) described an Insectivore fauna from Hundsheim, Austria, including a new subspecies, *Sorex kennardi hundsheimensis*, of Middle Pleistocene age. RABEDER (1972: 408, Tab. 10) refers the material from Pottenstein to *S. k. kennardi* and that from Hundsheim, Erpfingen and Raumgrotte to *S. k. hundsheimensis*.

HINTON's (1911) original description of the holotype was unfortunately rather brief, but included the following important diagnostic points: Size distinctly smaller than *S. araneus*, larger than *S. minutus*; mesopterygoid space proportionately broader (than *S. araneus*) and does not narrow behind; five upper unicuspids were present, decreasing regularly in size from before backwards as in *S. alpinus* and *S. minutus*, not in rough pairs as in *S. araneus* (determined from the alveoli only); maxillary cheekteeth P4-M2 with posterior emargination less deep than in *S. araneus*; mandibular ramus distinguished by its form (unspecified) and size; condyle agrees better with *S. minutus* and *S. alpinus* than with *S. araneus*.

This description requires a detailed revision in view of the greatly increased knowledge of Pleistocene shrews now available. The terminology and methods of measurement employed here follow REUMER (1984).

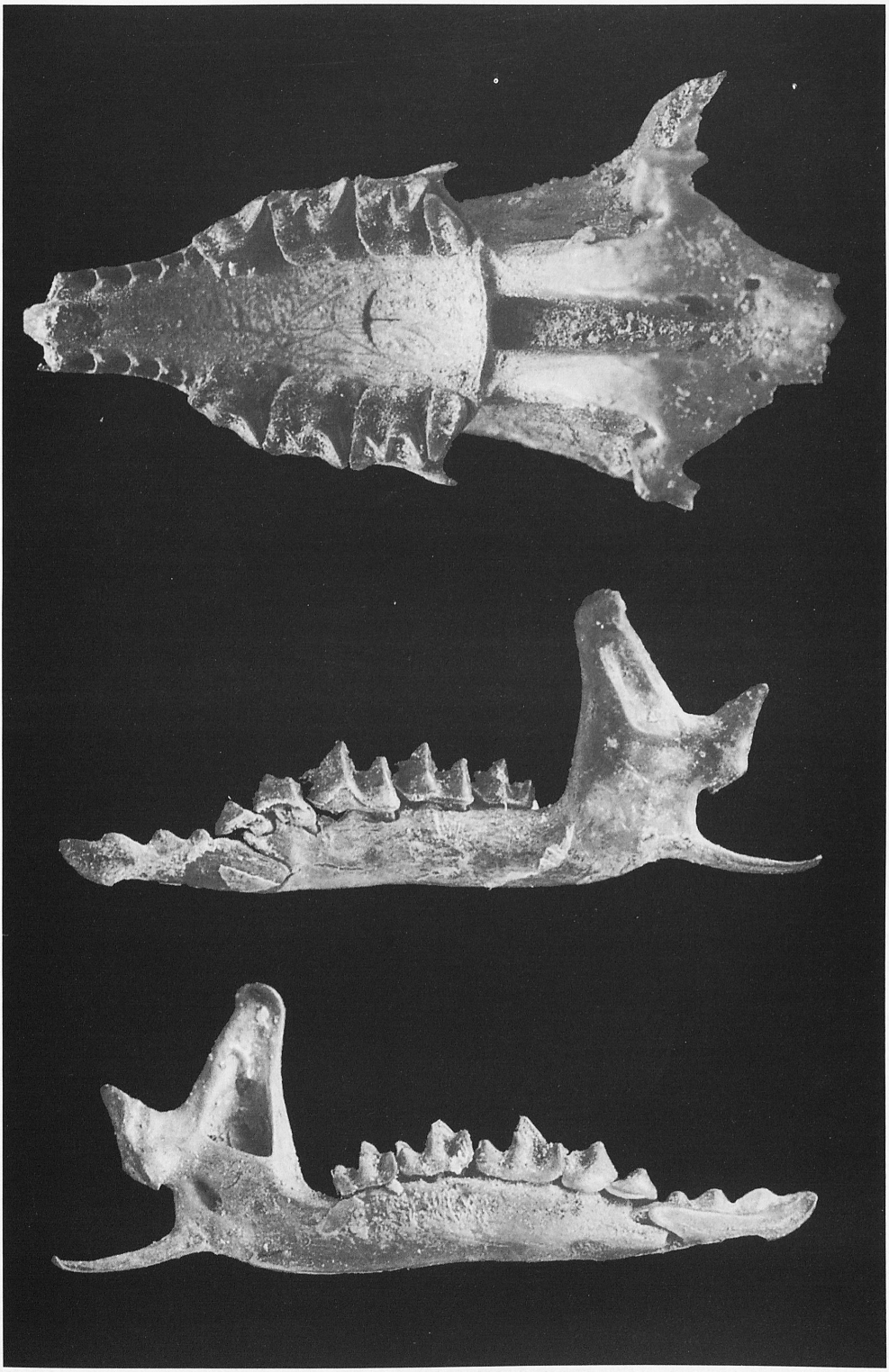

Plate 1. Cranium and left mandibular ramus of *Sorex kennardi* holotype, BM M37004.

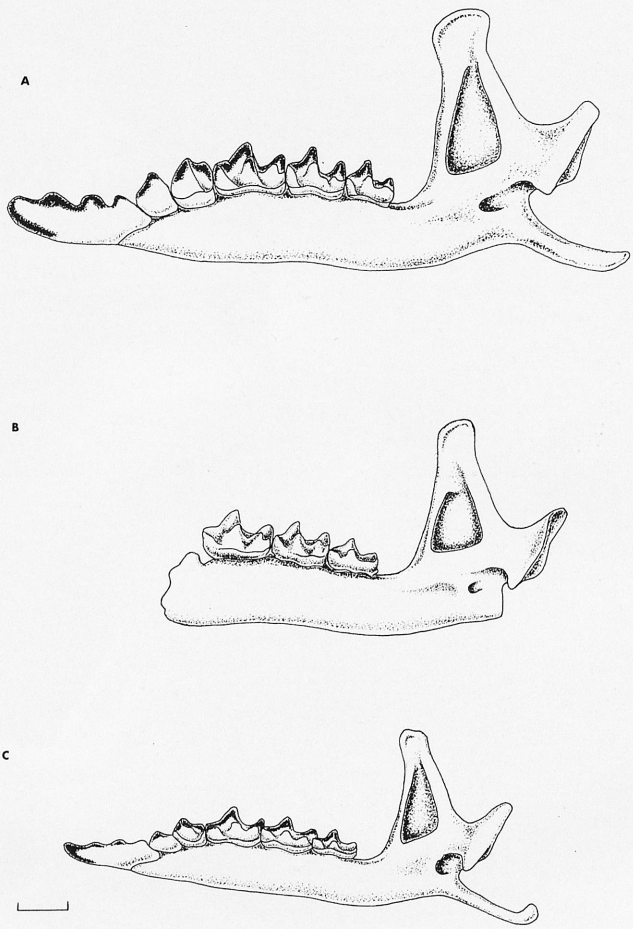

Fig. 1. Left mandibular rami, labial aspect, of [A] *Sorex araneus*, HZM.278.13037, Wells, Somerset, UK, (Recent); [B] *Sorex kennardi*, HZM.3.13623, Conningbrook, Kennington, Kent, UK, (Devensian Pleistocene); [C] *Sorex minutus*, HZM.77.13035, Upper Milton, near Wells, Somerset, UK. Scale = 1 mm.

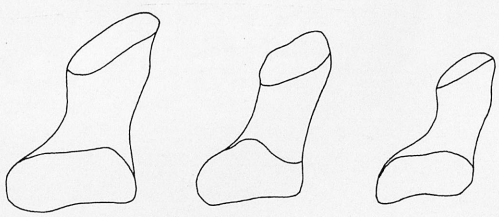

Fig. 2. Mandibular condyles of the same specimens as Fig. 1, outline drawings. Left: *Sorex araneus*, Centre: *Sorex kennardi*, Right: *Sorex minutus*. Scale = 1 mm.

III. REDESCRIPTION OF HOLOTYPE

Sorex kennardi BM M37004 (Plate 1).

The intact mandibular rami are smaller than in *S. araneus* and larger than in *S. minutus*. The coronoid process is tall, narrow and delicate, appearing disproportionately small in relation to the size of the teeth. Its anterior border is less concave than either species, its tip less expanded than *S. araneus*. The mandibular foramen is strikingly small; the angular process is long and slender, with the tip unexpanded and only slightly curved upwards. The internal temporal fossa is indistinct above and partially divided above half its height by an irregular ridge. The external temporal fossa is provided with a median ridge parallel with its posterior border and curving backwards towards the condyle below. A second less distinct ridge is present close to the posterior margin of the coronoid. The condyle (HINTON 1911: Fig. 11a) has its lower articular facet projecting less mesially than in *S. minutus* and *S. alpinus* SCHINZ, 1837 but with the interarticular area relatively longer as in these species and noticeably longer in relation to its width than in *S. araneus*. The mental foramen lies behind the level of the trigonid of m1. The relatively broad and parallel-sided mesopterygoid space described by HINTON (1911) is illustrated here in Plate 1, which also shows the gently convex posterior palatal margin.

D e n t i t i o n. The teeth were evidently quite deeply pigmented on the cusp tips as is usual in *Sorex*, but the pigmentation is poorly preserved in the holotype. The mandibular dentition is complete. The lower incisor is tricuspulate; a1 is single cusped and low, overlapped by p4 for less than half its length; p4 is robust and bicuspid with the anterior cusp considerably higher. The postero-lingual basin is well developed and the tooth is relatively short and broad; m1 is decidedly larger than m2, but essentially similar in the morphology of the sharp, well developed cusps. The protoconid is the dominant cusp, the paraconid distinctly lower than the metaconid. The hypoconid is higher than the entoconid, which is conical and with a rather high entoconid crest. There is a distinct post-entoconid ledge. The cingulum is somewhat eroded in the holotype, but seems to have been developed both buccally and lingually. The talonid of m3 is narrower than the trigonid, but with distinct basin, hypoconid and entoconid.

The upper incisors and five antemolars are all missing in the holotype. The alveoli of the antemolars as described by HINTON (1911) decrease regularly in size from A1 to A5. P4 has a well developed hypocone, which is individualised from the lingual cingulum; it is connected to the protocone by a curving postprotocrista. The parastyle is prominent and the posterior emargination moderate. No protoconule is present in the holotype. M1 is larger than M2, each subquadrate in shape. The hypocones are well developed, the postprotocristae curving lingually to their bases. Indistinct metalophs separate the trigon basins from the hypoconal flanges. The posterior emargination is moderately developed. M3 has a well developed protocone basin, paracone, parastyle, traces of three commissures and metacone (details of morphology are somewhat obscured by adherent matrix in the holotype).

The cranial and dental measurements are listed in Tables I-III.

IV. REFERRED MATERIAL FROM OBŁAZOWA CAVE

Material studied in detail here, located in the Harrison Zoological Museum, is listed below.

Site Obłazowa 2. Four left and three right mandibular rami with complete dentition (i-m3) represented (HZM.1.25859; 2.25905; 3.25906 Fig. 4; 4.25907 Fig. 3; 10.26436; 318.20643; 319.20644). Three right and two left maxillae with P4-M3 represented (HZM.7.25910 Fig. 5; 8.25911; 9.25912; 6.25909). One left I sup. (HZM.5.25908 Fig. 5). One upper antemolar (HZM.1.20661). Site Obłazowa 1 (layer 4/5). One left ramus with i, p4-m2 (HZM.11.26527).

Table I

Measurements of the mandibular rami. CH: Coronoid height; HC: Height of condyle; LUF: Length of upper facet; LLF: Length of lower facet

Coll.No:	i-m3	p4-m3	m1-m3	CH	HC	LUF	LLF
Locality: Obłazowa 2, Poland							
ISEK	7.62	–	–	–	–	–	–
ISEK	–	4.42	3.71	–	–	–	–
ISEK 8	–	–	–	4.22	–	–	–
ISEK 12	7.26	4.29	3.52	–	–	–	–
ISEK 13	–	4.35	3.58	–	–	–	–
ISEK 15	–	–	3.58	–	–	–	–
ISEK 20	–	–	–	4.03	–	–	–
ISEK 21	–	–	–	4.03	–	–	–
ISEK 23	–	4.42	3.71	–	–	–	–
ISEK 25	–	3.33	–	3.97	–	–	–
ISEK 26	–	–	–	4.16	–	–	–
ISEK 27	–	–	–	3.78	–	–	–
ISEK 32	–	–	3.71	–	–	–	–
ISEK 35	–	4.45	3.65	–	–	–	–
HZM.2.25905	–	4.32	3.62	–	–	–	–
HZM.3.25906	–	–	–	4.03	1.79	0.74	1.09
HZM.4.25907	–	–	3.49	4.03	1.79	0.90	1.12
HZM.10.26436	–	–	–	–	1.76	0.83	1.15
HZM.318.20643	–	4.35	3.65	–	–	–	–
HZM.319.20644	–	–	–	3.71	–	–	–
Locality: Conningbrook, Kent, England							
HZM.3.13623	–	–	3.58	4.03	1.76	0.74	1.02
Locality: Ponders End, Middlesex, England							
BM M37004	7.10	4.16	3.52	3.90	–	–	–

Table II

Measurements of the mandibular teeth. L: Crown length; TRW: Trigonid width; TAW: Talonid width; W: Crown width

Coll.No:	I inf.	m1			m2			m3	
	L	TRW	TAW	L	TRW	TAW	L	W	L
Locality: Obłazowa 2, Poland									
HZM.2.25905	–	0.74	0.83	1.57	0.77	0.80	1.41	0.64	1.02
HZM.3.25906	3.58	0.77	0.80	1.89	–	–	–	–	–
HZM.4.25907	–	0.64	0.77	1.38	0.64	0.70	1.22	0.58	0.96
HZM.318.20643	–	0.80	0.90	1.60	0.77	0.80	1.34	0.64	1.02
Locality: Obłazowa 1, Poland									
HZM.11.26527	3.42	0.77	0.83	1.54	0.77	0.77	1.28	–	–
Locality: Conningbrook, Kent, England									
HZM.3.13623	–	0.80	0.90	1.57	0.74	0.80	1.28	0.64	1.02
Locality: Ponders End, Middlesex, England									
BM M37004	3.46	–	0.74	1.41	–	0.70	1.22	0.54	0.90

Table III

Measurements of the maxilla. BL: buccal length; LL: lingual length; W: width of crown; AW: anterior width; PW: posterior width

Coll.No:	P4-M2	P4			M1				M2			
		BL	LL	W	BL	LL	AW	PW	BL	LL	AW	PW
Locality: Obłazowa 2, Poland												
ISEK 66	3.97	1.47	1.12	1.41	1.41	1.41	1.38	1.54	1.22	1.22	1.34	1.31
ISEK 77	3.84	1.41	1.09	1.31	1.34	1.34	1.34	1.47	1.22	1.22	1.34	1.31
HZM.6.25909	3.90	1.44	0.96	1.41	1.34	1.34	1.41	1.47	1.18	1.22	1.44	1.34
HZM.7.25912	3.90	1.41	0.96	1.41	1.34	1.34	1.31	1.47	1.22	1.25	1.41	1.34
HZM.8.25911	3.90	1.44	0.83	1.41	1.34	1.34	1.38	1.47	1.15	1.18	1.41	1.31
HZM.9.25912	3.97	1.41	1.02	1.28	1.38	1.34	1.28	1.47	1.22	1.22	1.34	
Locality: Ponders End, Middlesex, England												
BM M37004	3.65	1.31	0.89	1.31	1.25	–	–	1.41	1.15	–	–	1.28

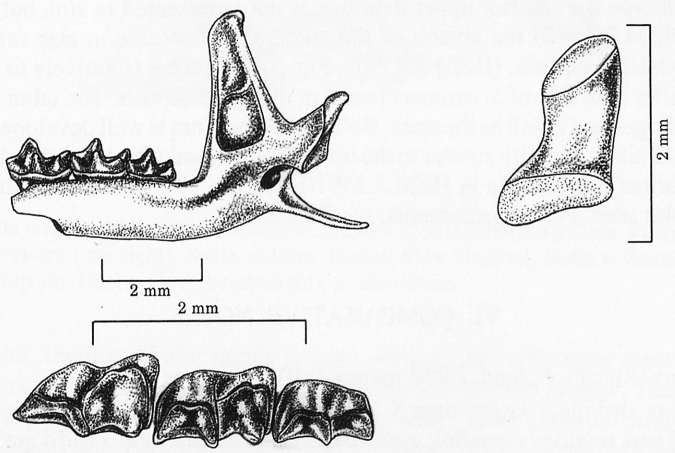

Fig. 3. Right posterior ramus with m1-m3, processes intact of *Sorex kennardi* HZM.4.25907, Obłazowa Cave, Poland. Lingual view of specimen (top left), Occlusal view of m1-m3 (below), Condyle (top right). Scale = 2 mm for each.

V. DESCRIPTION OF MATERIAL FROM OBŁAZOWA

The mandible is essentially identical in size and morphology with the holotype, and only some minor differences are noted here. The development of a coronoid spicule is variable and the transverse bar dividing the internal temporal fossa in the holotype is variably developed or absent in the Polish material.

The dentition is essentially similar to the holotype, but in m3 the cristid obliqua sometimes has a distinct small mesoconid, as in HZM.4.25907. This may also be present in unworn examples of m1 and m2 as in HZM.318.20643.

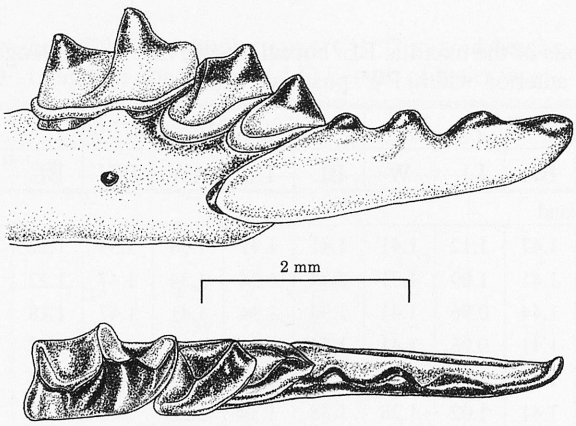

Fig. 4. Right mandibular ramus i-m1 of *Sorex kennardi* HZM.3.25906, Obłazowa Cave, Poland. Buccal (above) and occlusal views (below). Scale = 2mm.

As in the holotype the anterior upper dentition is not represented *in situ*, but so far as can be ascertained in HZM.7.25910 the alveoli of the antemolars decrease in size regularly as in the holotype. An isolated I sup. sin. (HZM.5.25908, Fig. 5) is referred tentatively to this species as it is distinctly smaller than that of *S. araneus* found in the same deposit. The talon in *S. kennardi* is relatively much larger and as tall as the apex; the buccal cingulum is well developed. The maxillary cheekteeth P4-M2 are essentially similar to the holotype, but it may be noted that the preprotocrista of P4 bears a distinct protoconule in HZM.7.25910 (Fig. 5). This is little developed or absent in the other examples seen. For measurements, see Tables I-III.

VI. COMPARATIVE NOTES

Sorex araneus (Recent, Poland; HZM material, 10 specimens).

This species is strikingly larger than *S. kennardi* and differs in a number of morphological details: talon of I sup. relatively smaller; upper unicuspids 1 and 2, and 3 and 4 are in roughly equal sized pairs; P4-M2 with deeper posterior emarginations; processes of mandibular ramus heavier, especially coronoid, with broader base; angular process heavier with upward curving tip; mandibular foramen larger; condyle with interarticular area broader, especially below, in relation to its length; mandibular dentition noticeably heavier, the crown of p4 more elongated in relation to its width.

Sorex minutus (Recent, Poland; HZM material, 7 specimens).

This species is distinctly smaller. Morphological differences include I sup. fissident; cheekteeth P4-M2 with the hypocones much less evident, especially P4; posterior border of infraorbital foramen more caudally situated above the back of the mesostyle of M1; mandibular ramus much more delicate; mandibular foramen relatively larger; condyle smaller, shaped as in Fig. 2; mental foramen more anterior, situated at a level in front of the protoconid of m1; mandibular dentition much smaller; p4 more elongated and narrow, its posterolingual basin more widely open.

Sorex caecutiens (Recent, Poland; HZM material, 3 specimens).

This Recent taxon is more compatible in size with *S. kennardi* but the teeth are distinctly smaller; P4-M2 have more deep and abrupt posterior emarginations; hypocones of these teeth

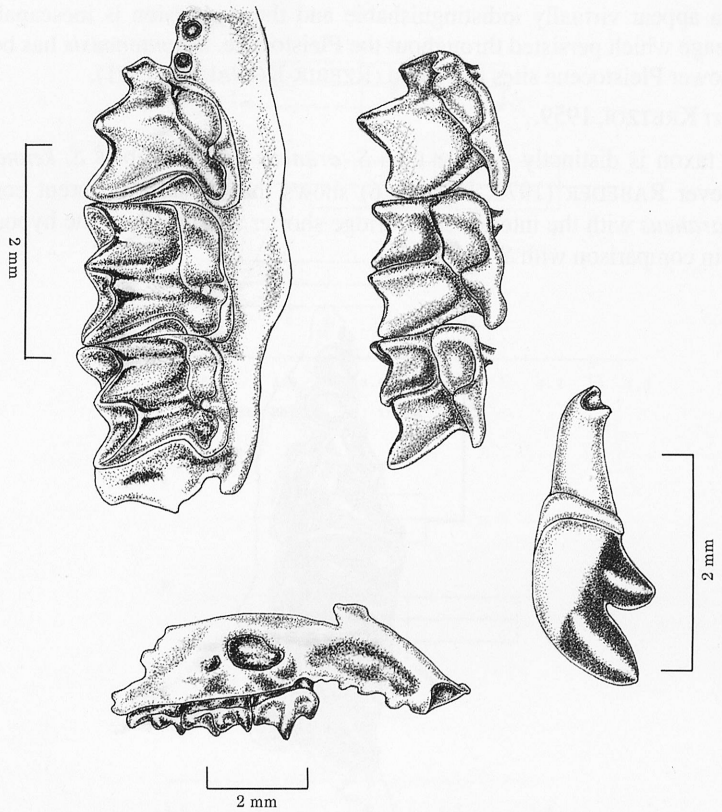

Fig. 5. Right maxilla with P4-M2 of *Sorex kennardi*, HZM.7.25910, Obłazowa Cave, Poland. Occlusal (top left) and lingual views (top right), Scale = 2mm. Buccal view (below), Scale = 2mm. *Sorex kennardi* HZM.5.25908 I sup.sin. Buccal view (below right), Scale = 2mm.

discrete but smaller; the mandibular ramus is more delicate, but with some resemblances in the form of the processes, the coronoid, however, relatively less tall and narrow. The crown of i inf. may be bi- or tricuspulate; p4 is similar in its relatively short, broad bicuspid crown. RZEBIK-KOWALSKA (1991) regards *Sorex bor* REUMER (1984) as the most likely ancestor of *Sorex caecutiens*.

Sorex runtonensis (West Runton, Norfolk, U.K. Cromerian ca. 700 000 y. b. p.)

HINTON (1911) did not compare *S. kennardi* with this taxon, described on the previous page of his paper. They are very similar in size (Fig. 8) and careful comparison of the material now available reveals very little significant morphological difference. The processes of the mandible are closely similar, especially the tall, narrow coronoid. The morphology of the dentition is very similar (Figs. 6, 7). It may be noted that the upper unicuspids are represented in two specimens in the HZM; A1 to A4 (HZM.36.16717) and A4 to A5 (HZM.109.22263, Fig.6). These show A1 to A4 decreasing regularly in size posteriorly, but A5 larger than A4. As noted above although the actual teeth are unknown in *S. kennardi* the alveoli of the holotype suggested that A5 may be smaller than A4. Two specimens of *S. runtonensis* have the alveoli of both these unicuspids present. In one (HZM.29.16163 West Runton) alv. A5 is larger than alv. A4, while in the other (HZM.127.23311 West Runton) alv. A5 is actually smaller. Either A5 is thus variable in size or perhaps more likely the size of the alveoli of these tiny teeth is an unreliable guide to the size of the actual teeth. It may be noted also that the depth of the posterior emargination of P4-M2 is variable in *S. runtonensis*.

These two taxa appear virtually indistinguishable and the conclusion is inescapable that they represent a lineage which persisted throughout the Pleistocene. *S. runtonensis* has been recorded from several Lower Pleistocene sites in Poland (RZEBIK-KOWALSKA 1991).

Sorex helleri KRETZOI, 1959.

This fossil taxon is distinctly smaller than *S. araneus* and resembles *S. kennardi* in some respects. However RABEDER (1972, Figs. 5, 6) shows that it has a different condyle shape, resembling *S. araneus* with the interarticular bridge shorter and broader. The hypocone of P4 is much reduced in comparison with *S. kennardi*.

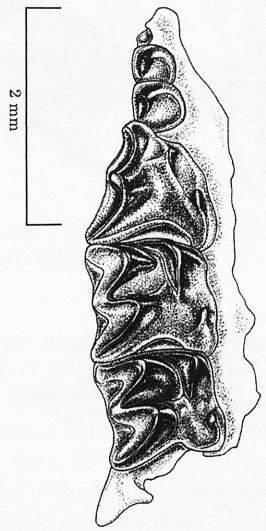

Fig. 6. Right maxilla with A4-M2 of *Sorex runtonensis*, HZM.109.22263, Cromerian Freshwater Bed, West Runton, Norfolk. Occlusal view. Scale = 2mm.

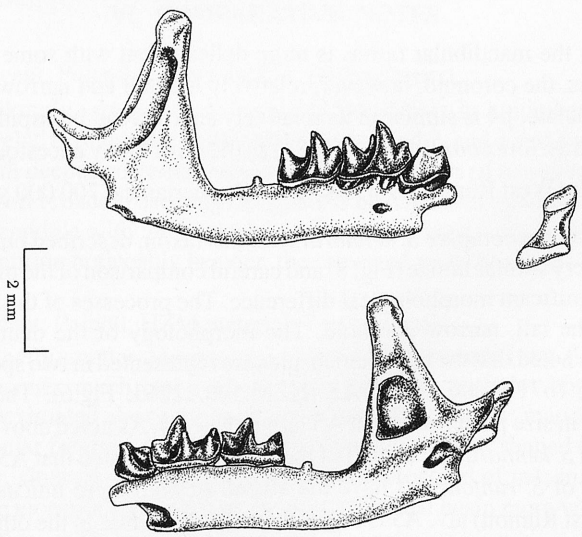

Fig. 7. Right ramus with p4-m2 and processes (except angular) of *Sorex runtonensis*, HZM.93.21172, West Runton, Norfolk. Buccal (above) and lingual (below) views. Condyle (right). Scale = 2 mm.

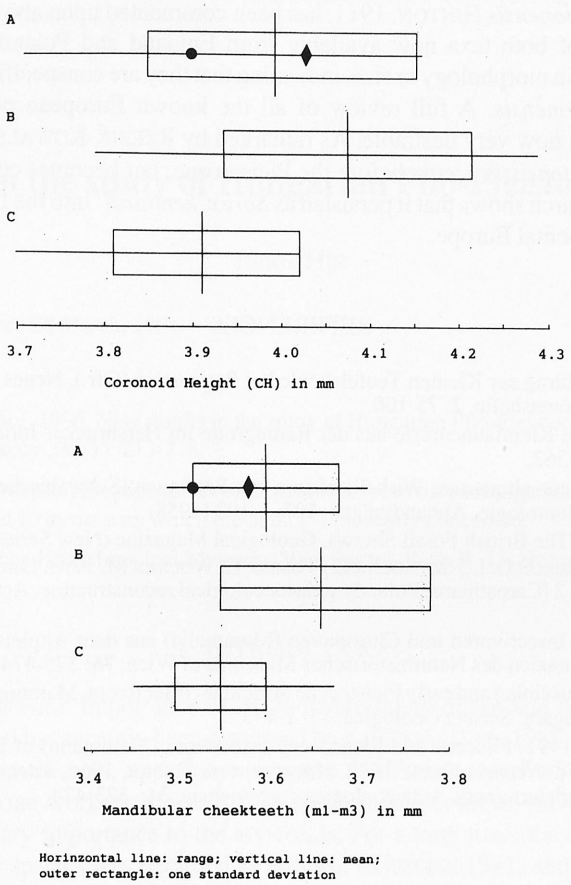

Fig. 8. Size comparison in mm of coronoid height (CH) and cheekteeth m1-m3. A: *Sorex kennardi* England and Poland – coronoid height: range= 3.71-4.16; x= 3.99;s= 0.15; n= 11; mandibular cheekteeth: range= 3.49-3.71; x= 3.60; s= 0.08; n= 13. B: *Sorex runtonensis* West Runton, Norfolk – coronoid height: range= 3.78-4.29; x= 4.07; s= 0.14; n= 19; mandibular cheekteeth: range= 3.55-3.71; x= 3.64; s= 0.09; n= 6. C: *Sorex runtonensis* Kozi Grzbiet, Poland (after RZEBIK-KOWALSKA 1991) – coronoid height: range= 3.70-4.02; x= 3.92; s= 0.10; n= 10; mandibular cheekteeth: range= 3.46-3.67; x= 3.55; s= 0.05; n= 19. ● = holotype *Sorex kennardi*; ♦ = *Sorex kennardi* (HZM.3.13623, Conningbrook, Kent).

VII. DISCUSSION

Careful comparison of the smaller *Sorex* species from Oblazowa Caves, Poland with the holotype of *Sorex kennardi* HINTON, 1911 confirms that they are conspecific. The Hundsheim fossil shrew described by RABEDER (1972) as *Sorex kennardi hundsheimensis* appears to have characters that are not typical of *Sorex kennardi* as here defined. In particular it lacks the tall, narrow coronoid process so characteristic of *S. kennardi* having instead a rather short, stout and square-topped process (RABEDER 1972, Taf. 5, Fig. 12a, b). The horizontal ramus also seems more robust and the lower incisor less narrow and elongated. The taxonomic status of *S. hundsheimensis* and the populations from Erpfingen and Raumgrotte referred to it by RABEDER (1972) should be reassessed.

The close relationship of the Late Pleistocene *Sorex kennardi* to the Lower and Middle Pleistocene *Sorex runtonensis* HINTON, 1911, has been commented upon above. Careful comparison of the material of both taxa now available from England and Poland fails to reveal any significant difference in morphology or size, indicating that they are conspecific. The specific name would be *Sorex runtonensis*. A full review of all the known European populations of the *S. runtonensis* lineage is now very desirable. As remarked by RZEBIK-KOWALSKA (1991, p. 374) it is unlikely that *S. runtonensis* occurs before the Pleistocene, but becomes common in the Lower Pleistocene. This research shows that it persisted as *Sorex 'kennardi'* into the Late Pleistocene both in England and continental Europe.

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