ACTA THERIOLOGICA
Vol. 34, 3: 55—65, 1989

Occurrence of Lemmus kowalskii Carls and Rabeder, 1988 (Rodentia: Microtinae: Lemmus) in the Lower Pleistocene of East Anglia

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Harrison D. L., Bates P. J. J. & Clayden J. D., 1989: Occurrence of *Lemmus kowalskii* Carls and Rabeder, 1988 in the Lower Pleistocene of East Anglia. Acta theriol., 34, 3: 55—65, [With 1 Table & 5 Figs].

Remains of a lemming from Lower Pleistocene crags at Sidestrand, Norfolk are here identified as *Lemmus kowalskii*, a recently described species from the Earliest Pleistocene of Bavaria. It differs from Recent *Lemmus lemmus* and *Myopus schisticolor* in details of dental morphology, especially the distinctively different structure of m^3.

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1. INTRODUCTION

During recent years the authors have made an intensive investigation of the Lower Pleistocene Crags and sands exposed in the cliff and seashore at Sidestrand, Norfolk. More than six hundred identifiable remains of small mammals have been recovered, comprising a typical Late Villanyian small mammal fauna, dominated by Microtines of genus *Mimomys*. This fauna has been briefly listed and reported elsewhere Harrison, Bates & Clayden, 1988) and will be fully reported later. Meanwhile the presence of *Lemmus kowalskii* Carls et Rabeder, 1988 requires a special report. The associated small mammal species indicative of a Late Villanyian age for this fauna are *Mimomys newtoni, M. reidi, M. pitymyoides, M. blanci, M. pliocaenicus, Clethrionomys kretzoii, Talpa cf. minor, Galemys kormosi, Desmana thermalis, Soricidae spp.* and *Mustela praenivalis.*

2. MATERIAL OF *LEMMUS KOWALSKII*

HZM.4.18247	Anterior mandible with m_1, part incisor, m_2 found associated, restored. Site S-S3. Sidestrand, Norfolk. Fig. 2(J) & 3
HZM.3.18116	Isolated m^1 . Site S-S3. Fig. 2(A)
HZM.6.18373	Isolated m_1 . Site S-S3. Fig. 4(A)

HZM.8.18808 Isolated m^1 . Site S-S3. Fig. 5(B)
HZM.1.17845 Isolated m^2 . Site S-SD. Fig. 2(D)
HZM.7.18376 Isolated m^2 . Site S-S3. Fig. 4(C)
HZM.2.17995 Isolated m^3 . Site S-S3. Fig. 2(G)
HZM.5.18310 Isolated m^3 . Site S-S3. Fig. 4(D)

3. REMARKS

The species is one of the rarer members of the Sidestrand fauna and is of unique interest, being the first occurrence of lemming in the British Lower Pleistocene. It was not included in the recent review of Lower Pleistocene British voles by Mayhew and Stuart (1986). It is interesting that all specimens so far recovered have been found in the Weybourne Crag deposits (Sites S-S3 and S-SD) of the cliff section and beach; none were found in the overlying Pastonian Sands (Harrison, Bates & Clayden, 1988). While it is generally accepted that it is difficult, if not impossible to distinguish the teeth of the Recent lemming (*Lemmus lemmus*) from those of the Wood lemming (*Myopus schisticolor*), apart from disparity in size, this Lower Pleistocene species is clearly distinguishable from both.

Diagnostic description: The teeth of this species are readily distinguishable from all other voles in the Sidestrand fauna by their persistently rootless condition and from the very young molars of the co-existing *Mimomys* species by their broad enamel-free areas, narrow beaked anterocone of the m_1, and arcuate lobes.

In comparison with Recent *Lemmus lemmus* and *Myopus schisticolor* (see Fig. 1 for the simple numerical terminology of the dental structures employed here) the teeth have a somewhat primitive aspect, with triangles better preserved and the lobes generally less compressed antero-posteriorly (Fig. 2).

It is however, in the m^3 that the most diagnostic features are found, distinguishing *L. kowalskii* from *L. lemmus* and *M. schisticolor*.

In the m^3 of this species T1 is a closed triangle, lacking the open enamel-free area present in the first lingual salient angle (LSA1) of *L. lemmus* and *M. schisticolor*. In association with this primitive feature the first lingual re-entrant fold (LR1) of *L. kowalskii* is shallower than the second buccal re-entrant fold (BR2). The reverse is the case in both *L. lemmus* and *M. schisticolor*, (Fig. 2). In *L. kowalskii* the third lingual re-entrant fold (LR3) of m^3 is virtually suppressed whereas in modern *Lemmus* and *Myopus* it is well developed. This feature is better preserved in the second m^3 recovered (HZM.5.18310).

The size of all the teeth recovered falls well within the range of

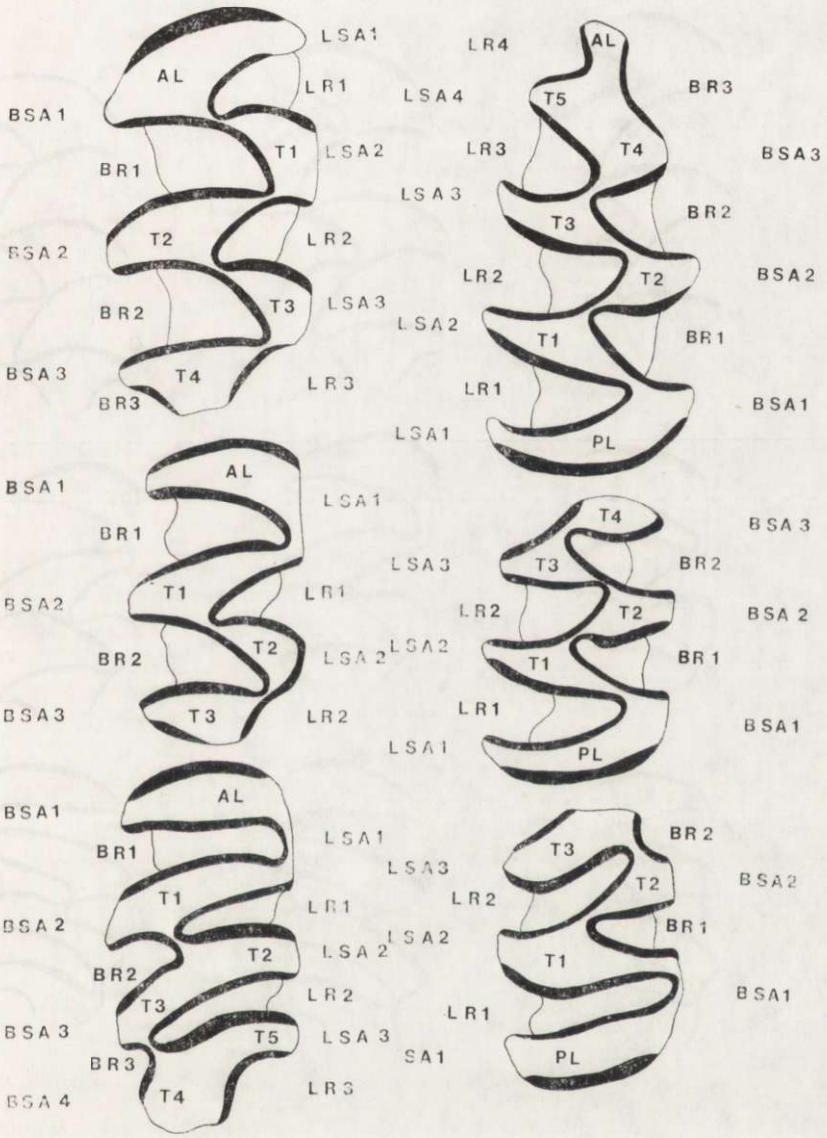

Fig. 1. Terminology of the dental structures of lemming cheekteeth. (Right maxillary and mandibular toothrows). B= Buccal; L= Lingual; SA= Salient angle; R= Re-entrant fold; AL= Anterior lobe; PL= Posterior lobe.

variation of Recent *Lemmus lemmus* (Table 1) and the material at present available is not adequate to confirm the impression that the teeth are generally narrower in relation to their length than in the modern lem-

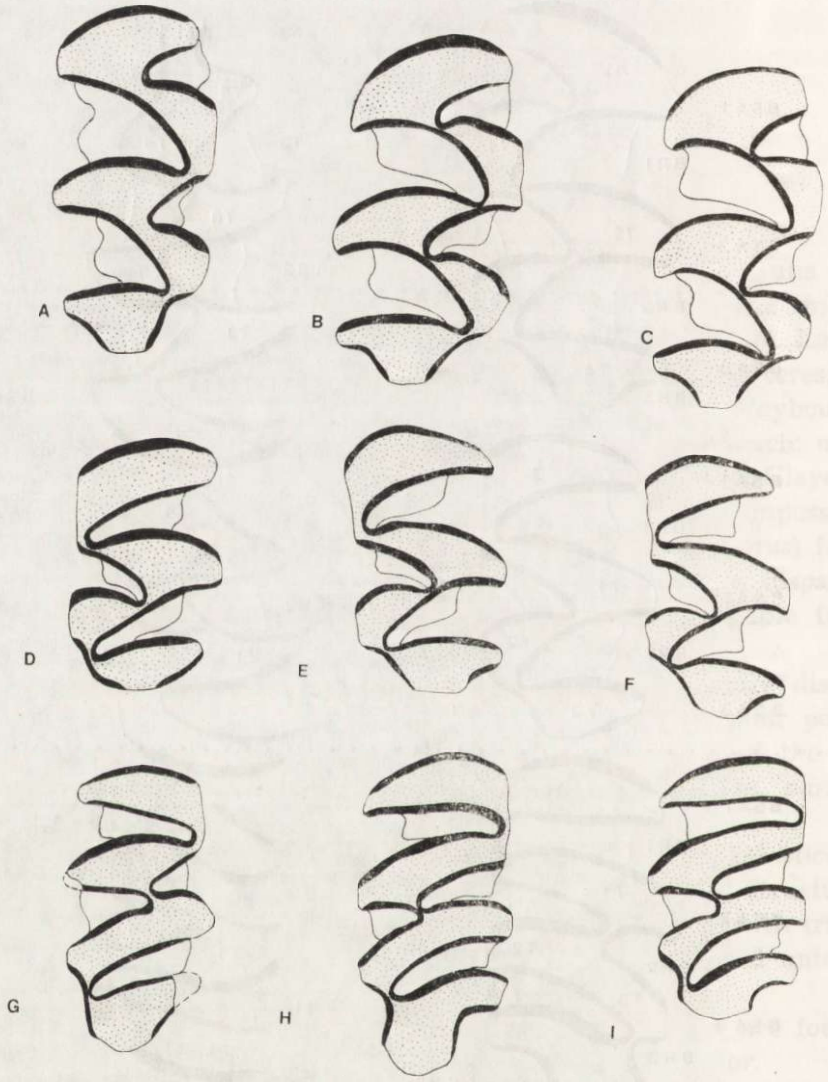

Fig. 2. Comparison of the cheekteeth of *Lemmus kowalskii* and two species of recent lemmings.

Maxillary cheekteeth. A: m^1 dex., *L. kowalskii*, HZM.3.18116. B: m^1 dex., *L. lemmus*, HZM.24.9587. C: m^1 dex., *M. schisticolor*, HZM.2.18094. D: m^2 sin., *L. kowalskii*, HZM.1.17845. E: m^2 sin., *L. lemmus*, HZM.24.9587. F: m^2 sin., *M. schisticolor*, HZM.2.18094. G: m^3 dex., *L. kowalskii*, HZM.2.17995. H: m^3 dex., *L. lemmus*, HZM.24.9587. I: m^3 dex., *M. schisticolor*, HZM.1.18093.

Mandibular cheekteeth. J: m_1 — m_2 sin., *L. kowalskii*, HZM.4.18247. K: m_1 — m_3 sin., *L. lemmus*, HZM.13.5948. L: m_1 — m_3 sin., *M. schisticolor*, HZM.1.18093. (All four recent specimens included are from Scandinavia). Scale=1 mm.

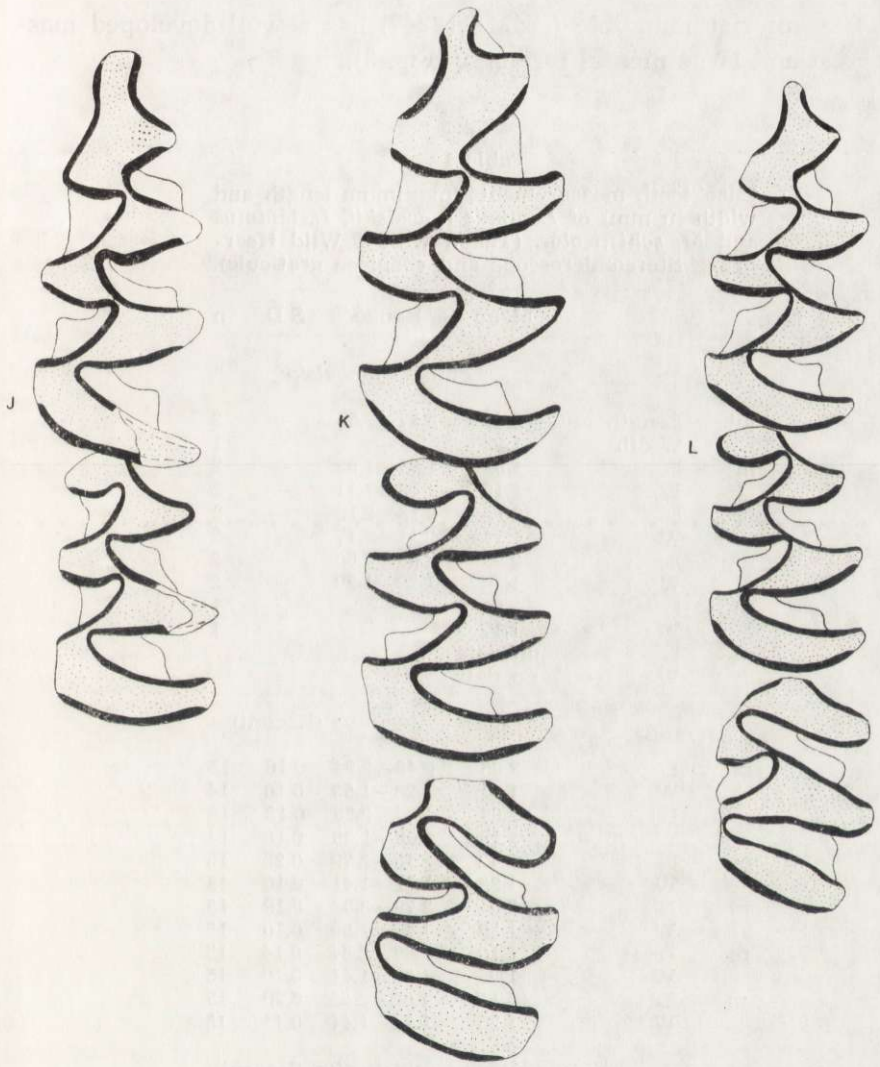

Fig. 2. concluded

Fig. 3. Anterior left mandible of *Lemmus kowalskii* (Lateral view of HZM.4.18247). Scale=2 mm,

mings. The anterior mandible (HZM.4.18247) has a well developed masseteric crest and large mental foramen, (Fig. 3).

Table 1

Cheekteeth measurements (maximum length and width in mm) of *Lemmus kowalskii*, *L. lemmus* and *M. schisticolor*. (Taken with a Wild Heerbrugg Stereomicroscope and eyepiece graticule).

		Mean	Range	S.D.	n
		Lemmus kowalskii			
m^1	Length	2.46	2.37—2.55	—	2
	Width	1.23	—	—	1
m^2	L	1.89	1.83—1.95	—	2
	W	1.10	1.08—1.11	—	2
m^3	L	2.15	2.13—2.16	—	2
	W	1.14	2.11—2.17	—	2
m_1	L	2.93	2.85—3.00	—	2
	W	1.28	1.26—1.29	—	2
m_2	L	2.04	—	—	1
	W	1.17	—	—	1
m_3	L	no data			
	W	no data			
		Lemmus lemmus (Recent)			
m^1	L	2.66	2.43—2.94	0.16	15
	W	1.41	1.26—1.53	0.10	14
m^2	L	2.04	1.83—2.25	0.13	15
	W	1.18	1.08—1.35	0.10	14
m^3	L	2.42	2.13—2.79	0.23	15
	W	1.23	1.11—1.41	0.10	15
m_1	L	3.04	2.79—3.33	0.19	15
	W	1.36	1.20—1.50	0.10	15
m_2	L	2.10	1.89—2.34	0.14	15
	W	1.25	1.08—1.41	0.10	15
m_3	L	1.87	1.62—2.25	0.20	15
	W	1.25	1.14—1.44	0.11	15
		Myopus schisticolor (Recent)			
m^1	L	2.44	2.43—2.46	—	2
	W	1.20	1.20—1.20	—	2
m^2	L	1.85	1.83—1.86	—	2
	W	1.07	1.05—1.08	—	2
m^3	L	1.98	1.92—2.04	—	2
	W	1.13	1.11—1.14	—	2
m_1	L	2.63	2.55—2.70	—	2
	W	1.16	1.14—1.17	—	2
m_2	L	1.89	1.83—1.95	—	2
	W	1.16	1.14—1.17	—	2
m_3	L	1.70	1.65—1.74	—	2
	W	1.17	1.14—1.20	—	2

4. DENTAL STRUCTURE AND VARIATION

(for measurements see Table 1)

m^1: Both examples recovered, HZM.3.18116, (Fig. 2A) and HZM.8.18808 (Fig. 4B), are remarkable on account of the degree of confluence between the anterior lobe and T1 and between T2 and T3. The tooth shows the general tendency to narrowness in relation to length, T1 and T4 are especially narrow in relation to length.

m^2: In both examples recovered, HZM.1.17845 (Fig. 2D) and HZM.7. 18376 (Fig. 4C), T1 is primitive in aspect, closed lingually at LSA1 and elongated antero-posteriorly in relation to its width. T2 is relatively large in comparison with *L. lemmus* and *M. schisticolor;* the preserved buccal salient angles of both teeth are notably rounded in comparison with the recent lemmings.

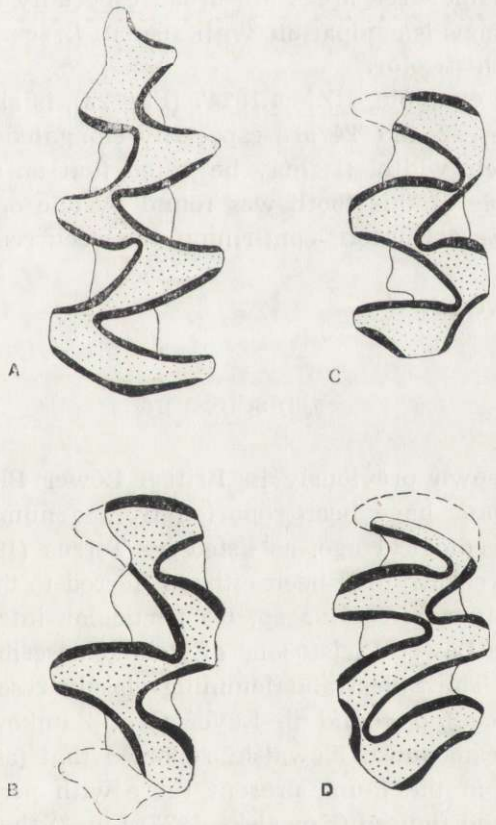

Fig. 4. Isolated cheekteeth of *Lemmus kowalskii*. A: HZM.6.18373, m_1 sin., S-S3, Sidestrand. B: HZM.8.18808, m^1 dex., S-S3, Sidestrand. C: HZM.7.18376, m^2 dex., S-S3, Sidestrand. D: HZM.5.18310, m^3 dex., S-S3, Sidestrand. Scale=1 mm.

m^3: Principal features already noted in the diagnostic description above and similar in both examples, HZM.2.17995 (Fig. 2G) and HZM.5.18310 (Fig. 4D), are the primitive aspect of T1, closed lingually at LSA1 and with LR1 shallower than BR2; the reverse is the case in *L. lemmus* and *M. schisticolor*. The junction between T1 and T2/3 is thus closer to the lingual side of the tooth. Both BR3 and LR3 are reduced, the latter virtually absent.

m_1: Both examples seen, HZM.4.18247 (Fig. 2J) & HZM.6.18373 (Fig. 4A), are narrow in relation to their length; the anterior lobe (AL) of the anterocone is rather broad. The triangles T1, T2 and T3 are all elongated antero-posteriorly in relation to their width, the posterior lobe contrastingly arcuate and narrow as in modern lemmings. Cementum in the re-entrants is abundant and as in all the teeth confined to the upper part of the rootless teeth. As in all lemmings enamel differentiation is slight but the enamel-free areas are broad especially on BSA1. The size of the two specimens is compatible with a small *L. lemmus*, but distinctly larger than *M. schisticolor*.

m_2: The single example, HZM.4.18247 (Fig. 2J), is also narrow in relation to its length, T2 and T4 are especially elongated antero-posteriorly in relation to their width. (It may be noted that an eroded and poorly preserved example of this tooth was found by one of us, J.D.C., in the beach clays at East Runton, confirming the occurrence of this species there also).

m_3: None recovered.

5. DISCUSSION

Although unknown previously in British Lower Pleistocene deposits, remains of *Lemmus* have been reported from a number of continental sites of similar geological age, as listed by Terzea (1972) and Kowalski (1977) and until recently had been either referred to the Recent *Lemmus lemmus* or simply as *Lemmus* sp. Of particular interest here are the remains from the Lower Pleistocene of Poland described and figured by Kowalski (1977). The Sidestrand lemming closely resembles the earliest known Polish *Lemmus* found in Layer C of Zamkowa Dolna Cave at Olsztyn near Częstochowa. Kowalski reported that (as at Sidestrand) it is the only vole in the fauna present there with permanently growing teeth. He noted and figured (Kowalski, 1977; Fig. 2) the peculiar structure of 5 examples of the m^3 with preservation of T1 and the other distinctive features noted above. Kowalski did not assign his material to a distinct taxon. However he recognised the evolution of the m^3 as a distinctive

feature and indicated the Zamkowa Dolna population (Kowalski, 1977; Fig. 6e) as a stage between the hypothetical ancestor and *L. lemmus*. Carls and Rabeder (1988) have now described extensive material of a new species *Lemmus kowalskii* from the Earliest Pleistocene of Schernfeld, Bavaria agreeing in all essentials with the specimens described here from Sidestrand, and with the Polish specimens from Zamkowa Dolna Cave. Devensian *Lemmus* are clearly referable to the modern *L. lemmus*, having the typical m^3 structure. Middle Pleistocene *Lemmus* require examination in view of the definition of the Lower Pleistocene species, as they could represent a further definable evolutionary stage.

Lemmus kowalskii may well prove to be a distinctive indicator of Villanyian rodent faunas. It is noteworthy that the Lower Pleistocene lemmings lived in a more temperate climate and were therefore less specialised than their modern descendants for arctic life. Contrary to the opinion of Hinton (1926) that lemmings are primitive, they were without doubt the most advanced voles existing in the Lower Pleistocene, having achieved ever-growing rootless cheekteeth before their contemporaries, even in the Pliocene (Kowalski, 1977). This was most likely an adaptation for feeding on coarse vegetation. The shortening of the incisors in lemmings, first noted by Hinton (1926) is probably not primitive but in fact a secondary event, as already noted by Kowalski (1977). The Pre-Pastonian environment at Sidestrand was an open park tundra, as determined by West (1980) with dominant *Pinus- Gramineae- Ericales* p.a.b.

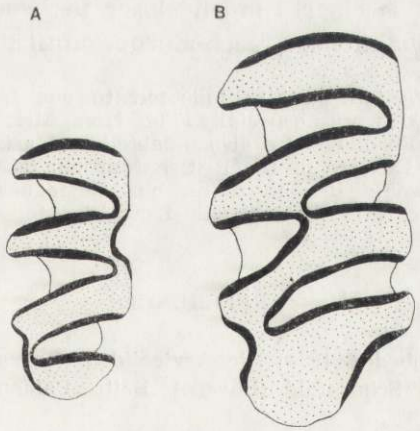

Fig. 5. Upper third right molar of *Lemmus sibiricus* and *Synaptomys cooperi* A: *Synaptomys cooperi*, HZM.2.10629. 5 miles N.E. of Mt. Cake, Virginia, U.S.A. B: *Lemmus sibiricus nigripes*, HZM.3.17.17473. St Paul, Pribilof Ids., Alaska. Scale= 1 mm.

Comparative notes: Comparison with *L. lemmus* and *M. schisticolor* has been effected above. In Recent *Lemmus sibiricus* the dental structure, and especially the m^3 is essentially as in *L. lemmus*, (Fig. 5B). It is interesting to note that in the Middle Villafranchian *Synaptomys (Praesynaptomys) europeaus* as described and figured by Kowalski (1977) the m^3 shows certain similarities to *L. kowalskii* although T3 and T2 are less confluent, owing to the deeper penetration of BR2 (Fig. 1, 13—15 of Kowalski, 1977). In Recent species of *Synaptomys* the m^3 has an even shallower LR1 than in *L. kowalskii*. T1 is similarly closed, with a narrow more vertically placed lingual enamel margin, but it is much more compressed antero-posteriorly, lacking the primitive triangular shape in *L. kowalskii* (Fig. 5A and Hinton, 1926, Fig. 5B). Carls and Rabeder (1988) consider that *"Synaptomys (Praeynaptomys)" europaeus* is best regarded as an early ancestral *Lemmus*. They postulate a series of phylogenetic chronospecies as follows: *Lemmus europaeus* (Late Csarnotium) — *L. kowalskii* (Villanyium) — *Lemmus* sp. (Biharium) — *L. lemmus* (Recent).

These comparisons underline the inherent difficulty of determining the generic status of these Lower Pleistocene ancestral lemmings. There is however no doubt that this Villanyian lemming of Bavaria, Britain and Poland does represent a distinct definable taxon and its occurrence over a wide European range in the Villanyium strongly supports the phylogenetic interpretation of Carls and Rabeder cited above.

Although *L. kowalskii* may possibly have resembled *Myopus* more than *Lemmus* in appearance this will never be known and is pure speculation. However, in size it is clearly much closer to *Lemmus*. Kowalski (1977) suggests that *Myopus* did not reach Europe until the Holocene.

Acknowledgements: We are greatly indebted to our friends who have kindly assisted with the field work, especially The Hon. Mrs. Jonathan Balcon, David Clayden and Michael Ford. We are also indebted to Martin Warren of the Cromer Museum and Andrew Currant of the British Museum (Nat. Hist.) for their helpful advice. Finally we would like to thank our colleagues Professor G. Rabeder, Professor K. Kowalski and Mrs. Rzebik-Kowalska for their kind co-operation.

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Received 13 June 1988, Accepted 5 November 1988.

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NOWY GATUNEK LEMINGA Z DOLNEGO PLEJSTOCENU ANGLII — *LEMMUS KOWALSKII (RODENTIA, MICROTINAE)*

Streszczenie

Odkryto resztki kostne leminga z Dolnego Plejstocenu (stanowisko w Sidestrand, Norfolk) opisane niedawno jako nowy gatunek — *Lemmus kowalskii*. Różni się on od współczesnych gatunków *Lemmus lemmus* i *Myopus schisticolor* szczegółami morfologii uzębienia, a zwłaszcza wyraźnie inną budową M^3.