Adres redakcji: Instytut Systematyki i Ewolucji Zwierząt Polskiej Akademii Nauk,
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Address of the Editor: Institute of Systematics and Evolution of Animals,
Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland

ISBN 83–900337–9-8
ISSN 0065–1710

Okładka – Cover: Jerzy ŚWIECIMSKI

Druk i oprawa: Drukarnia Kolejowa
ul. Bosacka 6, Kraków
nakład 800 egz. + 100

Acta zool. cracov. 36(2): 199-231, Kraków, 20 Dec.1993

Evolution of *Gliridae* (*Rodentia, Mammalia*) in the Pliocene and Quaternary of Poland

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Received: 14 April 1993
Accepted for publication: 4 May 1993

DAOUD A. 1993. Evolution of *Gliridae* (*Rodentia, Mammalia*) in the Pliocene and Quaternary of Poland. Acta zool. cracov. 36(2): 199-231.

Abstract. An analysis of the dental characters of Pliocene and Pleistocene glirids (*Myoxus minor, M. sackdillingenis, M. glis, Muscardinus pliocaenicus, M. avellanarius, M. dacicus, Dryomys nitedula, Eliomys quercinus, Glirulus pusillus*) from Poland was undertaken. The frequency of morphotypes and tooth measurements in samples of different geological age were compared with populations of the recent species. The observed intraspecific variation was in most cases casual. The morphotypes of cheek teeth have no adaptive value and are not subject to linear selection. The evolution is expressed by size increase (noted mainly in the *Myoxus* lineage) which is gradual with the exception of Pliocene populations.

Key words: Evolution, morphotypes, Pliocene, Quaternary, *Gliridae*.

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I. INTRODUCTION

Since the first description of the fossil dormice (*Gliridae*) of Poland by KOWALSKI (1956, 1963), new abundant materials have been collected. The oldest remains come from Opole 2 (Middle Miocene, Astaracian, MN 7?) and probably belong to *Myoxus* cf. *valesiensis* (AGUSTI, 1981) (KOWALSKI 1967, 1990). Another dozen species are present in a series of Miocene localities discovered recently at Bełchatów (Central Poland) (unpublished data). KOWALSKI (1990) mentioned the presence of *Glirudinus* sp. at Bełchatów 2 (Zone MN 5-6).

The Pliocene and Pleistocene *Gliridae* are better known in connection with the occurrence of numerous fossil-bearing localities of this age in Poland. The list of localities with remains of dormice was published by NADACHOWSKI (1990a).

The aim of the present study was the description of the Polish fossil glirids and an analysis of the patterns of dental evolution, especially in the genera *Myoxus* and *Muscardinus*.

Acknowledgments. I am most grateful to prof. dr K. KOWALSKI, whose help greatly contributed to the preparation of this paper. I appreciate discussions with colleagues from the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow. I am indebted to prof. dr Z. PUCEK, who made recent collections available for study. My special sincere thanks are extended to the late A. BEDNARCZYK for permission to study his fossil collections.

II. MATERIAL, LOCALITIES AND METHODS

The materials studied comprised isolated cheek-teeth belonging to the genera *Myoxus* ZIMMERMANN, 1780 (= *Glis* BRISSON, 1762), *Muscardinus* KAUP, 1829, *Dryomys* PALLAS, 1778, *Eliomys* WAGNER, 1840, and *Glirulus* THOMAS, 1905. More than 2000 fossil specimens and almost 900 teeth of recent individuals were used in the analyses (Tables I-VI).

The materials came from the following localities [age of the faunal assemblages after NADACHOWSKI et al. (1989b) and NADACHOWSKI (1990a)]:

Podlesice (PO). Age: Lower Ruscinian, MN 14. Type locality of *Myoxus minor* (KOWALSKI, 1956).

Pańska Góra (PN). Age: Lower Ruscinian, MN 14. Details on the stratigraphy and fauna were published by BEDNARCZYK (1993).

Węże 1 (WE1). Age: Upper Ruscinian, MN 15. Type locality of *Muscardinus pliocaenicus* KOWALSKI, 1963.

Rębielice Królewskie 1A (RK1A). Age: Early Villanyian, MN 16.

Kadzielnia 1 (KD1). Age: Upper Villanyian – Early Biharian, MN 17 - Ql.

Table I

Frequency of cheek teeth of *Myoxus* studied in this paper

Locality \ Tooth	Pd_4	P_4	M_1	M_2	M_3	Pd^4	P^4	M^1	M^2	M^3	N
Podlesice (PO)	2	3	28	11	12	–	6	14	21	7	104
Pańska Góra (PN)	2	3	8	4	5	–	1	3	4	5	35
Węże 1 (WE1)	–	1	19	11	6	–	1	14	21	1	74
Rębielice Królewskie 1A (RK1A)	1	3	25	12	2	–	1	7	9	–	60
Kadzielnia 1 (KD1)	–	1	5	8	–	–	3	6	3	1	27
Kamyk (KA)	–	55	56	64	53	–	60	78	48	15	429
Kielniki 1 (KI1)	1	30	38	40	24	–	21	27	35	8	224
Zalesiaki 1 (ZA1)	1	–	5	4	1	1	–	3	6	–	21
Kozi Grzbiet (KG)	12	50	122	96	94	5	50	90	96	77	692
Late Quaternary, Poland (LQ)	1	4	18	12	5	–	2	8	3	3	56
Recent, Poland (REC)	6	54	50	48	54	6	37	50	47	40	392
Total	26	204	374	310	256	12	182	300	293	157	2114

Table II

Frequency of cheek teeth of *Muscardinus pliocaenicus – avellanarius* group studied in this paper

Locality \ Tooth	Pd_4	P_4	M_1	M_2	M_3	Pd^4	P^4	M^1	M^2	M^3	N
Podlesice (PO)	–	–	29	18	5	–	1	17	6	1	77
Pańska Góra (PN)	–	2	1	1	1	–	1	2	2	–	10
Węże 1 (WE1)	–	1	1	4	–	–	–	1	1	–	8
Rębielice Królewskie 1A (RK1A)	–	–	3	1	1	–	–	3	1	–	9
Kozi Grzbiet (KG)	–	–	11	13	–	–	–	25	7	2	58
Late Quaternary, Poland (LQ)	–	–	3	3	–	–	–	3	–	–	9
Recent, Poland (REC)	–	40	56	50	66	–	10	60	50	50	382
Total	–	43	104	90	73	–	12	111	67	53	553

Table III

Frequency of cheek teeth of *Muscardinus dacicus* studied in this paper

Locality \ Tooth	Pd_4	P_4	M_1	M_2	M_3	Pd^4	P^4	M^1	M^2	M^3	N
Podlesice (PO)	–	–	7	4	–	–	–	5	2	2	20
Pańska Góra (PN)	–	2	1	1	–	–	–	1	–	1	6
Total	–	2	8	5	–	–	–	6	2	3	26

Table IV

Frequency of cheek teeth of *Dryomys nitedula* studied in this paper

Locality \ Tooth	Pd_4	P_4	M_1	M_2	M_3	Pd^4	P^4	M^1	M^2	M^3	N
Kozi Grzbiet (KG)	–	–	5	4	2	–	4	5	5	–	25
Recent, Poland (REC)	–	–	6	6	4	–	4	8	6	–	34
Total	–	–	11	10	6	–	8	13	11	–	59

Kamyk (KA). Age: Early Biharian, Q1.

Zalesiaki 1 (ZA1). Age: Biharian, Q1/Q2. Materials come from several samples (nos 1, 2, 3, 4, 9, 11, 12 and 15).

Kielniki 1 (KI1). Age: Upper Biharian, Q2.

Kozi Grzbiet (KG). Age: Upper Biharian, Q2.

Table V

Frequency of cheek teeth of *Eliomys quercinus* studied in this paper

Locality \ Tooth	Pd_4	P_4	M_1	M_2	M_3	Pd^4	P^4	M^1	M^2	M^3	N
Kozi Grzbiet (KG)	–	–	2	2	–	–	1	6	5	3	19
Late Quaternary, Poland (LQ)	–	–	–	1	–	–	–	3	3	1	8
Recent, Poland, Germany (REC)	–	6	10	10	10	–	6	10	10	10	72
Total	–	6	12	13	10	–	7	19	18	14	99

Table VI

Frequency of cheek teeth of *Glirulus pusillus* studied in this paper

Locality \ Tooth	Pd_4	P_4	M_1	M_2	M_3	Pd^4	P^4	M^1	M^2	M^3	N
Podlesice (PO)	–	4	12	8	1	–	3	6	6	2	42
Pańska Góra (PN)	–	3	4	4	1	–	3	3	2	2	22
Total	–	7	16	12	2	–	6	9	8	4	64

The materials from the Late Quaternary (Eemian – Holocene) (LQ) were pooled for analyses. They come from the following localities (for age see NADACHOWSKI 1982, 1990a): Bramka, Ciemna Cave, Dużej Sowy Cave, Dziadowa Skała, Koziarnia Cave, Raj Cave, Nad Jaskinią Niedostępną rock-shelter, Nad Mosurem Starym Duża Cave, Sąspowska Zachodnia Cave, Tunel Wielki, and Żytnia Skała.

The nomenclature of the parts of the *Gliridae* cheek teeth was assumed after DE BRUIJN (1966) (Fig. 1). A study was undertaken on lower and upper premolars and molars, using morphotype analysis. Particular morphotypes were distinguished on the basis of the crown shape, number of main and additional enamel ridges and their composition. To exclude the morphological differences in shape connected with the individual age of the specimens being studied, only teeth with a similar level of abrasion were compared. The tendencies of morphological changes were analyzed in particular lineages for all the cheek teeth. Species were distinguished on the basis of changes in the frequency of morphotypes and measurements.

The tooth length (L) is the greatest antero-posterior dimension. The width (W) was measured in different ways: along the posterolophid (Pd_4, P_4, M_1), along the metalophid (M_2, M_3), along the posteroloph (Pd^4), along the metaloph (P^4) and along the anteroloph (M^1, M^2, M^3).

For comparison, the teeth of recent animals were used in analyses. The fossil materials are in the possession of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow.

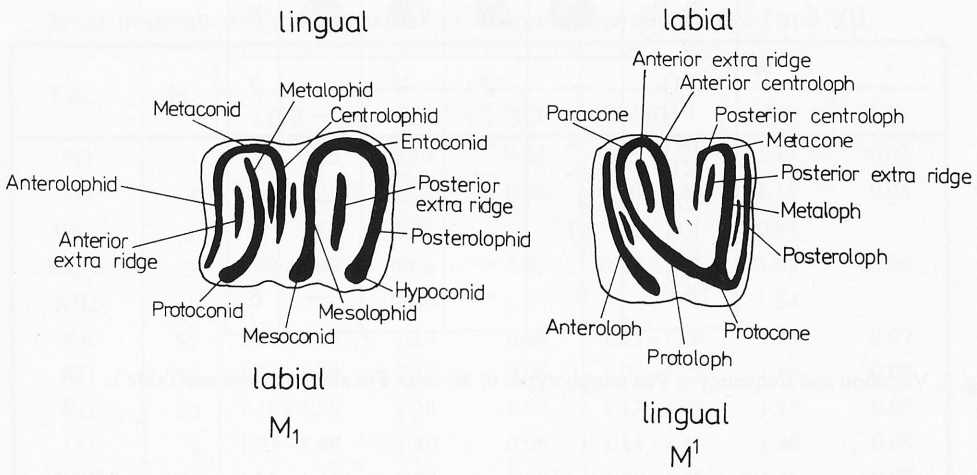

Fig. 1. Nomenclature of parts of *Gliridae* cheek teeth (after DE BRUIJN 1966, suplemented)

III. MORPHOTYPE ANALYSIS AND MEASUREMENTS

The morphotypes of cheek teeth were analyzed separately for particular genera. Schematic drawings of the morphotypes of *Myoxus* (=*Glis*), *Muscardinus* and *Dryomys* and their frequency are presented in Figures 2-28. The teeth of *Eliomys* and *Glirulus* did not show any significant morphological variability (Fig. 29).

1. Description of the dental pattern in *Myoxus*

Pd_4 two-rooted; crown triangular in shape, with four or five main and one or two extra ridges placed between them. For measurements see Table VII.

Table VII

Measurements of Pd_4 of *Myoxus*. L – length, W – width, Loc. – locality, N – number of specimens studied, OR – observed range, M – mean, SD – standard deviation. For abbreviations of localities see Table I

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	2	0.98 - 0.98	0.98		0.91 - 0.95	0.93	0.02
PN	2	0.91 - 0.87	0.94	0.03	0.83 - 0.89	0.86	0.03
RK1A	1		1.00			0.89	
KI1	1		1.03			1.03	
ZA1	1		1.11			1.11	
KG	12	1.08 - 1.21	1.15	0.04	1.01 - 1.12	1.08	0.03
LQ	1		1.31			1.22	
REC	6	1.20 - 1.33	1.26	0.05	1.11 - 1.21	1.15	0.03

Types / Pd_4 / Loc.	 1	 2	 3	 4	N
PO	–	2	–	–	2
PN	–	2	–	–	2
RK1A	–	–	1	–	1
KI1	–	–	–	1	1
ZA1	1	–	–	–	1
KG	10	–	–	2	12
LQ	1	–	–	–	1
REC	6	–	–	–	6

Fig. 2. Variation and frequency of Pd_4 morphotypes of *Myoxus*. For abbreviations see Table I.

Morphotype 1 (Fig. 2/1). Anterolophid, metalophid, mesolophid and posterolophid interconnected; centrolophid absent.

Morphotype 2 (Fig. 2/2). Anterolophid, mesolophid and posterolophid well developed; one additional ridge present. Anterolophid attached to metalophid forms a closed loop.

Morphotype 3 (Fig. 2/3). Anterolophid connected with metalophid forming a loop with an extra ridge inside it. Other ridges fused on lingual side; a very small central extra ridge adjacent to metalophid; centrolophid absent.

Morphotype 4 (Fig. 2/4). Anterolophid attached to metalophid. The other ridges form a complicated irregular pattern.

P_4. Occlusal surface of P_4 triangular with 4-5 main ridges and 1-2 extra ridges. Single root is very thick. For measurements see Table VIII.

Morphotype 1 (Fig. 3/1). All five main ridges present. One extra ridge between mesolophid and posterolophid; anterolophid connected with metalophid, forming a loop; posterolophid small ending free; mesolophid attached to posterolophid on lingual side; with posterior extra ridge between them.

Morphotype 2 (Fig. 3/2) very similar to morphotype 1; centrolophid absent.

Morphotype 3 (Fig. 3/3). Most ridges developed as in morphotype 1; posterior extra ridge absent; centrolophid fused with metalophid.

Morphotype 4 (Fig. 3/4). Anterolophid, attached to metalophid on both sides of tooth, forming a loop with small ridge inside it; the other ridges form an irregular pattern.

Morphotype 5 (Fig. 3/5). The characteristic feature of this morphotype is diagonal position of the anterolophid and metalophid in relation to the tooth axis. The centrolophid and posterior extra ridge are developed as in morphotype 1.

Morphotype 6 (Fig. 3/6). Anterolophid with a small groove, connected with metalophid on lingual side; centrolophid very small.

Morphotype 7 (Fig. 3/7). Anterolophid connected with metalophid on lingual and labial sides; mesolophid attached both to anterolophid (labially) and to posterolophid (lingually). The posterior extra ridge ends free.

Table VIII

Measurements of P_4 of *Myoxus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	3	1.07 - 1.23	1.13	0.06	1.15 - 1.21	1.17	0.02
PN	3	1.06 - 1.23	1.14	0.06	1.10 - 1.20	1.15	0.05
WE1	1		1.03			0.94	
RK1A	3	1.02 - 1.09	1.06	0.03	0.97 - 1.12	1.05	0.06
KD1	1		1.38			1.54	
KA	55	1.01 - 1.29	1.14	0.06	1.03 - 1.26	1.14	0.07
KI1	30	1.01 - 1.30	1.16	0.06	1.01 - 1.23	1.13	0.05
KG	50	1.19 - 1.38	1.28	0.03	1.17 - 1.42	1.27	0.05
LQ	4	1.23 - 1.49	1.40	0.06	1.24 - 1.48	1.36	0.08
REC	54	1.28 - 1.46	1.38	0.08	1.26 - 1.46	1.36	0.07

Types P_4 / Loc.	 1	 2	 3	 4	 5	 6	 7	N
PO	3	—	—	—	—	—	—	3
PN	3	—	—	—	—	—	—	3
WE1	—	—	—	—	—	—	—	1
RK1A	2	—	—	1	—	—	—	3
KD1	—	1	—	—	—	—	—	1
KA	50	5	—	—	—	—	—	55
KI1	28	2	—	—	—	—	—	30
KG	20	1	—	—	2	26	1	50
LQ	3	1	—	—	—	—	—	4
REC	38	11	5	—	—	—	—	54

Fig. 3. Variation and frequency of P_4 morphotypes of *Myoxus*. For abbreviations see Table I.

M_1 two-rooted; crown rectangular in outline, with five main and two additional ridges. For measurements see Table IX.

Morphotype 1 (Fig. 4/1). Anterolophid connected with metalophid on lingual rarely on labial, side. Centrolophid ending free distinctly shorter than other main ridges; mesolophid attached to posterolophid lingually. In some teeth the metaconid and/or entoconid is absent.

Morphotype 2 (Fig. 4/2). The characteristic feature of this morphotype is connection between the metalophid and mesolophid by a small transverse ridge. Other elements as in morphotype 1.

Morphotype 3 (Fig. 4/3). Metalophid divided into two parts; one, connected with anterior extra ridge on lingual side and forming a loop, the other part forming semicircle on labial side.

M_2 very similar to M_1, subrectangular in outline. For measurements see Table X.

Morphotype 1 (Fig. 5/1), with five main ridges. Centrolophid ending free (very rarely connected with metalophid); anterolophid attached to metalophid lingually, not reaching metalophid on labial side; mesolophid connected with posterolophid lingually.

Morphotype 2 (Fig. 5/2). Its distinguishing feature is the connection of the metalophid with the mesolophid by a short transverse ridge on the labial side. The other ridges are developed as in morphotype 1.

Types M_1 / Loc.	 1	 2	 3	N
PO	28	—	—	28
PN	8	—	—	8
WE1	19	—	—	19
RK1A	25	—	—	25
KD1	5	—	—	5
KA	56	—	—	56
KI1	38	—	—	38
ZA1	5	—	—	5
KG	116	6	—	122
LQ	17	—	1	18
REC	50	—	—	50

Types M_2 / Loc.	 1	 2	N
PO	11	—	11
PN	4	—	4
WE1	11	—	11
RK1A	12	—	12
KD1	8	—	8
KA	64	—	64
KI1	40	—	40
ZA1	4	—	4
KG	91	5	96
LQ	12	—	12
REC	48	—	48

Fig. 4-5. Variation and frequency of M_1 (Fig. 4) and M_2 (Fig. 5) morphotypes of *Myoxus*. For abbreviations see Table I.

Table IX

Measurements of M_1 of *Myoxus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	28	1.48 - 1.77	1.62	0.08	1.36 - 1.69	1.53	0.08
PN	8	1.55 - 1.77	1.63	0.08	1.46 - 1.62	1.53	0.06
WE1	19	1.42 - 1.69	1.55	0.08	1.29 - 1.59	1.43	0.07
RK1A	25	1.48 - 1.73	1.59	0.06	1.36 - 1.66	1.51	0.07
KD1	5	1.65 - 1.84	1.76	0.06	1.60 - 1.83	1.68	0.09
KA	56	1.52 - 1.77	1.65	0.05	1.36 - 1.72	1.55	0.07
ZA1	5	1.61 - 1.78	1.71	0.06	1.54 - 1.80	1.70	0.10
KG	122	1.65 - 1.95	1.81	0.07	1.57 - 1.83	1.72	0.06
LQ	18	1.89 - 2.06	1.97	0.04	1.71 - 2.03	1.91	0.08
REC	50	1.88 - 2.12	2.00	0.05	1.84 - 2.04	1.94	0.06

Table X

Measurements of M_2 of *Myoxus* abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	11	1.62 - 1.75	1.70	0.04	1.58 - 1.81	1.71	0.06
PN	4	1.59 - 1.76	1.66	0.06	1.56 - 1.68	1.62	0.04
WE1	11	1.49 - 1.77	1.58	0.07	1.48 - 1.69	1.57	0.05
RK1A	12	1.48 - 1.70	1.58	0.05	1.47 - 1.65	1.58	0.05
KD1	4	1.68 - 2.09	1.86	0.14	1.66 - 2.06	1.82	0.13
KA	64	1.54 - 1.85	1.71	0.05	1.51 - 1.81	1.68	0.05
KI1	40	1.61 - 1.91	1.71	0.05	1.55 - 1.75	1.69	0.04
ZA1	4	1.65 - 1.89	1.78	0.08	1.70 - 1.91	1.87	0.04
KG	96	1.77 - 2.00	1.90	0.06	1.68 - 1.95	1.82	0.05
LQ	12	1.83 - 2.16	2.04	0.08	1.83 - 2.19	2.06	0.08
REC	48	1.95 - 2.18	2.05	0.06	1.98 - 2.20	2.12	0.07

M_3 trapezoid in outline, with five main and two additional ridges. The tooth has two roots: the anterior is flattened, the posterior cylindrical. For measurements see Table XI.

Morphotype 1 (Fig. 6/1). Anterolophid is attached to metalophid lingually; centrolophid short, metalophid ending free. Posterior extra ridge connected with posterolophid on lingual side.

Morphotype 2 (Fig. 6/2). Main ridges developed as in previous morphotype. Centrolophid absent.

Morphotype 3 (Fig. 6/3). Main ridges developed as in morphotype 1. Posterior extra ridge connected with posterolophid by a small transverse ridge.

Morphotype 4 (Fig. 6/4). The anterolophid ends free; centrolophid attached to anterior extra ridge; end of mesolophid free; posterior extra ridge connected with posterolophid.

Morphotype 5 (Fig. 6/5). The characteristic feature of this morphotype is the occurrence of a very small additional ridge between the posterior extra ridge and the posterolophid.

Morphotype 6 (Fig. 6/6). The posterior extra ridge and posterolophid form a closed loop.

M_3 from Kozi Grzbiet shows a peculiar, local pattern which cannot be considered in terms of the previously described variability. Most of teeth have a characteristic depression on the posterolophid. Additionally, the posterior extra ridge is divided into two parts which are attached to the anterolophid and/or metalophid in various ways (Fig. 7).

Table XI

Measurements of M_3 of *Myoxus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	12	1.48 - 1.68	1.59	0.05	1.35 - 1.58	1.45	0.06
PN	5	1.52 - 1.63	1.58	0.04	1.44 - 1.48	1.46	0.02
WE1	6	1.41 - 1.58	1.51	0.05	1.29 - 1.44	1.38	0.04
RK1A	2	1.46 - 1.58	1.52	0.06	1.30 - 1.45	1.38	0.07
KA	53	1.36 - 1.74	1.61	0.07	1.29 - 1.59	1.49	0.06
KI1	24	1.55 - 1.77	1.65	0.05	1.35 - 1.63	1.50	0.06
ZA1	1		1.65			1.59	
KG	94	1.65 - 1.97	1.83	0.06	1.45 - 1.71	1.61	0.05
LQ	5	1.99 - 2.15	2.07	0.05	1.77 - 1.87	1.83	0.03
REC	54	1.95 - 2.20	2.09	0.05	1.73 - 1.92	1.87	0.04

Types M_3 / Loc.	1	2	3	4	5	6	N
PO	9	2	—	1	—	—	12
PN	2	3	—	—	—	—	5
WE1	5	1	—	—	—	—	6
RK1A	1	1	—	—	—	—	2
KA	51	2	—	—	—	—	53
KI1	18	—	—	—	2	4	24
ZA1	1	—	—	—	—	—	1
KG	93	—	—	—	1	—	94
LQ	5	—	—	—	—	—	5
REC	47	—	5	—	—	—	52

Fig. 6. Variation and frequency of M_3 morphotypes of *Myoxus*. For abbreviations see Table I.

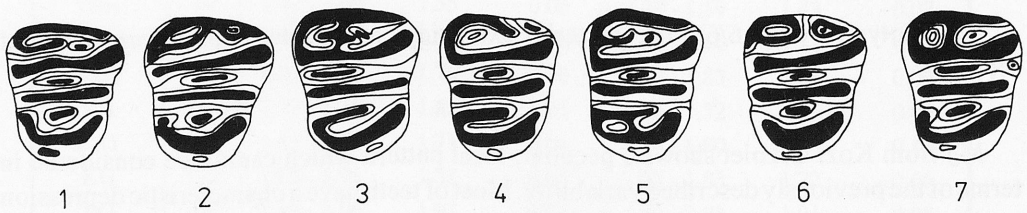

Fig. 7. Variation and frequency of M_3 morphotypes of *Myoxus* from Kozi Grzbiet. For abbreviations see Table I.

Types / Pd^4 / Loc.	 1	 2	N
ZA1	1	—	1
KG	5	—	5
REC	—	6	6

Fig. 8. Variation and frequency of Pd^4 morphotypes of *Myoxus*. For abbreviations see Table I.

Pd^4 three-rooted; crown triangular in outline, with four ridges and additional cusp placed centrally. For measurements see Table XII.

Morphotype 1 (Fig. 8/1). Anteroloph short, mataloph attached to mesoloph on both sides of tooth. The mesoloph connceted with posteroloph in the shape of a loop.

Morphotype 2 (Fig. 8/2). Both main and extra ridges interconnected; several small cusps present in marginal parts of tooth.

Table XII

Measurements of Pd^4 of *Myoxus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
ZA1	1		1.11			1.16	
KG	5	1.19 - 1.23	1.21	0.01	1.35 - 1.41	1.38	0.02
REC	6	1.20 - 1.23	1.21	0.01	1.30 - 1.39	1.35	0.03

P^4 two-rooted (rarely with one or three roots). Anterior root relatively short and thin, posterior one much longer and thick. Crown oval in outline, with five main and one or two extra ridges. For measurements see Table XIII.

Morphotype 1 (Fig. 9/1). Anteroloph ending free; protoloph attached to centroloph labially; metaloph connected with posteroloph. An extra ridge between the metaloph and posteroloph.

Morphotype 2 (Fig. 9/2). Anteroloph very short, protoloph, centroloph, metaloph and posteroloph ending free. Posterior extra ridge absent.

Morphotype 3 (Fig. 9/3), with a cusp in the central part of the tooth. Main ridges fused as in Pd^4 (morphotype 1).

M^1. Crown subrectangular in shape, with five main and two extra ridges. Tooth three-rooted (sometimes with four roots), one on the lingual side and two on labial side. For measurements see Table XIV.

Morphotype 1 (Fig. 10/1). Anteroloph, posteroloph and centroloph with free ends; metaloph connected with posteroloph labially.

Morphotype 2 (Fig. 10/2). Anteroloph attached to metaloph labially; centroloph large, placed diagonally to tooth axis. Small additional ridge between posteroloph and centroloph.

Table XIII

Measurements of P^4 of *Myoxus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	6	1.05 - 1.14	1.10	0.03	1.19 - 1.33	1.26	0.04
PN	1		1.10			1.20	
WE1	1		0.93			1.08	
RK1A	1		1.06			1.13	
KD1	3	1.24 - 1.41	1.31	0.07	1.40 - 1.71	1.52	0.13
KA	60	1.03 - 1.21	1.15	0.04	1.18 - 1.40	1.26	0.05
KI1	21	1.11 - 1.23	1.18	0.03	1.18 - 1.32	1.27	0.04
KG	50	1.11 - 1.36	1.27	0.06	1.43 - 1.61	1.52	0.05
LQ	2	1.44 - 1.45	1.44		1.54 - 1.64	1.59	0.05
REC	37	1.33 - 1.49	1.44	0.04	1.53 - 1.68	1.60	0.04

Table XIV

Measurements of M^1 of *Myoxus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	14	1.42 - 1.67	1.54	0.07	1.48 - 1.80	1.60	0.08
PN	3	1.48 - 1.61	1.53	0.05	1.56 - 1.76	1.62	0.04
WE1	14	1.31 - 1.59	1.48	0.07	1.33 - 1.58	1.50	0.07
RK1A	7	1.35 - 1.59	1.51	0.07	1.47 - 1.57	1.53	0.03
KD1	6	1.80 - 1.93	1.84	0.04	1.89 - 2.07	1.98	0.06
KA	78	1.41 - 1.79	1.56	0.05	1.40 - 1.74	1.54	0.06
KI1	27	1.51 - 1.69	1.60	0.05	1.51 - 1.69	1.61	0.05
ZA1	3	1.50 - 1.55	1.53	0.02	1.55 - 1.57	1.56	0.01
KG	90	1.54 - 1.89	1.78	0.08	1.48 - 2.00	1.81	0.09
LQ	8	1.75 - 1.99	1.89	0.05	1.92 - 2.05	2.00	0.05
REC	50	1.81 - 1.96	1.89	0.04	1.91 - 2.10	2.04	0.05

Types P^4 / Loc.	 1	 2	 3	N
PO	5	—	1	6
PN	1	—	—	1
WE1	1	—	—	1
RK1A	—	—	1	1
KD1	3	—	—	3
KA	45	2	13	60
KI1	19	—	2	21
KG	50	—	—	50
LQ	2	—	—	2
REC	37	—	—	37

Types M^1 / Loc.	 1	 2	N
PO	13	1	14
PN	3	—	3
WE1	13	1	14
RK1A	7	—	7
KD1	6	—	6
KA	78	—	78
KI1	27	—	27
ZA1	3	—	3
KG	90	—	90
LQ	8	—	8
REC	50	—	50

Fig. 9-10. Variation and frequency of P^4 (Fig. 9) and M^1 (Fig. 10) morphotypes of *Myoxus*. For abbreviations see Table I.

M^2 very similar to M^1, main ridges slightly bent diagonally to tooth axis. For measurements see Table XV.

Morphotype 1 (Fig. 11/1). All main ridges well developed. Two extra ridges between anteroloph and protoloph as well as between metaloph and posteroloph.

Morphotype 2 (Fig. 11/2). The characteristic feature is the occurrence of a small additional ridge between the protoloph and centroloph.

Morphotype 3 (Fig. 11/3). Two extra ridges on both sides of centroloph.

Types M^2 / Loc.	 1	 2	 3	N
PO	17	—	4	21
PN	2	—	2	4
WE1	14	—	7	21
RK1A	5	—	4	9
KD1	2	—	1	3
KA	6	1	41	48
KI1	13	7	15	35
ZA1	1	—	5	6
KG	22	12	62	96
LQ	3	—	—	3
REC	47	—	—	47

Types M^3 / Loc.	 1	 2	 3	 4	N
PO	—	5	—	2	7
PN	2	2	—	1	5
WE1	—	1	—	—	1
KD1	—	1	—	—	1
KA	11	4	—	—	15
KI1	7	1	—	—	8
KG	1	71	5	—	77
LQ	3	—	—	—	3
REC	40	—	—	—	40

Fig. 11-12. Variation and frequency of M^2 (Fig.11) and M^3 (Fig. 12) morphotypes of *Myoxus*. For abbreviations see Table I.

M^3 three-rooted (only occasionaly with four roots); crown trapezoid in outline, with five main and two additional ridges. For measurements see Table XVI.

Morphotype 1 (Fig. 12/1). Anteroloph attached to metaloph labially; protoloph connected with metaloph lingually; posterior loop formed by metaloph and posteroloph; centroloph ending free.

Morphotype 2 (Fig. 12/2). Centroloph branching on labial side; small extra ridge between centroloph and metaloph.

Morphotype 3 (Fig. 12/3). Its characteristic feature is the presence of two small extra ridges on both sides of the centroloph.

Morphotype 4 (Fig. 12/4). Main ridges are distributed irregularly and forming a very complicated pattern.

Table XV

Measurements of M^2 of *Myoxus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	21	1.44 - 1.71	1.57	0.08	1.62 - 1.83	1.73	0.06
PN	4	1.54 - 1.61	1.58	0.02	1.71 - 1.79	1.75	0.03
WE1	21	1.42 - 1.69	1.54	0.08	1.48 - 1.69	1.60	0.06
RK1A	9	1.45 - 1.71	1.60	0.09	1.53 - 1.73	1.64	0.05
KD1	3	1.65 - 1.70	1.68	0.02	1.71 - 1.77	1.74	0.02
KA	48	1.52 - 1.77	1.64	0.06	1.59 - 1.77	1.70	0.06
KI1	35	1.51 - 1.72	1.65	0.05	1.58 - 1.79	1.72	0.04
ZA1	6	1.64 - 1.90	1.74	0.08	1.82 - 2.08	1.89	0.09
KG	96	1.65 - 1.87	1.78	0.07	1.72 - 2.05	1.92	0.07
LQ	3	1.86 - 1.93	1.90	0.03	2.04 - 2.11	2.07	0.02
REC	47	1.82 - 2.00	1.91	0.04	2.05 - 2.20	2.14	0.04

Table XVI

Measurements of M^3 of *Myoxus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	7	1.19 - 1.38	1.30	0.06	1.43 - 1.64	1.54	0.06
PN	5	1.24 - 1.35	1.29	0.03	1.34 - 1.58	1.48	0.06
WE1	1		1.19			1.40	
KD1	1		1.68			1.80	
KA	15	1.14 - 1.38	1.31	0.06	1.38 - 1.63	1.54	0.06
KI1	8	1.17 - 1.40	1.31	0.06	1.46 - 1.60	1.55	0.05
KG	77	1.35 - 1.55	1.47	0.07	1.60 - 1.76	1.69	0.06
LQ	2	1.52 - 1.59	1.56	0.02	1.69 - 1.92	1.81	0.09
REC	40	1.59 - 1.70	1.64	0.07	1.73 - 1.96	1.91	0.08

2. Results of morphotype and measurement analysis in *Myoxus*

The morphological pattern of most teeth of the genus *Myoxus* is rather variable. However, the frequency of the morphotypes either does not change significantly e. g. M_1, M_2, and M^1 (Figs 4, 5, 10) or the change seems to be accidental in the case of Pd_4, P_4, M_3, P^4 and M^3 (Figs 2, 3, 6, 9, 12). Only for M^2 the frequency distribution of the morphotypes in particular localities differs significantly (Fig. 11). In the Pliocene populations (PO, PN, WE1, RK1A and KD1) morphotype 1 is predominant (50-80%), while morphotype 3 is less frequent (20-50%). The samples of Lower Pleistocene age are characterized by reversed proportions. Morphotype 3 distinctly prevails (43-85%), while morphotype 1 is much more rare (12-37%). An additional important difference is the presence in localities KA, KI1 and KG of morphotype 2 with a frequency ranging from 2 to 20 percent. The Late Quaternary and recent populations are morphologically very stable and show only the occurrence of morphotype 1. These differences constitute the basis for distinguishing three species: *Myoxus minor* (Pliocene), *M. sackdillingensis* (Lower Pleistocene) and *M. glis*. This lineage is characterized by a general increase in size (Tables VII-XVI). However, it is not a simple gradual process. The individuals of *Myoxus minor* from the Lower Ruscinian (PO and PN) are larger than the younger Upper Ruscinian (WE1) and Lower Villanyian (RK1A) specimens of this species. A constant size increase is observed from the beginning of the Pleistocene (Fig. 13).

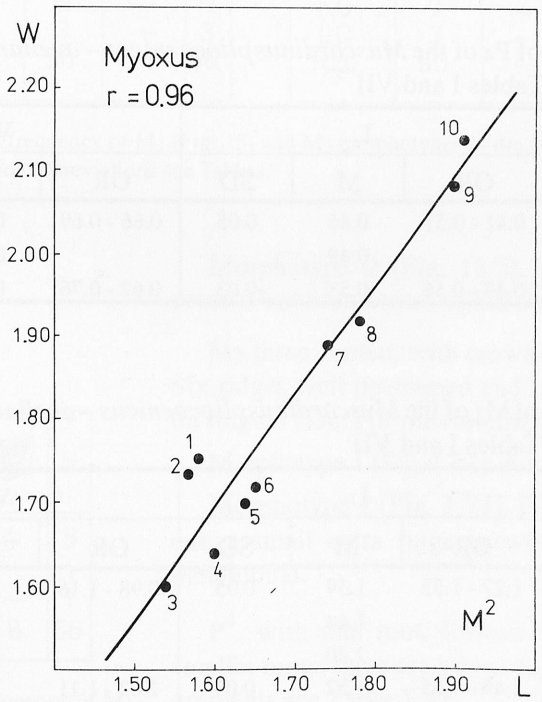

Fig. 13. Relation between the mean values of length (L) and width (W) of the M^2 assemblages of *Myoxus*. 1 – Pańska Góra, 2 – Podlesice, 3 – Węże 1, 4 – Rębielice Królewskie 1A, 5 – Kamyk, 6 – Kielniki 1, 7 – Zalesiaki 1A, 8 – Kozi Grzbiet, 9 – Late Quaternary, 10 – recent population from Poland. Measurements in mm.

3. Description of the dental pattern in *Muscardinus*

P_4 one-rooted; crown isomeric trapezoid in outline, with three ridges on occlusal surface. They end free (*M. dacicus*) or are interconnected on the lingual side (*M. pliocaenicus – avellanarius* group) (Figs 14 and 22). For measurements see Table XVII.

Loc. \ Types P_4	1
PN	2
WE1	1
REC	40

Fig. 14. Variation and frequency of P_4 morphotypes of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Table I.

M_1 three-rooted; crown trapezoid in outline, with six subparallel ridges. For measurements see Tables XVIII and XXV.

Morphotype 1 (Fig. 15/1) with typically developed main ridges.

Morphotype 2 (Fig. 15/2). One extra ridge placed labially between mesolophid and posterolophid.

M_2 four-rooted, with six ridges on occlusal surface; middle parts of ridges bent anteriorly (in the *M. pliocaenicus - avellanarius* group). For measurements see Tables XIX and XXV.

Morphotype 1 (Fig. 16/1). Accesorial ridges absent.

Table XVII

Measurements of P_4 of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PN	2	0.41 - 0.51	0.46	0.05	0.66 - 0.69	0.69	0.02
WE1	1		0.49			0.67	
REC	40	0.43 - 0.56	0.53	0.03	0.62 - 0.76	0.70	0.03

Table XVIII

Measurements of M_1 of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	29	1.27 - 1.52	1.39	0.05	0.98 - 1.16	1.08	0.04
PN	1		1.44			1.12	
WE1	1		1.40			1.03	
RK1A	3	1.49 - 1.55	1.52	0.03	1.02 - 1.11	1.06	0.02
KG	11	1.50 - 1.62	1.56	0.04	1.06 - 1.28	1.20	0.05
LQ	3	1.60 - 1.70	1.64	0.03	1.18 - 1.30	1.24	0.04
REC	56	1.52 - 1.66	1.61	0.04	1.10 - 1.30	1.25	0.04

Table XIX

Measurements of M_2 of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	18	1.17 - 1.35	1.26	0.05	0.98 - 1.25	1.08	0.05
PN	1		1.28			1.11	
WE1	4	1.16 - 1.27	1.24	0.03	0.95 - 1.20	1.06	0.04
RK1A	1		1.28			1.19	
KG	13	1.21 - 1.40	1.34	0.05	1.16 - 1.34	1.23	0.05
LQ	3	1.36 - 1.42	1.39	0.02	1.29 - 1.35	1.31	0.02
REC	50	1.26 - 1.44	1.36	0.04	1.18 - 1.31	1.26	0.04

Types M_1 / Loc.	1	2	N
PO	27	2	29
PN	1	—	1
WE1	1	—	1
RK1A	3	—	3
KG	11	—	11
LQ	3	—	3
REC	56	—	56

Types M_2 / Loc.	1	2	N
PO	14	4	18
PN	1	—	1
WE1	3	1	4
RK1A	1	—	1
KG	9	4	13
LQ	3	—	3
REC	50	—	50

Fig. 15-16. Variation and frequency of M_1 (Fig. 15) and M_2 morphotypes of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Table I.

Types M_3 / Loc.	1	2	N
PO	1	4	5
PN	1	—	1
RKIA	1	—	1
REC	58	8	66

Fig. 17. Variation and frequency of M_3 morphotypes of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Table I.

Morphotype 2 (Fig. 16/2). A small extra ridge present between centrolophid and mesolophid.

M_3 three-rooted, with crown trapezoid in outline. Six ridges well developed and partly interconnected on lingual side. For measurements see Table XX.

Morphotype 1 (Fig. 17/1). Accesorial ridges absent.

Morphotype 2 (Fig. 17/2). Five main ridges present; a small extra ridge between anterolophid and metalophid.

P^4, with one root, formed from three accreted smaller roots; there are two or three ridges. For measurements see Table XXI.

Morphotype 1 (Fig. 18/1). The main ridges interconnected lingually, forming a U-shape pattern.

Table XX

Measurements of M_3 of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	5	0.95 - 1.19	1.05	0.04	0.96 - 1.10	1.04	0.04
PN	1		1.18			1.14	
RK1A	1		1.00			1.00	
REC	66	0.99 - 1.31	1.16	0.08	1.00 - 1.22	1.16	0.06

Table XXI

Measurements of P^4 of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	1		0.60			1.00	
PN	1		0.62			0.84	
REC	10	0.62 - 0.74	0.68	0.03	0.70 - 0.99	0.82	0.04

Types / Loc.	P^4 1	2	N
PO	1	—	1
PN	—	1	1
REC	10	—	10

Types / Loc.	M^3 1	N
PO	1	1
KG	2	2
REC	50	50

Types / Loc.	M^1 1	2	3	N
PO	1	16	—	17
PN	—	2	—	2
WE1	—	1	—	1
RK1A	2	1	—	3
KG	16	7	—	23
LQ	3	—	—	3
REC	58	—	2	60

Types / Loc.	M^2 1	N
PO	6	6
PN	2	2
WE1	1	1
RK1A	1	1
KG	7	7
REC	50	50

Fig. 18-21. Variation and frequency of P^4 (Fig. 18), M^1 (Fig. 19), M^2 (Fig. 20) and M^3 (Fig. 21) morphotypes of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Table I.

Morphotype 2 (Fig. 18/2). Three ridges and a small extra cusp in central part of the tooth.

M^1 as a rule four-rooted, sometimes smaller fifth root (in *M. pliocaenicus - avellanarius* group) or additional two roots present (in *M. dacicus*) (Fig. 22). Crown with five or six main ridges; anteroloph ending free in both *M. pliocaenicus - avellanarius* lineage and *M. dacicus*; other ridges interconnected lingually. Moreover, in *M. dacicus* the metaloph ends free as well. For measurements see Tables XXII and XXV.

Morphotype 1 (Fig. 18/1). Five main ridges present.

Morphotype 2 (Fig. 18/2). An extra ridge present between centroloph and metaloph.

Morphotype 3 (Fig. 18/3). The occurrence of a transverse ridge linking anteroloph and protoloph together, is a characteristic feature.

M^2 four-rooted; crown built of six ridges interconnected on lingual side. Distances between three anterior ridges rather great, other ridges are placed very close to each other; one additional ridge situated lingually (Fig. 20). For measurements see Tables XXIII and XXV.

M^3 four-rooted; crown trapezoid in outline. Five or six main ridges on occlusal surface, two extra ridges placed on both lingual and labial sides of tooth (Fig. 21). For measurements see Tables XXIV and XXV.

Table XXII

Measurements of M^1 of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	17	1.36 - 1.69	1.60	0.06	0.94 - 1.18	1.10	0.06
PN	2	1.48 - 1.61	1.54	0.06	0.95 - 1.16	1.06	0.09
WE1	1		1.62			1.10	
RK1A	3	1.62 - 1.73	1.67	0.05	1.11 - 1.15	1.13	0.02
KG	25	1.61 - 1.86	1.76	0.07	1.08 - 1.28	1.18	0.06
LQ	3	1.80 - 1.91	1.85	0.04	1.20 - 1.30	1.26	0.03
REC	60	1.70 - 1.94	1.80	0.06	1.20 - 1.37	1.30	0.05

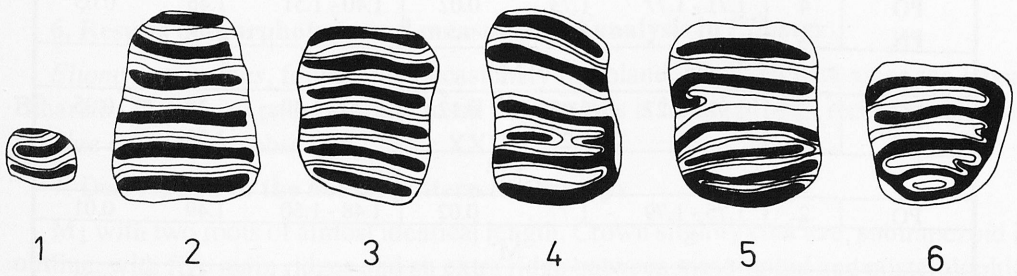

Fig. 22. Morphology of cheek teeth of *Muscardinus dacicus*. 1 – P_4, 2 – M_1, 3 – M_2, 4 – M^1, 5 – M^2, 6 – M^3.

Table XXIII

Measurements of M^2 of the *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	6	1.17 - 1.33	1.23	0.05	1.23 - 1.36	1.27	0.04
PN	2	1.20 - 1.34	1.27	0.07	1.26 - 1.35	1.30	0.04
WE1	1		1.19			1.22	
RK1A	1		1.17			1.22	
KG	7	1.24 - 1.44	1.35	0.07	1.25 - 1.39	1.32	0.04
REC	50	1.24 - 1.46	1.36	0.06	1.25 - 1.40	1.33	0.06

Table XXIV

Measurements of M^3 of *Muscardinus pliocaenicus – avellanarius* group. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
PO	1		1.04			1.14	
KG	2	1.02 - 1.07	1.04	0.02	1.27 - 1.29	1.28	0.01
REC	50	0.98 - 1.13	1.08	0.05	1.21 - 1.33	1.28	0.04

Table XXV

Measurements of cheek teeth of *Muscardinus dacicus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
Pd_4							
PN	2	0.69 - 0.74	0.71	0.02	0.75 - 0.79	0.76	0.01
M_1							
PO	7	1.74 - 2.20	1.95	0.14	1.25 - 1.75	1.44	0.15
PN	1		2.08			1.52	
M_2							
PO	4	1.71 - 1.77	1.73	0.02	1.40 - 1.51	1.46	0.03
PN	1		1.82			1.48	
M^1							
PO	5	1.91 - 2.27	2.09	0.12	1.30 - 1.47	1.39	0.05
PN	1		2.20			1.56	
M^2							
PO	2	1.75 - 1.79	1.77	0.02	1.48 - 1.50	1.49	0.01
M^3							
PO	2	1.28 - 1.34	1.31	0.03	1.44 - 1.50	1.47	0.03
PN	1		1.48			1.51	

4. Results of morphotype and measurement analysis in *Muscardinus*

The fossil remains of the genus *Muscardinus* from Poland belong to two different lineages. The first one is represented by the medium-sized *Muscardinus pliocaenicus-avellanarius* group. The dental pattern of fossil species is very similar to that of the recent taxon. The differences in the frequency of particular morphotypes are random in most teeth (Figs 14-21). The M^1 of *Muscardinus pliocaenicus* is characterized by the predominance of morphotype 2 which is distinguished by the presence of an extra ridge. In the recent species *M. avellanarius* the frequency of this pattern gradually diminishes during the Lower Pleistocene. In the recent populations morphotype 1 is absolutely predominant (Fig. 19). *M. pliocaenicus* is distinctly smaller than the recent descendant (Tables XVII-XXIV). In most teeth the size increase is gradual. However, in the case of M_2 and M^2, the populations of Late Ruscinian age (WE1, RK1A) are smaller than the Early Ruscinian ones (PO, PN).

The second lineage is represented by a large-sized species – *Muscardinus dacicus*. Its tooth morphology is generally similar to that of the *M. pliocaenicus – avellanarius* group (Fig. 22), while dimensions are distinctly greater (Table XXV).

5. Description of the dental pattern in *Eliomys*

P_4 two-rooted; crown triangular in outline; its surface distinctly concave with three cusps.

M_1 three-rooted, two of roots in the anterior part of tooth. Crown rectangular, concave, with three cusps. Five main and two extra ridges present.

M_2 very similar to M_1 as far as morphology is concerned.

M_3 three-rooted; crown oval in outline and concave, with three cusps on labial side as well as five main and two additional ridges.

P^4 three-rooted; thicker root on lingual side, two thinner ones on labial side. Crown triangular in outline, with two cusps and four main ridges on concave surface; an extra ridge placed centrally.

M^1 three-rooted (one thicker root and two thinner). Crown subrectangular and concave, five ridges; three of them (anteroloph, protoloph and centroloph) interconnected on labial side. Two other ridges (metaloph and posteroloph) also interconnected on labial side.

M^2. All its structures developed as in M^1.

M^3 three-rooted. Crown triangular in outline, with five main and one extra ridges.

For measurements of all teeth see Table XXVI.

6. Results of morphotype and measurement analysis in *Eliomys*

Eliomys quercinus, found only occasionaly in Poland, has lived here since the Upper Biharian. The dental pattern of the fossil populations is identical with recent specimens. No size changes are observed (Table XXVI).

7. Description of the dental pattern in *Dryomys*

M_1 with two roots of almost identical length. Crown slightly concave, subtrapezoid in outline, with five main ridges and an extra ridge between mesolophid and posterolophid. Endolophid absent in some specimens (Fig. 23).

Table XXVI

Measurements of cheek teeth of *Eliomys quercinus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
P_4							
REC	6	1.13 - 1.18	1.16	0.02	1.12 - 1.28	1.21	0.05
M_1							
KG	2	1.39 - 1.42	1.40	0.01	1.58 - 1.61	1.59	0.01
REC	10	1.23 - 1.38	1.29	0.05	1.57 - 1.62	1.60	0.02
M_2							
KG	2	1.32 - 1.34	1.33	0.01	1.60 - 1.64	1.62	0.01
LQ	1		1.39			1.58	
REC	10	1.32 - 1.41	1.34	0.05	1.58 - 1.74	1.65	0.06
M_3							
REC	10	1.09 - 1.15	1.12	0.02	1.35 - 1.39	1.37	0.02
P^4							
KG	1		1.01			1.30	
REC	6	1.03 - 1.10	1.06	0.03	1.36 - 1.41	1.38	0.02
M^1							
KG	6	1.22 - 1.28	1.26	0.02	1.71 - 1.81	1.76	0.04
LQ	3	1.23 - 1.28	1.24	0.04	1.74 - 1.83	1.78	0.04
REC	10	1.24 - 1.34	1.31	0.03	1.66 - 1.85	1.77	0.06
M^2							
KG	5	1.30 - 1.34	1.32	0.02	1.78 - 1.83	1.80	0.02
LQ	1		1.32			1.78	
REC	10	1.30 - 1.37	1.33	0.03	1.66 - 1.84	1.81	0.02
M^3							
KG	3	1.03 - 1.10	1.07	0.03	1.19 - 1.33	1.26	0.05
LQ	1		1.11			1.28	
REC	10	1.04 - 1.19	1.11	0.05	1.26 - 1.38	1.33	0.04

M_2 very similar to M_1. One or two extra ridges present.

Morphotype 1 (Fig. 24/1). One extra ridge between mesolophid and the posterolophid.

Morphotype 2 (Fig. 24/2) characterized by absence of centrolophid; extra ridge between anterolophid and metalophid.

M_3 two-rooted. Crown trapezoid in outline, with five main and two extra ridges.

Morphotype 1 (Fig. 25/1). Anterior extra ridge placed between anterolophid and metalophid and posterior one between mesolophid and posterolophid.

Morphotype 2 (Fig. 25/2), is distinguished by the absence of the centrolophid and the occurrence of only one extra ridge.

P^4 two-rooted (one tooth thick and one short and thin). Crown oval in outline, with five ridges (Fig. 26).

M^1 with three roots, one thicker and two thinner. Slightly concave crown, rectangular in outline, with five or six main and one or two extra ridges.

Morphotype 1 (Fig. 27/1) with six main ridges and an extra ridge between anterior centroloph and protoloph; anterior centroloph connected with protoloph on labial side, posterior centroloph distinctly shorter, attached to metaloph. Endoloph entirely developed.

Morphotype 2 (Fig. 27/2). The absence of the posterior centroloph is its characteristic feature.

Morphotype 3 (Fig. 27/3), with only five main ridges on the occlusal surface.

M^2 three-rooted. Crown similar to that in M^1, with five or six main and one extra ridges. Endoloph always entirely developed.

Morphotype 1 (Fig. 28/1), with six main ridges; extra ridge between metaloph and posterior centroloph.

Morphotype 2 (Fig. 28/2). The absence of an extra ridge is its distinguishing feature.

Morphotype 3 (Fig. 28/3), with only five main ridges.

For measurements of all teeth see Table XXVII.

Types / Loc.	M_1 1
KG	5
REC	6

Types / Loc.	M_2 1	2	N
KG	3	1	4
REC	6	–	6

Types / Loc.	M_3 1	2	N
KG	–	2	2
REC	4	–	4

Types / Loc.	P^4 1
KG	4
REC	4

Types / Loc.	M^1 1	2	3	N
KG	3	1	1	5
REC	8	–	–	8

Types / Loc.	M^2 1	2	3	N
KG	2	4	–	6
REC	–	3	2	5

Fig. 23-28. Variation and frequency of morphotypes of M_1 (Fig. 23), M_2 (Fig. 24), M_3 (Fig. 25), P^4 (Fig. 26), M^1 (Fig. 27), and M^2 (Fig. 28) of *Dryomys nitedula*. For abbreviations see Table I.

Table XXVII

Measurements of cheek teeth of *Dryomys nitedula*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
M_1							
KG	5	1.09 - 1.13	1.10	0.03	0.98 - 1.05	1.03	0.03
REC	6	1.07 - 1.12	1.10	0.04	0.99 - 1.03	1.01	0.03
M_2							
KG	4	1.14 - 1.35	1.26	0.07	1.16 - 1.36	1.25	0.07
REC	6	1.16 - 1.30	1.29	0.05	1.17 - 1.34	1.27	0.06
M_3							
KG	2	1.17 - 1.19	1.18	0.01	1.14 - 1.16	1.15	0.01
REC	4	1.17 - 1.22	1.19	0.04	1.14 - 1.18	1.16	0.02
P^4							
KG	4	0.95 - 1.00	0.97	0.02	0.73 - 0.77	0.74	0.02
REC	4	0.98 - 1.04	1.01	0.03	0.71 - 0.78	0.75	0.03
M^1							
KG	5	1.00 - 1.06	1.03	0.03	1.14 - 1.20	1.17	0.04
REC	8	0.99 - 1.04	1.02	0.03	1.18 - 1.22	1.20	0.04
M^2							
KG	5	1.10 - 1.16	1.14	0.04	1.22 - 1.30	1.26	0.06
REC	6	1.07 - 1.14	1.11	0.05	1.30 - 1.38	1.34	0.06

8. Results of morphotype and measurement analysis in *Dryomys*

The find from Kozi Grzbiet is the only fossil record of *Dryomys nitedula* from Poland. The dental pattern and dimentions of the teeth from this locality do not differ from those of the recent population (Fis. 23-28, Table XXVII).

9. Description of the dental pattern in *Glirulus*

P_4, with two roots of almost the same length. Crown ovate in outline, with five main and two extra ridges; two very short accessory ridges are also present. Endolophid is entirely developed (Fig. 29/1).

M_1, two-rooted. Crown rectangular in outline. Besides five main and two extra ridges there are some accessory ridges. Endolophid entirely developed in all speciemens studied (Fig. 29/2).

M_2 two-rooted; anterior root distinctly thicker. Occlusal surface very similar to M_1 pattern. Three accessory ridges present (Fig. 29/3).

M_3 two-rooted. Crown oval in outline. Occlusal pattern generally similar to that in previous teeth (Fig. 29/4).

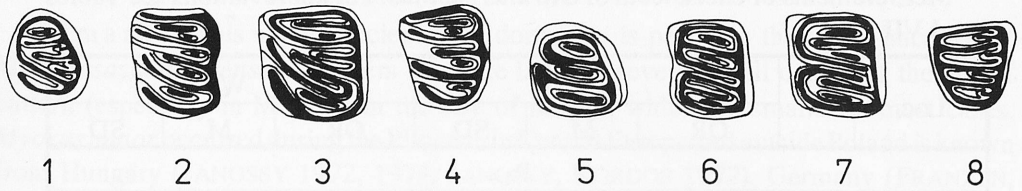

Fig. 29. Morphology of cheek teeth of *Glirulus pusillus*. 1 – P_4, 2 – M_1, 3 – M_2, 3 – M_3, 5 – P^4, 6 – M^1, 7 – M^2, 8 – M^3

P^4 three-rooted. Crown broadly ovate in outline, with five main and two extra ridges. Anteroloph attached to protoloph on both sides of the tooth, forming a closed loop (Fig. 29/5).

M^1 three-rooted, one root thicker, two thinner. Crown rectangular in outline, with seven main ridges and two extra ones. Anteroloph, protoloph and anterior centroloph interconnected, forming a closed loop. Posterior closed loop formed by posterior centroloph, metaloph and posteroloph (Fig. 29/6).

M^2 almost identical with M^1. They differ slightly in crown shape (Fig. 29/7).

M^3 three-rooted. Crown oval in outline, with seven main and two extra ridges (Fig. 29/8).

For measurements of all the teeth see Table XXVIII.

10. Results of morphotype and measurement analysis in *Glirulus*

Remains of *Glirulus pusillus* do not show any distinct differences in size and morphology between populations (Fig. 28, Table XXVIII). The teeth of this species are distinctly smaller than in the recent members of this genus from Japan.

IV. SYSTEMATIC DESCRIPTIONS

Family *Gliridae* THOMAS, 1897

Subfamily *Glirinae* THOMAS, 1897

Genus *Myoxus* ZIMMERMANN, 1780

Myoxus minor (KOWALSKI, 1956)

Glis sackdillingensis minor n. subsp. – KOWALSKI 1956: 384-386, Pl. IV, Fig. 8, Text-fig. 2f.

cf. *Glis* sp. – KOWALSKI 1960a: 189-190.

Glis cf. *minor* – SULIMSKI 1962: 221.

Glis minor – KOWALSKI 1963: 545-550, Figs 8-10.

Table XXVIII

Measurements of cheek teeth of *Glirulus pusillus*. For abbreviations see Tables I and VII

Loc.	N	L			W		
		OR	M	SD	OR	M	SD
P_4							
PO	4	0.74 - 0.82	0.77	0.06	0.70 - 0.77	0.73	0.04
PN	3	0.79 - 0.84	0.82	0.03	0.67 - 0.71	0.69	0.02
M_1							
PO	12	0.89 - 0.96	0.92	0.06	0.80 - 0.88	0.84	0.05
PN	4	0.91 - 0.97	0.94	0.03	0.80 - 0.85	0.83	0.04
M_2							
PO	8	0.98 - 1.06	1.01	0.06	0.96 - 1.02	0.98	0.04
PN	4	0.99 - 1.08	1.03	0.07	0.96 - 1.03	1.00	0.03
M_3							
PO	1		1.02			0.95	
PN	1		1.03			0.96	
P^4							
PO	3	0.72 - 0.73	0.73	0.01	0.71 - 0.74	0.73	0.02
PN	3	0.70 - 0.73	0.72	0.02	0.74 - 0.80	0.76	0.04
M^1							
PO	6	0.90 - 0.97	0.95	0.05	0.92 - 0.98	0.96	0.04
PN	3	0.93 - 0.99	0.96	0.04	0.94 - 0.99	0.97	0.04
M^2							
PO	6	0.96 - 1.01	0.99	0.03	0.96 - 1.03	1.00	0.03
PN	2	0.98 - 1.00	0.99	0.01	0.99 - 1.01	1.00	0.01
M^3							
PO	2	0.79 - 0.88	0.84	0.03	0.82 - 0.91	0.87	0.04
PN	2	0.78 - 0.86	0.82	0.03	0.88 - 1.01	0.94	0.04

Gliridae, gen et sp. indet. – KOWALSKI 1963: 559-560, Fig. 14

Glis minor – SULIMSKI 1964: 228-229.

Glis cf. *minor* – GŁAZEK et al. 1980: 264.

Glis sp. – NADACHOWSKI 1989: 157, Table II.

Diagnosis: Small *Myoxus* whose second upper molar has two extra ridges in most specimens (50-80%). In some individuals there are four extra ridges, two of them placed on both sides of the centroloph (20-50%)

Localities: Podlesice (KOWALSKI 1956), Pańska Góra (NADACHOWSKI 1989, BEDNARCZYK 1993), Mała Cave (SULIMSKI et al. 1979), Węże 1 (KOWALSKI 1963), Ewy

Cave (GŁAZEK et al. 1980), Mokra 1 (NADACHOWSKI 1989), Raciszyn 1 (NADACHOWSKI 1989), Węże 2 (SULIMSKI 1962), Rębielice Królewskie lA (KOWALSKI 1963).

Remarks: This small species of fat dormouse is probably the direct ancestor of *Myoxus sackdillingensis*. It differs from the latter in several small details of the dental pattern (especially in M^2) and in the size of molars, which are smaller in most cases. *Myoxus minor* occurred during the Pliocene in Central Europe and outside Poland is known from Hungary (JÁNOSSY 1972, 1974; JÁNOSSY, KORDOS 1977), Germany (FRANZEN, STORCH 1975; FEJFAR, STORCH 1990) and Roumania (TERZEA 1973; TERZEA, JURCSAK 1976).

Myoxus sackdillingensis HELLER, 1930

Myoxus glis var. *sackdillingensis* n. var. – HELLER 1930: 281-283, Pl. XVI, Fig. 5a-b, 6.

Glis sackdillingensis – KOWALSKI 1960b: 20-21.

Glis sackdillingensis – KOWALSKI 1963: 553-558, Fig. 12.

Glis sp. – GŁAZEK et al. 1977: 212.

Glis cf. *sackdillingensis* – BOSÁK et al. 1982: Table 1.

Glis sp. – NADACHOWSKI 1989: 161, Table III.

Glis sackdillingensis – NADACHOWSKI 1989: 161, Table III.

Glis sp. – NADACHOWSKI 1990b: 220, Table 3.

Glis sp. – NADACHOWSKI et al. 1991: 431.

Diagnosis: Medium-sized *Myoxus* whose M^2 differs from that of *M. minor* in the higher frequency of morphotypes with four extra ridges (43-85%) and sometimes in the occurrence of teeth with three additional ridges (2-20%).

Localities: Przymiłowice 3 (NADACHOWSKI et al. 1991), Kadzielnia 1 (KOWALSKI 1963), Kamyk (KOWALSKI 1960b), Kielniki 3A (KOWALSKI 1975), Żabia Cave (BOSÁK et al. 1982), Zalesiaki 1A (NADACHOWSKI 1990b), Kielniki 1 (NADACHOWSKI 1989), Zamkowa Dolna C (NADACHOWSKI 1989), Kozi Grzbiet (GŁAZEK et al. 1977).

Remarks: This species was common in Poland in the Early Pleistocene. It seems to be the ancestor of the recent *M. glis*. It is also relatively widely distributed all over the continent of Europe.

Myoxus glis LINNAEUS, 1766

Diagnosis: Large species of *Myoxus* which differs from other species belonging to the same lineage in having only two extra ridges in M^2.

Localities: The species was described in Poland from 13 localities, ranging in age from the Eemian to the Holocene (ALEXANDROWICZ et al., 1992; DAGNAN-GINTER et al., 1992; NADACHOWSKI 1982, 1990a).

Remarks: In the Middle and Late Pleistocene the fat dormice were distributed throughout Europe but everywhere its frequency in the fossil assemblages is low.

Genus *Muscardinus* KAUP, 1829

Muscardinus pliocaenicus KOWALSKI, 1963

Muscardinus avellanarioides (nomen nudum) – SULIMSKI 1962: 221.

Muscardinus pliocaenicus sp. n. – KOWALSKI 1963: 538-543, Figs 3-5.

Muscardinus sp. – KOWALSKI 1963: 544, Fig. 7.

Muscardinus pliocaenicus – SULIMSKI 1964: 229.

Muscardinus cf. *pliocaenicus* – GŁAZEK et al. 1980: 264.

Muscardinus cf. *pliocaenicus* – NADACHOWSKI 1989: 157, Table II.

Diagnosis: Small *Muscardinus* morphologically very similar to the recent species. Dimensions of teeth distinctly smaller in comparison with *M. avellanarius*.

Localities: Podlesice (KOWALSKI 1963), Pańska Góra (NADACHOWSKI 1989, BEDNARCZYK 1993), Mała Cave (SULIMSKI et al. 1979), Węże 1 (KOWALSKI 1963), Ewy Cave (GŁAZEK et al. 1980), Mokra 1 (NADACHOWSKI 1989), Raciszyn 1 (NADACHOWSKI 1989), Węże 2 (SULIMSKI 1962), Rębielice Królewskie 1A (KOWALSKI 1963).

Remarks: This species is probably the direct ancestor of the recent common dormouse. It occurs in Polish localities together with *Myoxus minor,* but is less frequent. *M. pliocaenicus* was described from Pliocene localities of almost whole Europe (e.g. DAXNER-HÖCK, DE BRUIJN 1981; FEJFAR, STORCH 1990; GUERIN, MEIN 1971; JÁNOSSY 1972, 1974)

Muscardinus avellanarius (LINNAEUS, 1758)

Muscardinus sp. – KOWALSKI 1958: 39-40, Fig. 24.

Muscardinus cf. *avellanarius* – KOWALSKI 1963: 544-545.

Muscardinus sp. – KOWALSKI 1975: 101.

Muscardinus cf. *avellanarius* – BOSÁK et al. 1982: 221, Table 1, Pl. 2.

Muscardinus cf. *avellanarius* – NADACHOWSKI 1989: 161, Table III.

Muscardinus sp. – NADACHOWSKI 1990b: 220, Table 3.

Diagnosis: Medium-sized species which differs from its ancestor *M. pliocaenicus* in larger tooth dimensions.

Localities: Kadzielnia 1 (KOWALSKI 1958), Kielniki 3A (KOWALSKI 1975), Żabia Cave (BOSÁK et al. 1982), Zalesiaki 1A (NADACHOWSKI 1990b), Kozi Grzbiet (GŁAZEK et al. 1976), and 8 localities of Late Quaternary age (DAGNAN-GINTER et al. 1992; NADACHOWSKI 1982, 1990a).

Remarks: The recent species of *Muscardinus* has lived in Europe since the Early Pleistocene but its remains are nowhere numerous.

Muscardinus dacicus KORMOS, 1930

Muscardinus dacicus n. sp. – KORMOS 1930: 243-244.

Muscardinus aff. *dacicus* – KOWALSKI 1963: 543, Fig. 6.

Muscardinus cf. *dacicus* – NADACHOWSKI 1989: 157, Table II.

Diagnosis: Large-sized *Muscardinus* generally similar to the *M. pliocaenicus-avellanarius* group as far as tooth morphology is concerned.

Localities: Podlesice (KOWALSKI 1963), Pańska Góra (NADACHOWSKI 1989, BADNARCZYK 1993).

Remarks: The large species of *Muscardinus* is known, in addition to Polish localities, from Hungary (e.g. JÁNOSSY, KORDOS 1977).

Subfamily *Dryomyinae* DE BRUIJN, 1967

Genus *Dryomys* PALLAS, 1778

Dryomys nitedula (PALLAS, 1778)

Localities: Kozi Grzbiet

Remarks: The only fossil record from Poland is that from Kozi Grzbiet. GŁAZEK et al. (1980) mentioned the probable occurrence of this genus (?*Dryomys* sp.) in Ewy Cave. This supposition needs confirmation.

Genus *Eliomys* WAGNER, 1840

Eliomys quercinus (LINNAEUS, 1766)

Eliomys sp. – NADACHOWSKI 1989: 161, Table III.

Eliomys cf. *quercinus* – NADACHOWSKI 1989: 161, Table III.

Localities: Kielniki 1 (NADACHOWSKI 1989), Kozi Grzbiet (NADACHOWSKI 1989), Żytnia Skała (KOWALSKI et al. 1967), Nad Jaskinią Niedostępną Rock-shelter (NADACHOWSKI 1982), Nad Mosurem Starym Duża Cave (NADACHOWSKI et al. 1989a), Duża Cave at Mączna Skała (DAGNAN-GINTER et al. 1992), Zawalona Cave (ALEXANDROWICZ et al. 1992).

Remarks: This species has lived in Poland since the Upper Biharian. Its frequency is always very low in fossil assemblages.

Genus *Glirulus* THOMAS, 1905

Glirulus pusillus (HELLER, 1936)

Amphidyromus pusillus n.g. n. sp. – HELLER 1936: 125-126, Taf. X: 1

Glirulus (Amphidyromys) pusillus – KOWALSKI 1963: 535-538, Fig. 2.

Glirulus pusillus – KOWALSKI 1975: 101.

Glirulus sp. – NADACHOWSKI 1989: 161, Table III.

Glirulus cf. *pusillus* – NADACHOWSKI 1989: 157, Table II.

Glirulus pusillus – BEDNARCZYK 1993: 233-240, Fig. 3.

Localities: Podlesice (KOWALSKI 1963), Pańska Góra (NADACHOWSKI 1989, BEDNARCZYK 1993), Zalesiaki 1B (NADACHOWSKI 1989), Zamkowa Dolna B (NADACHOWSKI 1989), Mokra 1 (NADACHOWSKI 1989), Kielniki 3A (KOWALSKI 1975), Żabia Cave (NADACHOWSKI 1989).

Remarks: This species is characeristic of the Pliocene faunas. It survived in Poland up to the Early Pleistocene. A description of part of the materials from Pańska Góra was given by BEDNARCZYK (1993).

V. DISCUSSION

At present the *Gliridae* comprise about 20 species belonging to 8 genera (CORBET, HILL 1991); 5 of these species are almost entirely of European location (STORCH 1978). In the Neogene this family was very diversified, especially on our continent. Its diversification began in the Miocene and very soon yielded more than 20 genera (e.g. DAAMS 1976, 1981; WU WENYU 1990). Only a reduced number of forms survived until the Pliocene and Quaternary.

The morphological patterns of cheek teeth of the *Gliridae* show variation which can be considered in terms of morphotype variability, as it is done with other groups of rodents. These morphotypes are distinguished on the basis of (1) the shape of enamel ridges visible on the occlusal surface, (2) the manner of interconnection between them and (3) the occurrence of extra ridges. Most often only one morphotype predominates in the population studied and the others occur only occasionally. In a few cases (e.g. M^2 of *Myoxus*), in particular localities, different morphotypes prevail, which suggests a hereditary background of these changes. The morphological dental patterns of the *Gliridae* do not change gradually with time as it is seen with other groups of the Neogene and Quaternary rodents. Various taxonomical studies have shown that particular genera or groups of species are characterized by a combination of features and not by their exclusion. Thus, particular morphotypes of glirid cheek teeth have no adaptive value and are not subject to linear selection. This last supposition is based on the fact that the glirids which are one of the oldest families of rodents, fixed the morphological structure of their teeth very early, already as early as the beginning of the Miocene. In spite of the great intrapopulational variability preserved in some genera, the later morphological directional changes, especially during the Pliocene and Quaternary, were slight and even negligible in most species.

In the materials of *Gliridae* from Poland at least two evolutionary lineages can be distinguished. The first one consists of three species of *Myoxus*: *M. minor, M. sackdillingensis* and *M. glis*. The second one is represented by the ancestor-descendant pair of *Muscardinus pliocaenicus* and *M. avellanarius*.

Generally, in both lineages the evolution is expressed by a size increase in the cheek teeth. These tendencies, in most cases, seem to be gradual processes. It means probably also the increase of the whole body size of these dormice from the Pliocene to the recent times. However, especially in the *Myoxus* lineage, the populations from the Early Pliocene (Podlesice, Pańska Góra) are distinctly larger than the younger Late Pliocene samples (Węże 1, Rębielice Królewskie 1A) (Fig. 13). The same tendency is observed in the *Muscardinus* lineage, although it is not so distinctly expressed.

Various explanations of this phenomenon can be offered. The first one are possible climatic changes during the Pliocene. In this case the body size changed according to Bergmann's rule, which states that the body size of homoiothermic vertebrates is larger in a cool climate. However, no direct information about climatic fluctuations in Poland during that period is available. The second explanation is based on the possibility of natural selection between glirids and members of new, very expansive families of rodents (e.g. *Muridae, Arvicolidae*), which had undergone important development during the Pliocene. The changes in body size can be accounted for as an adaptation to the new arrangement

of the ecological niches. The third supposition, less probable, is that the Late Pliocene populations are immigrants from some territories out of Central Europe.

It is known that *Gliridae* are very rare members of the recent vertebrate communities. However, it is interesting to note, that the frequency of glirids found in some fossil assemblages, especially at the end of the Early Pleistocene, often happens to be very high. Such a situation is observed, for instance, in Kielniki 1 where 90% of the fossil remains belong to *Myoxus sackdillingensis*, whereas in Kozi Grzbiet this species forms nearly 35% of the assemblage. In most Pliocene and Early Pleistocene localities the occurrence of *Myoxus* fluctuates between 3% and 15%. The Late Quaternary and Holocene assemblages are characterized by a very low percentage of *Myoxus* remains, which, in most cases, does not exceed 1%. These distinct differences result possibly from different taphonomic processes, which lead to the accumulation of fossil assemblages. However, we cannot exclude that the *Gliridae* were once much more numerous, in contrast with the situation observed in recent rodent communities of Europe, especially during the Early Pleistocene.

At present the European dormice are mainly woodland dwellers, with the exception of *Eliomys*, which ihabits open, rocky terrains, as well. Thus, the occurrence of representatives of the *Gliridae* in fossil assemblages seems to indicate the occurrence of woodland or shrubby landscapes in the vicinity of the site during the period when fossil remains had been accumulating.

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