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Evolution of *Anomalomys* GAILLARD, 1900 (*Rodentia, Mammalia*) in the Miocene of Poland

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Abstract. Isolated molars of *Anomalomys* from three different levels of sediments in the brown-coal mine of Bełchatów, representing mammalian zones MN 4 to MN 9 have been studied. They illustrate the evolution of dimensions and pattern of teeth in this evolutionary lineage of rodents. Bełchatów is a unique fossil locality with populations of *Anomalomys* from three different horizons. They belong to *A. minor* and *A. gaudryi*. The material of *Anomalomys kowalskii* KORDOS, 1989 from the Miocene of Opole has also been studied.

Key-words: fossil mammals, *Rodentia*, *Anomalomys*, Miocene, Poland, evolution.

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I. INTRODUCTION

Miocene sediments of the brown-coal mine of Bełchatów in Central Poland yielded, besides molluscs, also remains of mammals (KOWALSKI 1993 a, b, KOWALSKI, KUBIAK 1993, RZEBIK-KOWALSKA 1993). The oldest horizon with mammalian remains, Bełchatów C contained a fauna of mammalian zone MN 4, the middle one, Bełchatów B, that of MN 5/6 and the upper one, Bełchatów A, of MN 9. All the three horizons contained isolated teeth belonging to the genus *Anomalomys* and representing successive stages of one evolutionary lineage.

Anomalomys GAILLARD, 1900, has been só far known in Poland only from the Miocene (MN 7/8) of Opole, from where it was described by KOWALSKI (1967) as *Anomalomys gaudryi*. KORDOS (1989) created a new name for the population of Opole, *Anomalomys* (*Miospalax*) *kowalskii*. The material from Opole is redescribed in the present study.

GAILLARD (1900) recognized a new species and genus of rodents, *Anomalomys gaudryi*, in the Miocene of La Grive St. Alban in France (MN 7/8). VIRET and SCHAUB (1946) completed the description of *Anomalomys gaudryi* and added a new species of the genus, the slightly more specialised *A. gaillardi*.

In the following years the presence of *A. gaudryi* GAILLARD, 1900 was noted in numerous Miocene fossil localities in Europe: at Nova Ves (Neudorf) in Slovakia (SCHAUB, ZAPFE 1953), Hostalets de Pierola and Sant Quirze in the Vallès Penedès Basin in Spain (AGUSTI, GIBERT 1982 b, AGUSTI 1989), at Anwil, Ergeten and Chlihörnli in Switzerland (ENGESSER 1972, BOLLINGER, EBERHARD 1986), at the German fossil localities Hammerschmiede (MAYR, FAHLBUSCH 1975), Grosslappen (STROMER 1928, 1940) and Steinheim (SCHAUB, ZAPFE, 1953), at Hasznos in Hungary (KORDOS 1989) and Sariçay in Turkey (ÜNAY 1978).

On the other hand, *Anomalomys gaillardi* VIRET and SCHAUB, 1946 was recognized at Trinxera Sud Autopista, Can Llobateres, La Bastida, Can Petit, Can Jofresa and Ballester in Spain (HARTENBERGER, THALER 1963, HARTENBERGER 1965, AGUSTI et al. 1982, AGUSTI, GIBERT 1982a, AGUSTI 1989), at Montredon (VIRET, SCHAUB 1946, AGUILAR 1982), Soblay and Mollon (VIRET, SCHAUB 1946, GUERIN, MEIN 1971) in France, at Csákvár in Hungary (KORDOS 1989), Suchomasty in the Czech Republic (FEJFAR 1989), Götzendorf in Austria (as "cf. *gaillardi*", BACHMAYER, WILSON 1984), and Buzhory in Moldavia (LUNGU 1981).

In 1972 FEJFAR described a primitive, small form of the genus *Anomalomys,* named by him *A. minor.* The type locality was Frantiskove Lazne (Franzensbad) in the Czech Republic. *A. minor* was identified later in numerous German localities: by SCHÖTZ (1980) at Niederaichbach, Massendorf, Langenmosen and Undorf, by FAHLBUSCH and WU (1981) and WU (1982) at Puttenhausen, by ZIEGLER and FAHLBUSCH (1986) in Rauscheröd, Rembach and Forsthart, by EBERHARD (1986) at Adelegg and by MAYR et al. (1989) at Goldern. It is also known from Hirschthal (ENGESSER 1989) and from Jona-Tägernaustrasse (BOLLIGER 1992 a, b) in Switzerland and from Váralja in Hungary (KORDOS 1989).

KLEIN HOFMEIJER and BRUIJN (1985) described another species of *Anomalomys,* called *A. aliverensis,* from Aliveri in Greece. This is so far the oldest representative of the genus, about as large as *A. minor,* but with different proportions of molars.

KORDOS (1989) created a new name, *Anomalomys rudabanyensis,* for the population from Rudabanya in Hungary (Zone MN 9). In the same paper (KORDOS 1989) he introduced another new name, *Anomalomys kowalskii,* for the material from Opole in Poland, known so far under the name of *A. gaudryi.* According to him, one molar belonging to the same taxon was found at Szentendre in Hungary.

DAXNER-HÖCK (1980) discovered the most derived form of *Anomalomys* at Eichkogel bei Mödling in Austria, and named it *A. gernoti.* According to KORDOS (1985, 1989) this species, as well as several others of similar age, represent another genus, *Anomospalax* KORDOS 1985, extending the evolutionary lineage of *Anomalomys.*

BOLLIGER (1992 a) diagnosed another species of *Anomalomys, A. minutus,* from Tobel – Hombrechtikon in Switzerland. According to him, the same taxon is probably present in Germany, listed as *A. minor* from Ponholz by FAHLBUSCH (1985) and from Gisseltshansen 1a by HEISSIG (1989).

According to existing data, *Anomalomys* was present in Europe from MN 4. The lack of its ancestors in earlier layers of Europe and Asia Minor suggests that it immigrated to

Europe from Asia, where it had evolved from unknown early cricetids at the beginning of the Miocene (KLEIN HOFMEIER, BRUIJN 1984). It soon became widespread in Central and Western Europe, reached the Iberian Peninsula in MN 6, and survived there until MN 10 (Late Vallesian - Early Turolian). The lineage of *Anomalomys* is represented in MN 4 – MN 5 by *A. minor,* in MN 6 – MN 9 by *A. gaudryi,* in MN 9 – MN 10 by *A. gaillardi* and in MN — 11 by *A. gernoti. A. minutus* seems to be a side-branch of *Anomalomys* which developed and became extinct in Western Europe in MN 5 (BOLLIGER 1992 a).

As mentioned above, the genus *Anomospalax* established by KORDOS (1985) developed, according to that author, from *Anomalomys* and existed in Central Europe from MN 11 to MN 13. Its descendant would be *Prospalax* MEHELY, 1908, which was common in eastern parts of Europe from MN 14 and survived until the Early Pleistocene.

The systematic position of *Anomalomys* has been debated by many paleontologists since its discovery and it has been recognized as the ancestor of the *Spalacidae.* After the discovery of Early and Middle Miocene members of the *Spalacidae,* which differed from the earliest forms of *Anomalomys* from the same periods, BRUIJN (1984) came to the conclusion that these two groups of subterranean rodents had developed independently. He suggested upgrading *Anomalomyinae* SCHAUB, 1925, to family level *(Anomalomyidae).*

Pronounced hypsodonty and evolution in the direction of the simplified crown pattern of molars point to the underground way of life of the *Anomalomyidae,* the teeth of subterranean rodents being subject to strong wear caused by quarz grains from soil in their food. The morphology of the *Anomalomys* humerus (MEIN 1967) is also typical of the fossorial rodent.

Bełchatów is a unique locality containing remains of *Anomalomys* on three different levels covering a period of some 9 MA of the evolution of this lineage (from MN 4 to MN 9).

Specimens from Bełchatów described in this paper are housed in the collection of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Cracow. Specimens from Opole belong to the Department of Paleozoology, Institute of Zoology, University of Wrocław, but are temporarily kept in the Institute in Cracow.

The study of the fossil fauna of Bełchatów was supported by grant N° 6 6219 92 03 of the Polish Scientific Committee. The author is indebted to Dr Adam SZYNKIEWICZ, who provided geological data on the locality, to Miss Beata SŁOWIK, who selected most of small mammal remains from the samples collected at Bełchatów and to Mr Marek KAPTURKIEWICZ who prepared the drawings. Dr Pierre MEIN kindly provided me with the specimens of *Anomalomys gaudryi* from La Grive St. Alban and Dr Thomas BOLLIGER gave me access to his unpublished paper on the evolution of *Anomalomys.*

II. SYSTEMATIC PART

Family *Anomalomyidae*

Genus *Anomalomys* GAILLARD, 1900

Anomalomys minor FEJFAR, 1972

Bełchatów C (Fig. 1: 1-4).

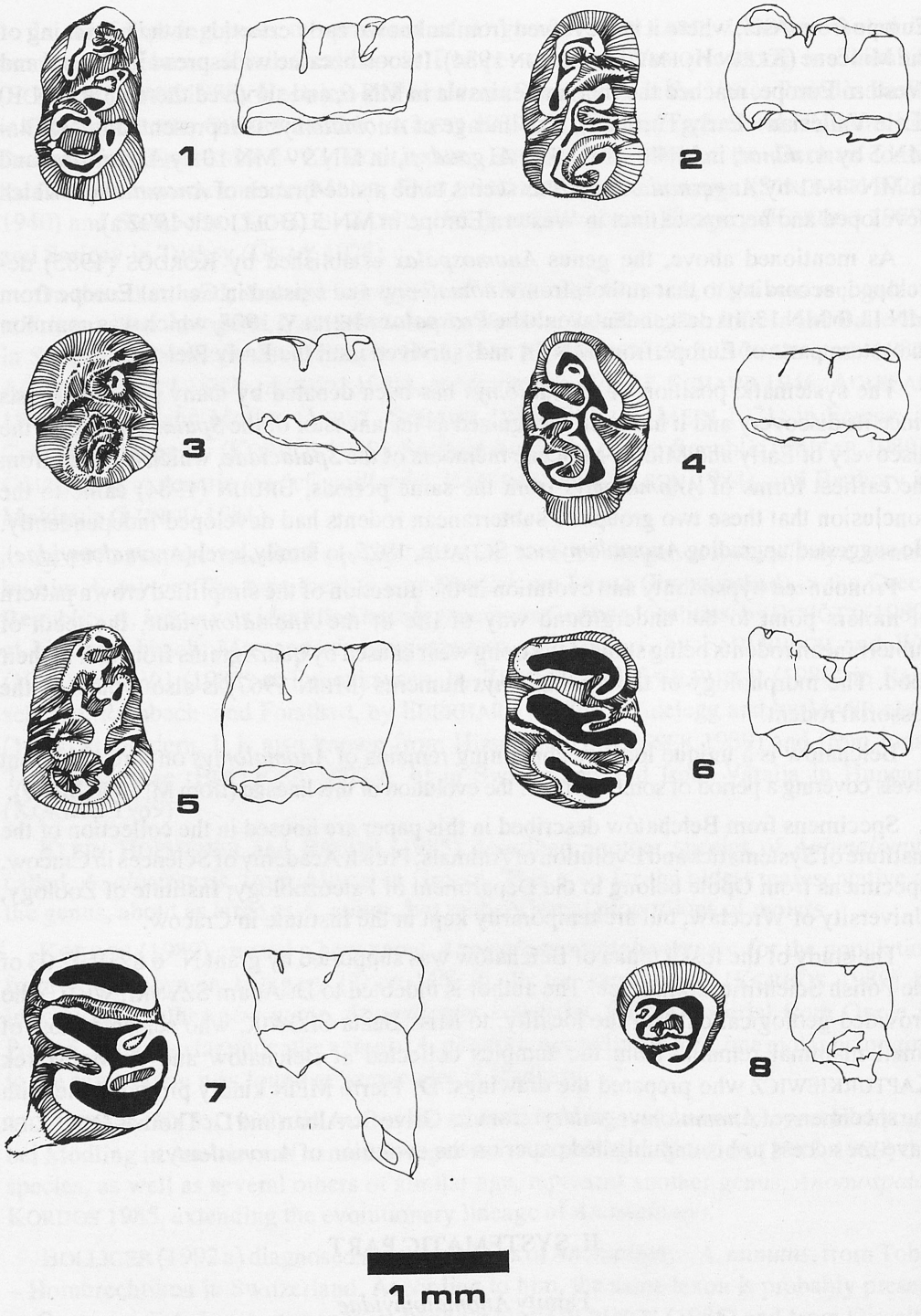

Fig. 1. *Anomalomys minor* from Bełchatów. 1-4: Bełchatów C; 1 – RM_1, No 2149/1; 2 – LM^1, No 2149/2; 3 – LM^2, No 2149/4; 4 – RM^1, No 2149/3; 5-8: Bełchatów B; 5 – RM_1, No 2150/1; 6 – LM_2, No 2150/2; 7 – LM_2, No 2150/3; 8 – RM^3, No 2150/4.

Material. 4 isolated molars: 1 M_1, 2 M^1, 1 M^2 (MF/ 2149). At least two individuals are represented in the material.

Description. M_1 (MF/2149/1) is only slightly worn. The tooth is very narrow, insignificantly broader in its posterior part. The anteroconid – metaconid complex is isolated from the remaining part of the crown by a deep lingual syncline connected with the anterior labial syncline. The mesolophid is well developed and reaches the labial border of the crown. The posterior arm of the hypoconid is also well developed.

There are two specimens of M^1. In MF/2149/2 the crown structure is identical with that in the tooth from Niedereichbach (SCHÖTZ 1980, Abb.1:3). In the second specimen, more worn, the mesoloph is very short and does not reach the border of the crown. The longitudinal ridge is interrupted in the younger specimen, continuous in the older one. Single M^2 (MF/2149/3) is unworn.

Dimensions: see Table I.

Bełchatów B (Fig. 1: 5-8).

Material. Four isolated molars: 1 M_1, 2 M_2, 1 M^3 (MF/2150). At least two individuals are represented in the material.

Description. M_1 (MF/2150/1) is only lightly worn. Its crown is distinctly broader in the posterior part. The crown-pattern is similar to that in the corresponding tooth from Bełchatów C. Two M_2 (MF/2150/2 - 3) are both rather heavily worn. Lingual and labial anterior synclines are connected. Single M^3 is short, rounded.

Dimensions: see Table I.

Table I

Dimensions of molars in *Anomalomys minor* from Bełchatów (in mm)

Tooth	L	W
Bełchatów C		
M_1, No 2149/1	1.24	0.55
M^1, No 2149/2	1.18	0.58
M^1, No 2149/3	1.10	0.67
M^2, No 2149/4	0.95	0.66
Bełchatów B		
M_1, No 2150/1	1.25	0.63
M_2, No 2150/2	1.24	0.90
M_2, No 2150/3	1.27	1.00
M^3, No 2150/4	0.60	0.68

Anomalomys gaudryi GAILLARD, 1900

Bełchatów A (Fig 2.: A-B).

Material: 52 isolated molars: 12 M_1, 10 M_2, 8 M_3, 10 M^1 9 M^2, 3 M^3 (MF/ 2151). At least 9 individuals are represented in the material.

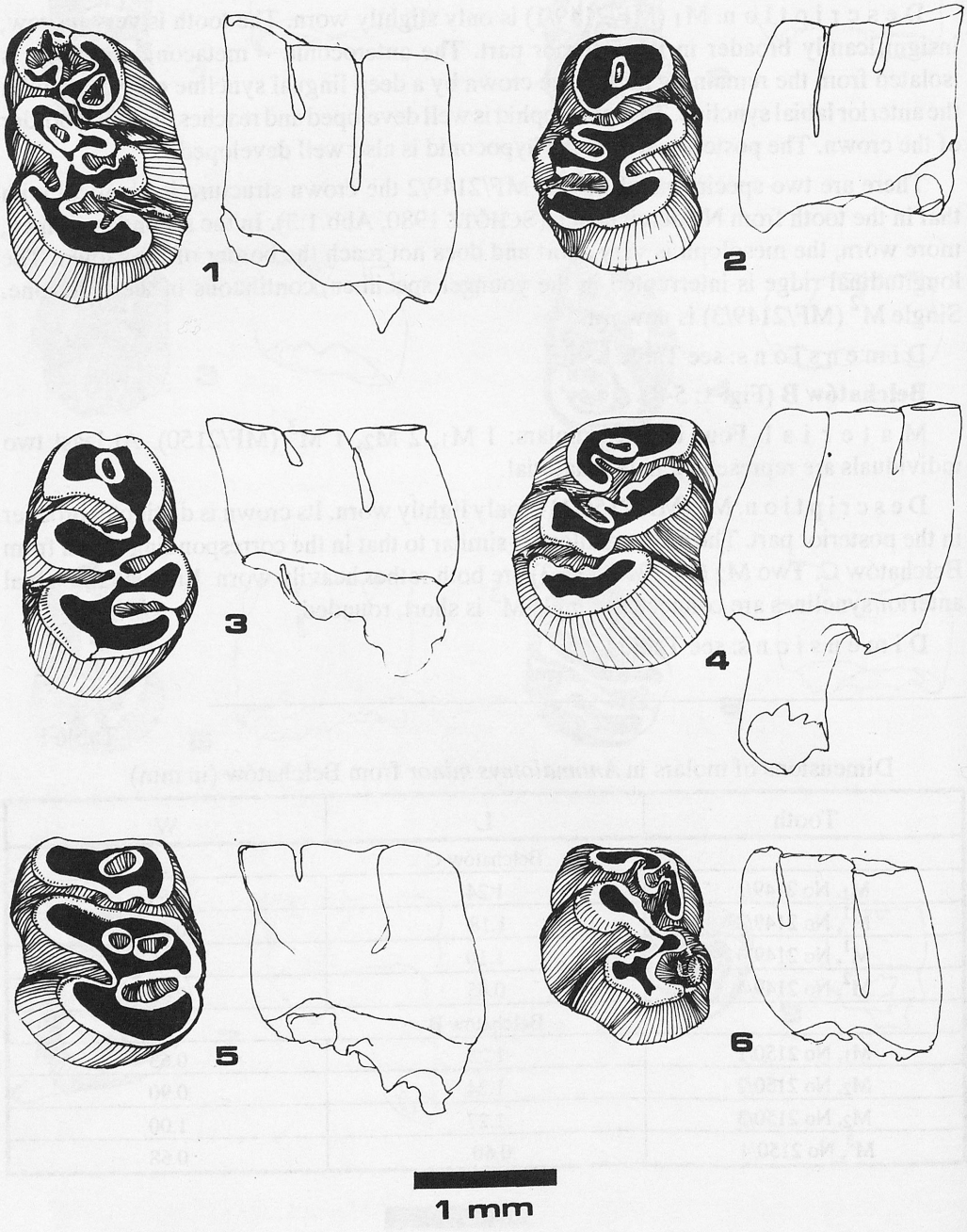

Fig. 2A. *Anomalomys gaudryi* from Bełchatów A. 1 – LM_1, No 2151/1; 2 – RM_1, No 2151/2; 3 – LM_1, No 2151/3; 4 – RM_2, No 2151/13; 5 – LM_2, No 2151/14; 6 – RM_3, No 2151/23.

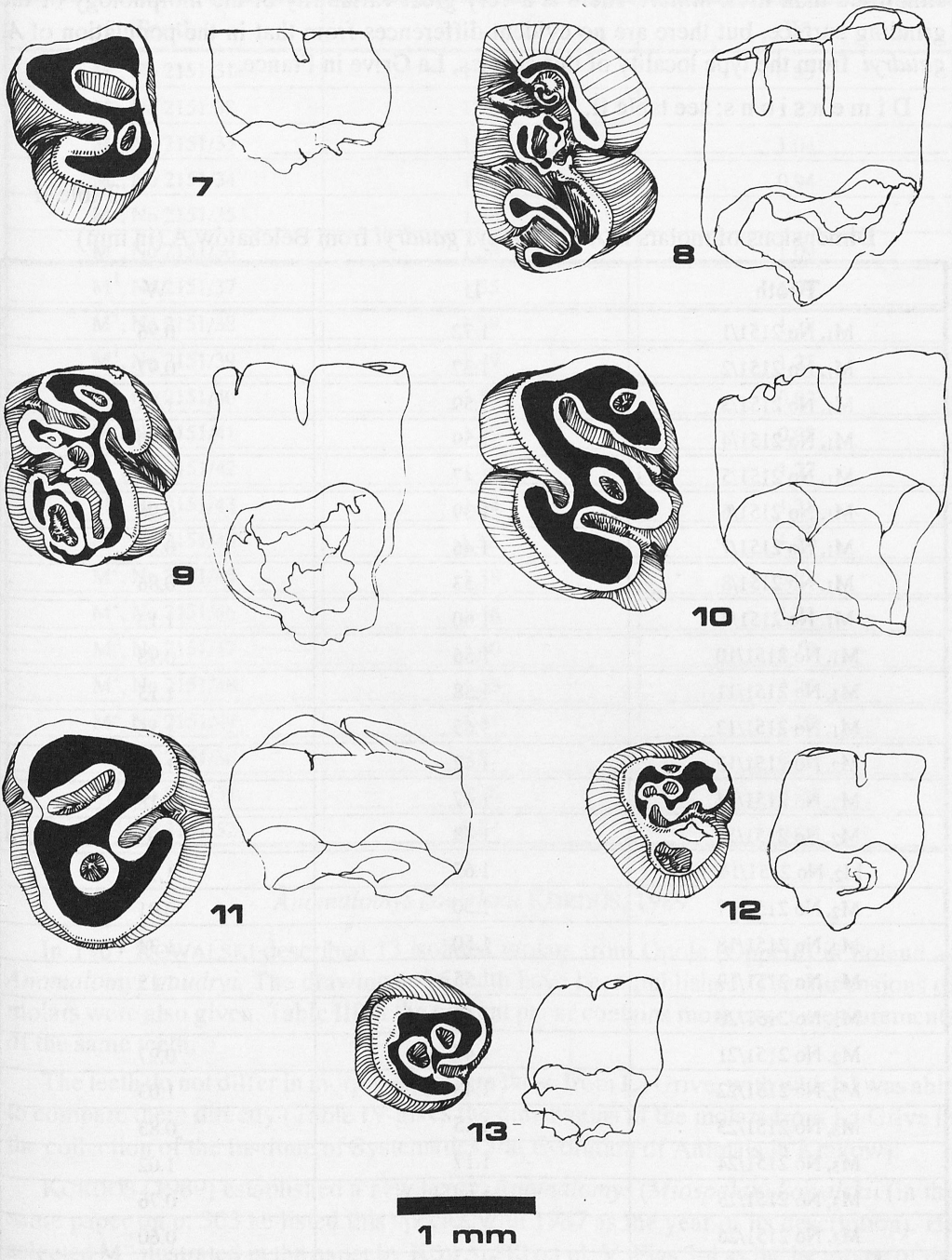

Fig. 2B. *Anomalomys gaudryi* from Bełchatów A. 7 – LM_3, No 2151/24; 8 – RM^1, No 2151/31; 9 – RM^1, No 2151/32; 10 – RM^2, No 2151/2151/40; 11 – LM^2, No 2151/42; 12 – LM^3, No 2151/50; 13 – LM^3, No 2151/51.

D e s c r i p t i o n. The molars are more hypsodont and their crown – pattern is more simplified than in *A. minor*. There is a very great variability of the morphology of the grinding surface, but there are no evident differences from that in the population of *A. gaudryi* from the type locality of this species, La Grive in France.

D i m e n s i o n s: see table II.

Table II

Dimensions of molars in *Anomalomys gaudryi* from Bełchatów A (in mm)

Tooth	L	W
M_1, No 2151/1	1.72	0.96
M_1, No 2151/2	1.37	0.97
M_1, No 2151/3	1.59	1.14
M_1, No 2151/4	1.59	0.90
M_1, No 2151/5	1.47	0.89
M_1, No 2151/6	1.39	0.96
M_1, No 2151/7	1.46	0.99
M_1, No 2151/8	1.53	0.86
M_1, No 2151/9	1.60	1.13
M_1, No 2151/10	1.56	0.98
M_1, No 2151/11	1.58	1.15
M_1, No 2151/12	1.65	1.15
M_2, No 2151/13	1.42	1.01
M_2, No 2151/14	1.47	1.18
M_2, No 2151/15	1.48	1.03
M_2, No 2151/16	1.65	1.14
M_2, No 2151/17	1.50	0.91
M_2, No 2151/18	1.50	1.34
M_2, No 2151/19	1.55	1.15
M_2, No 2151/20	1.43	–
M_2, No 2151/21	1.47	0.97
M_2, No 2151/22	1.48	1.03
M_3, No 2151/23	1.15	0.83
M_3, No 2151/24	1.17	1.02
M_3, No 2151/25	1.08	0.76
M_3, No 2151/26	0.99	0.60
M_3, No 2151/27	1.07	0.84
M_3, No 2151/28	0.98	0.71
M_3, No 2151/29	1.07	0.84
M_3, No 2151/30	1.02	0.86

Table II ctd.

Tooth	L	W
M^1, No 2151/31	1.58	0.85
M^1, No 2151/32	1.70	1.22
M^1, No 2151/33	1.55	1.04
M^1, No 2151/34	1.67	0.94
M^1, No 2151/35	1.58	–
M^1, No 2151/36	1.58	1.09
M^1, No 2151/37	1.55	1.09
M^1, No 2151/38	1.59	1.28
M^1, No 2151/39	1.49	1.25
M^1, No 2151/40	1.56	0.93
M^2, No 2151/41	1.39	0.98
M^2, No 2151/42	1.56	1.22
M^2, No 2151/43	1.54	1.35
M^2, No 2151/44	1.32	1.10
M^2, No 2151/45	1.38	0.92
M^2, No 2151/46	1.46	1.21
M^2, No 2151/47	1.40	1.19
M^2, No 2151/48	1.33	1.26
M^2, No 2151/49	1.41	1.18
M^3, No 2151/50	0.91	0.83
M^3, No 2151/51	0.78	0.92
M^3, No 2151/52	0.84	0.91

Anomalomys kowalskii KORDOS, 1989

In 1967 KOWALSKI described 13 isolated molars from Opole (Oppeln) in Poland as *Anomalomys gaudryi*. The drawings of 5 teeth have been published. The dimensions of molars were also given. Table III of the present paper contains more exact measurements of the same teeth.

The teeth do not differ in morphology from those from La Grive, with which I was able to compare them directly (Table IV gives the dimensions of the molars from La Grive in the collection of the Institute of Systematics and Evolution of Animals in Kraków).

KORDOS (1989) established a new taxon, *Anomalomys* (*Miospalax*) *kowalskii* (in the same paper on p. 305 he listed this species with 1987 as the year of its description). He selected M^2 ilustrated in the paper by KOWALSKI on pl. V, Figs 3-4 as the lectotype of the new species. KORDOS ascribed one tooth (M^2) from Szentendre in Hungary to the same species.

There is no reason to separate the form from Opole as a new species. In my opinion it is a younger synonym of *Anomalomys gaudryi*.

Table III

Dimensions of molars in *Anomalomys gaudryi* from Opole (in mm)

Tooth	L	W	Remarks
M_1	1.55	0.93	KOWALSKI 1967, Pl.VI, Figs. 2, 3
M_1	1.40	0.83	
M_2	1.50	0.97	KOWALSKI 1967, Pl. VII, Figs. 1, 2
M_2	1.48	1.23	
M_3	1.16	0.90	
M^1	1.69	1.23	KOWALSKI 1967, Pl. V, Figs. 1, 2
M^1	1.65	1.27	
M^1	1.49	1.17	
M^1	1.73	1.37	
M^2	1.45	1.12	KOWALSKI 1967, Pl. V, Figs. 3, 4 (lectotype of *A. kowalskii*)
M^2	1.43	1.48	
M^2	1.40	1.07	
M^2	1.36	1.33	

Table IV

Dimensions of molars of *Anomalomys gaudryi* from La Grive (in mm)

Tooth	L	W	Remarks
M_1, No 706/1	1.68	1.07	
M_1, No 706/2	1.87	0.98	
M_1, No 706/3	1.87	1.09	
M_1, No 706/4	1.79	1.18	
M_1, No 706/16	1.84	1.33	In mandible with M_1 - M_3
M_1, No 706/17	1.87	1.02	In mandible with M_1
M_2, No 706/5	1.67	1.36	
M_2, No 706/6	1.67	1.23	
M_2, No 706/7	1.76	1.27	
M_2, No 706/8	1.61	1.19	
M_2, No 706/16	1.67	1.42	In mandible with M_1 - M_3
M_3, No 706/9	1.29	0.95	
M_3, No 706/16	1.49	1.30	In mandible with M_1 - M_3
M^1, No 706/10	1.73	1.16	
M^1, No 706/18	1.75	1.21	In maxilla with M^1
M^1, No 706/19	1.70	1.33	In maxilla with M^1 - M^2
M^2, No 706/11	1.64	1.20	
M^2, No 706/13	1.62	1.48	
M^2, No 706/14	1.80	1.40	
M^2, No 706/15	1.84	1.31	
M^2, No 706/19	1.56	1.30	In maxilla with M^1 - M^3

III. DISCUSSION

The material of *Anomalomys* from Bełchatów belongs to three populations representing probably the same evolutionary lineage. Its evolution progressed in the direction of growing hypsodonty, of the simplification of the grinding surface pattern of molars and of larger dimensions. At the same time particular samples show a very high variability in the crown-pattern, partly connected with individual age and partly independent of it.

In describing taxa of *Anomalomys* KORDOS (1989) uses the "hypselodontic index" of molars without, however, giving any explanation how it was calculated.

In addition to *A. gaudryi,* STROMER (1928) described also a new species and genus, *Miospalax monacensis*, from Grosslappen in Germany. It was represented by very heavily worn teeth. On the basis of their pattern, which he believed to be simpler and different from that of *Anomalomys,* STROMER ascribed these remains to *Spalacidae.* In his later paper, after comparing his collections with the material from La Grive, STROMER (1940) came to the conclusion that the specimens described as *Miospalax monacensis* belonged to the same form as the remains identified as *A. gaudryi.* Other paleontologists also recognize *Miospalax monacensis* as a synonym of *Anomalomys gaudryi.*

KRETZOI (1971) in a short review of the phylogeny of mole-rats listed, without giving any reason for that, *Miospalax* STROMER, 1928 as a valid genus. KORDOS (1989), following him, used the same name as a name of the subgenus.

There are no morphological reasons for the separation of two groups of specimens from Grosslappen and, besides it is also highly improbable to find two sympatric subterranean rodents of the same size in one fauna. It seems obvious that *Miospalax* is a younger synonym of *Anomalomys.*

There is obvious that the populations of *Anomalomys* of different geological ages are slightly different and, in the case of larger samples, can be characterized by dimensions of their teeth. Giving a new name to each new sample, especially that represented by single or several specimens, does not contribute to the progress of paleontology.

The samples from Bełchatów C and B, both rather scarce, fit the group of *Anomalomys minor.* This group contains now three species of similar dimensions (*A. minor, A. aliveriensis* and *A. minutus).* The population from Bełchatów C consists of the smallest form of *Anomalomys* known so far (Fig. 3). It originates probably from mammalian zone MN 4 and is older than 18.1±1.7 MA (KOWALSKI, KUBIAK 1993). The specimens from Bełchatów B are larger and approach the dimensions of taxa belonging to the *A. minor* – group. The fauna of Bełchatów B probably represents zone MN 5/6. The differences between populations of *A. minor* – group from different localities may reflect temporal or geographical differentiation, or both.

A. gaudryi from Bełchatów A is slightly smaller than the material from La Grive and about the same size as the form from Opole. It is also distinctly smaller than *A. rudabanyensis* from Rudabanya in Hungary (MN 9). This is rather surprising, as the presence of *Microtocricetus* in Bełchatów A suggests zone MN 9 and the age identical with that of Rudabanya. Both La Grive and Opole are included into MN 7/8, La Grive being the reference locality of this zone. Perhaps the problem of the age of Bełchatów A needs a

further discussion. It is also possible that the size of particular populations of *Anomalomys* is connected not only with geological age but also with geographical variability of the species in each particular period.

A. rudabanyensis and *A. gaillardi*, both more derived than *A. gaudryi*, have not been discovered in Poland so far.

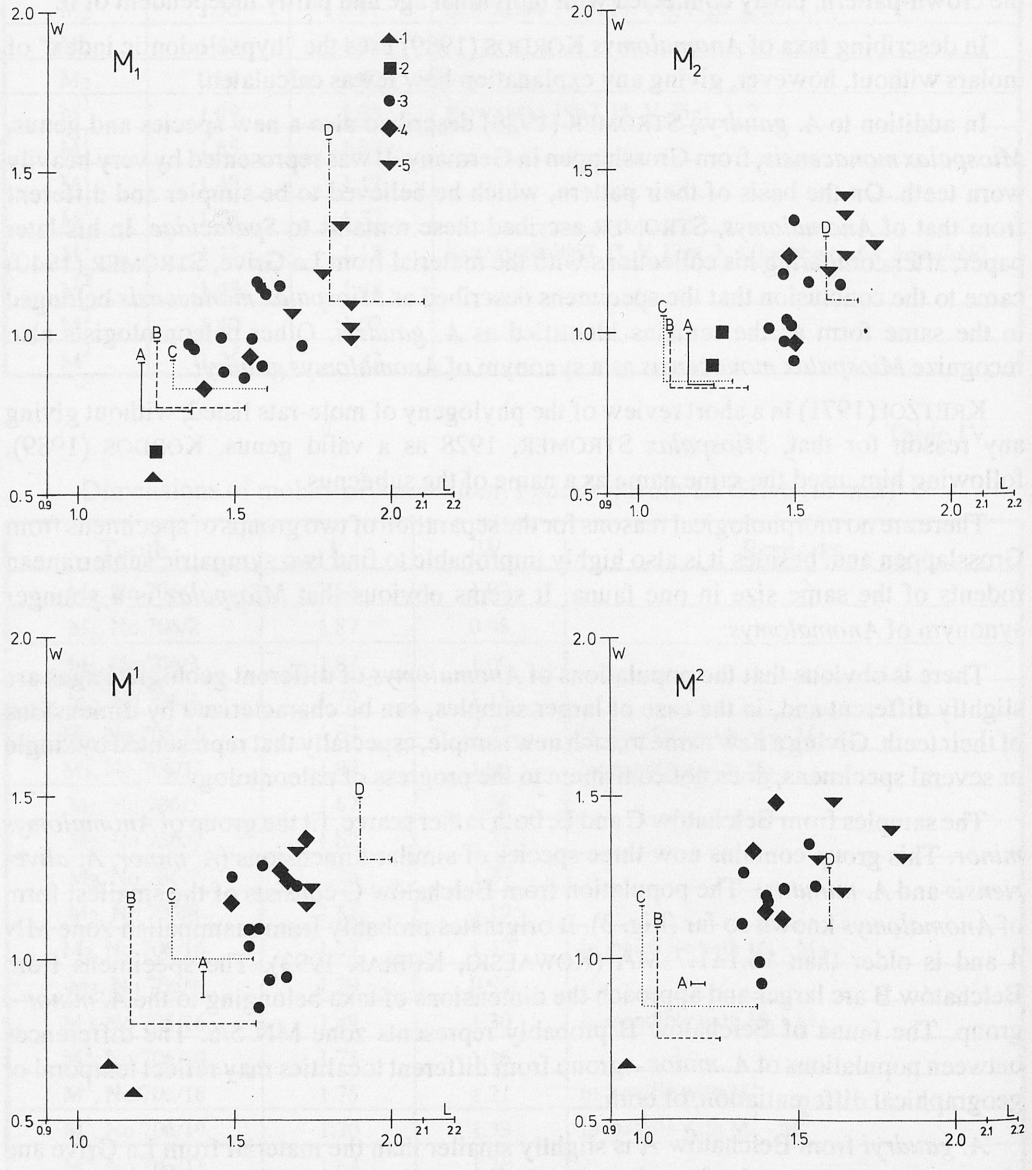

Fig. 3. Length/width scatter diagrams of M_1, M_2, M^1 and M^2 of *Anomalomys* from various localities. Original measurements: 1 – Bełchatów C, 2 – Bełchatów B, 3 – Bełchatów A, 4 – Opole, 5 – La Grive. Range of dimensions: A – *A. minutus* from Tobel Hombrechtikon, after BOLLIGER 1992a; *A. aliveriensis* from Aliveri, after KLEIN HOFMEIJER and BRUIJN, 1985; C – *A. minor* from Franzensbad and localities in Bavaria, after SCHÖTZ 1980; D – *A. rudabanyensis* from Rudabanya, after KORDOS 1989.

Anomalomys was in all probability a subterranean rodent. Recent rodents living underground are generally connected with an open country, because in forests a dense network of roots makes digging difficult. As a result they are widespread rather in arid regions where open landscapes dominate. The fauna and flora accompanying the remains of *Anomalomys* in its fossil localities point rather to forest and a wet environment. It is possible that *Anomalomys* inhabited meadows or other open spaces near waters in a generally mesic or wet environment.

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