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Prosomys insuliferus (KOWALSKI 1958) *(Rodentia, Mammalia)* from the Pliocene of Poland and of the European Part of the U.S.S.R.

[Pp. 29—54 , 53 text-figs.]

Prosomys insuliferus **(KOWALSKI 1958)** ***(Rodentia, Mammalia)*** **z pliocenu Polski i europejskiej części ZSRR ***

Prosomys insuliferus **(KOWALSKI 1958)** ***(Rodentia, Mammalia)*** **из плиоцена Польши и Европейской части СССР**

Abstract. Remains of the rodent *Prosomys insuliferus* (KOWALSKI 1958) *(Arvicolidae)* from the Pliocene of Podlesice in Poland and from Antipovka and Chugunovka in the European part of U.S.S.R. are described. The faunal lists of these fossil localities are given. *Prosomys insuliferus* is also known from the Pliocene of Vendargues in France and another species of this genus *P. mimus* SHOTWELL 1956 from the western part of the U.S.A. The systematic position of other primitive forms of *Arvicolidae* is discussed. *Prosomys* SHOTWELL 1956, primitive in many of its characteristics, nevertheless belongs to the family *Arvicolidae* and is its oldest well known member.

INTRODUCTION

In 1958 KOWALSKI described from Podlesice in Poland a new species of fossil rodents under the name of *Promimomys insuliferus*. In 1959 KRETZOI created a new genus for it, *Polonomys*, this name, however, was seldom used by later students. In 1968 REPENNING, comparing the material from Podlesice with *Prosomys mimus* SHOTWELL 1956 from the Hemphillian of Oregon, came to the conclusion that they belong to one genus and therefore included the American

* Praca wykonana w ramach problemu MR. II. 3.

form in the genus *Promimomys* KRETZOI 1955. Besides Podlesice, *P. insuliferus* has been found in Vendargues and Canterrane in France (MICHAUX 1971, 1976).

The collection of new specimens in Podlesice and the discovery of an identical form in new localities, Antipovka and Chugunovka in the Voronezh region (the U.S.S.R.) stimulated the authors to undertake a new description of the species known as *Promimomys insuliferus* and to revise its systematic position.

LOCALITIES

Podlesice. Fossil remains from Podlesice near Kroczyce in Central Poland (19°32'E, 50°34'N) were collected in a bone breccia filling a small karstic hole inside a cave in Jurassic limestone. It was discovered by K. KOWALSKI, who published a note on it in 1951 and a description of fauna in 1956. In the fossil materials bones of bats prevailed, remains of reptiles and small mammals from the orders of *Insectivora*, *Rodentia* and *Carnivora* were also found. Further contributions to the fauna of Podlesice were published by BLACK and KOWALSKI (1974), FAHLBUSCH (1969, 1978), KOWALSKI (1958, 1959, 1962, 1963, 1964, 1974), MŁYNARSKI (1962) and RZEBIK-KOWALSKA (1971, 1975, 1976). The geological age of the breccia can be determined only on the base of the fauna. It was first erroneously determined as Early Pleistocene (KOWALSKI 1956), later generally recognized as Lower Pliocene (KOWALSKI 1958, and others). The opinion of BERGGREN and van COUVERING (1974) that the fauna from Podlesice was accumulated in the uppermost Miocene does not seem justified.

The fauna from Podlesice contains the following forms (species marked with a cross need revision as to their systematic position):

Reptilia

Ophisaurus pannonicus KORMOS 1917
Anguis cf. *fragilis* LINNAEUS 1758
Lacerta sp.
Elaphe sp.

Mammalia

Insectivora
+ *Talpa minor* FREUDENBERG 1914
Desmana nehringi KORMOS 1913
+ *Sorex alpinoides* KOWALSKI 1956
+ *Sorex dehneli* KOWALSKI 1956
+ *Sorex runtonensis* HINTON 1911
+ *Sorex minutus* LINNAEUS 1766
+ *Petenyia hungarica* KORMOS 1934

Paranourosorex gigas RZEBIK-KOWALSKA 1975
Blarinoides mariae SULIMSKI 1959
+ *Petenyiella gracilis* (PETÉNYI 1864)
+ *Soriculus kubinyi* KORMOS 1934

Chiroptera
Rhinolophus delphinensis GAILLARD 1899
Rhinolopus grivensis (DEPÉRET 1892)
Miniopterus schreibersi (KUHL 1819)
Plecotus crassidens KORMOS 1930
Myotis podlesicensis KOWALSKI 1956
Myotis danutae KOWALSKI 1956
Myotis dasycneme subtilis KOWALSKI 1956
Myotis cf. *aemulus* HELLER 1936
Myotis cf. *exilis* HELLER 1936

Carnivora
Baranogale helbingi KORMOS 1934
Vormela cf. *petenyi* KRETZOI 1942
Mustela sp.

Rodentia
Sciurus cf. *warthae* SULIMSKI 1964
Tamias cf. *orlovi* (SULIMSKI 1964)
Pliopetaurista cf. *dehneli* (SULIMSKI 1964)
Blackia polonica BLACK and KOWALSKI 1974
Pliopetes hungaricus KRETZOI 1959
Pliopetaurista sp.
Sciurinae indet. (cf. *Sciurotamias*)
Leptodontomys aff. *catalaunicus* (HARTENBERGER 1967)
Keramidomys mohleri ENGESSER 1972
Estramomys sp.
+ *Sminthozapus* sp.
+ *Anomalomys* sp.
+ *Parapodemus coronensis* SCHAUB 1938
Kowalskia magna FAHLBUSCH 1969
Kowalskia polonica FAHLBUSCH 1969
Cricetus sp. 1
Cricetus sp. 2
Epimeriones progressus KOWALSKI 1974
Baranomys kowalskii KRETZOI 1962
Prosomys insuliferus (KOWALSKI 1968)
„*Trilophomys*" *canterranensis* MICHAUX 1976
Glirulus pusillus (HELLER 1936)
Muscardinus pliocaenicus KOWALSKI 1963
Muscardinus cf. *dacicus* KORMOS 1930
Glis minor KOWALSKI 1956

Lagomorpha

+ *Ochotonidae* gen. et sp. indet.
+ *Leporidae* gen. et sp. indet.

Antipovka and Chugunovka. The material described in the present paper comes from the collection made by a geologist, Dr. P. W. KRASNENKOV. It was obtained by washing and screening of old alluvial sediments of wide extent.

The terrain where the collections were made is situated between the rivers Bitiug and Don, near the villages Antipovka and Chugunovka in the Voronezh district. Outcrops of continental sediments of different origin and of different age (from Early Pliocene to Late Pleistocene) are to be found here in ravines and river valleys. Clays, loams, fossil soils, redeposited loesses, clayey limnic sediments, alluvial sands and gravels are represented among the sediments. River sediments from a well developed and well studied system of old terraces (KRASNENKOV et all. 1970, KRASNENKOV, AGADJANIAN 1975, 1976).

The central part of the Russian Plain has undergone a continual uplifting since the beginning of the Miocene. That is why new river valleys were formed on successively lower levels. As a result, river sediments on higher levels are older, lower ones younger. On the middle Don about twenty old river terraces were differentiated.

The relative age of each terrace was determined by detailed geological studies. In more complicated cases data from borings and from the study of sections helped to reconstruct the history of the geomorphological development and the sequence of layers of river sediments.

The geomorphological stratigraphy has to be supplemented by biostratigraphical data (JÁNOSSY 1974). In the region of the middle Don it is possible, because nearly all layers of the terraces contain ramains of small mamm als. These remains make it possible to determine the geological age of sediments by referring them to the relatively well known succession of faunas in Western as well as Eastern Europe. In dating the development of fauna localities, in which the layers containing rodent remains alternate with typical marine sediments are of particular importance. In the European part of the U.S.S.R. such localities include Kvabebi, Kuchurgan and many other sites in the Black See region, as well as Akulaevo in Bashkiria. They make it possible to refer the sediments of river terraces of the middle Don to the successive phases of the development of the Russian Plain. On the other hand, the succession of terraces helps to establish the sequence of faunas, which is not always clear, particularly when the difference in age is small.

In the vicinity of the villages Antipovka and Chugunovka the sands which belong to the uppermost level, and therefore represent the oldest complex of terraces, are exposed. The distance between these two villages is only about 1 km. In both localities the outcrops have identical sections and differ only slightly in thickness. Their profile is as follows:

In the floor there are chalks of the Cenomanian. They are overlaid by sand beds, 5 m (on the watershed) to 20 m thick. The lower part of them contain gra-

vel and coarse sand, in the upper they are interbedded by middle- and fine-grained sands with crossbedding typical of river sediments. They contain freshwater gastropods, remains of reptiles and of small mammals. This series of river sediments can be referred to the Middle Pliocene.

Higher in the section sands are interbedded by horizontal layers of clays of watershed fraction. They turn successively into red-brown fossil soil of steppe character with a well developed profile, up to 2 m thick. Similar fossil soils are of wide extent in the middle and southern parts of the Russian Plain. It is generally accepted that they developed in the Upper Pliocene. They are overlaid by ancient loesses. Above them there are Pleistocene sediments containing boulder-clay of the Middle Pleistocene (Riss I), fossil soil and finally loess from the period of the Würm glaciation. Their total thickness reaches 30 m.

In bone-bearing layers of Antipovka and Chugunovka R. V. KRASNENKOV collected about 200 specimens. The following mammalian forms were determined in the material:

Insectivora	
Desmana sp.	5 specimens
Talpa sp.	1 specimen
Erinaceus sp.	2 specimens
Crocidura sp.	1 specimen
Lagomorpha	
Ochotona pseudopusilla GUREEV and SHEVCHENKO 1964	76 specimens
Hypolagus ex. gr. *gromovi* GUREEV 1964	30 specimens
Rodentia	
Pliopetaurista sp.	1 specimen
Trogontherium minus NEWTON 1890	1 specimen
Microspalax ex. gr. *odessanus* TOPACHEVSKI 1969	19 specimens
Allocricetus sp.	5 specimens
Epimeriones sp.	1 specimen
Prosomys insuliferus (KOWALSKI 1968)	68 specimens

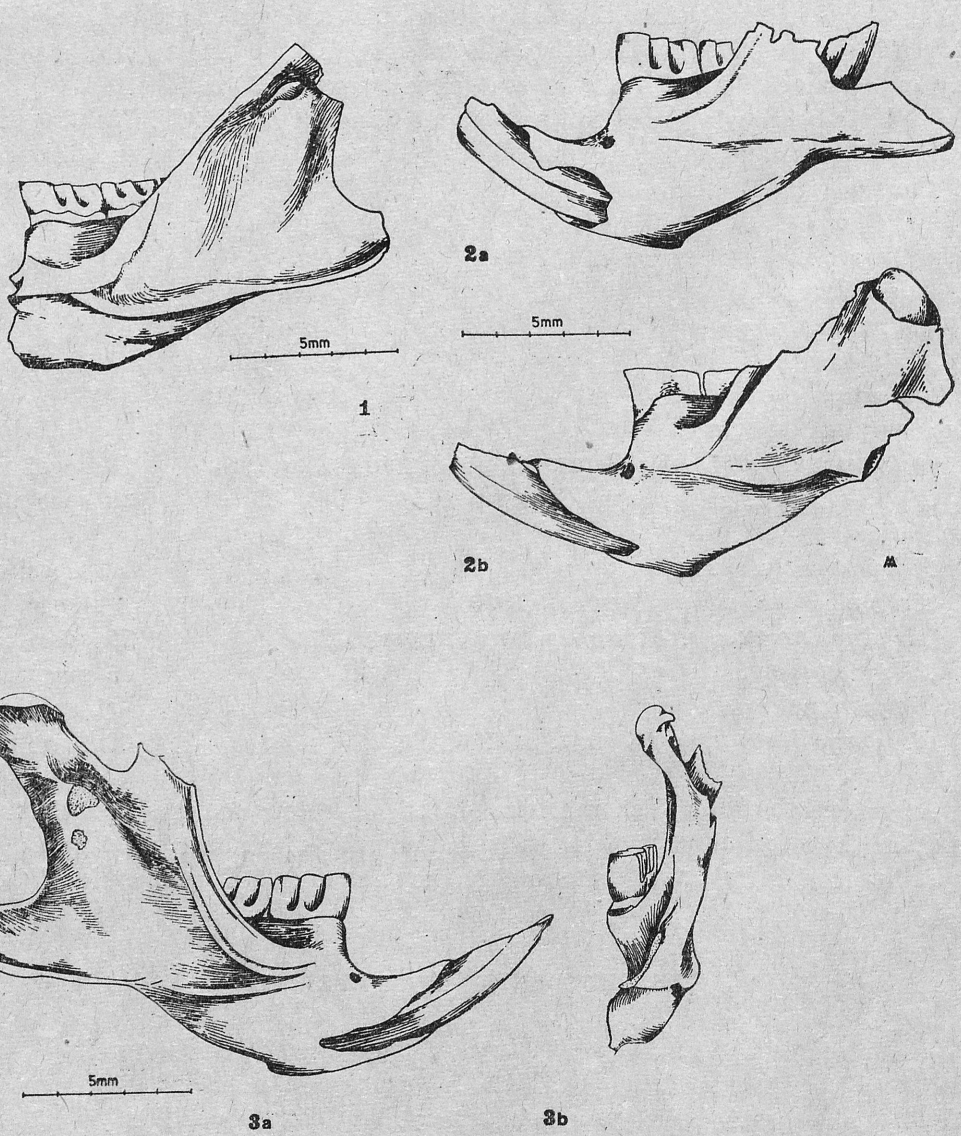
In general the fauna is characterized by the numerous occurrence of the lagomorphs, the small number of cricetids and complete lack of typical voles. Its most interesting feature is undoubtedly the presence of *Prosomys insuliferus*.

DESCRIPTION OF THE MATERIAL

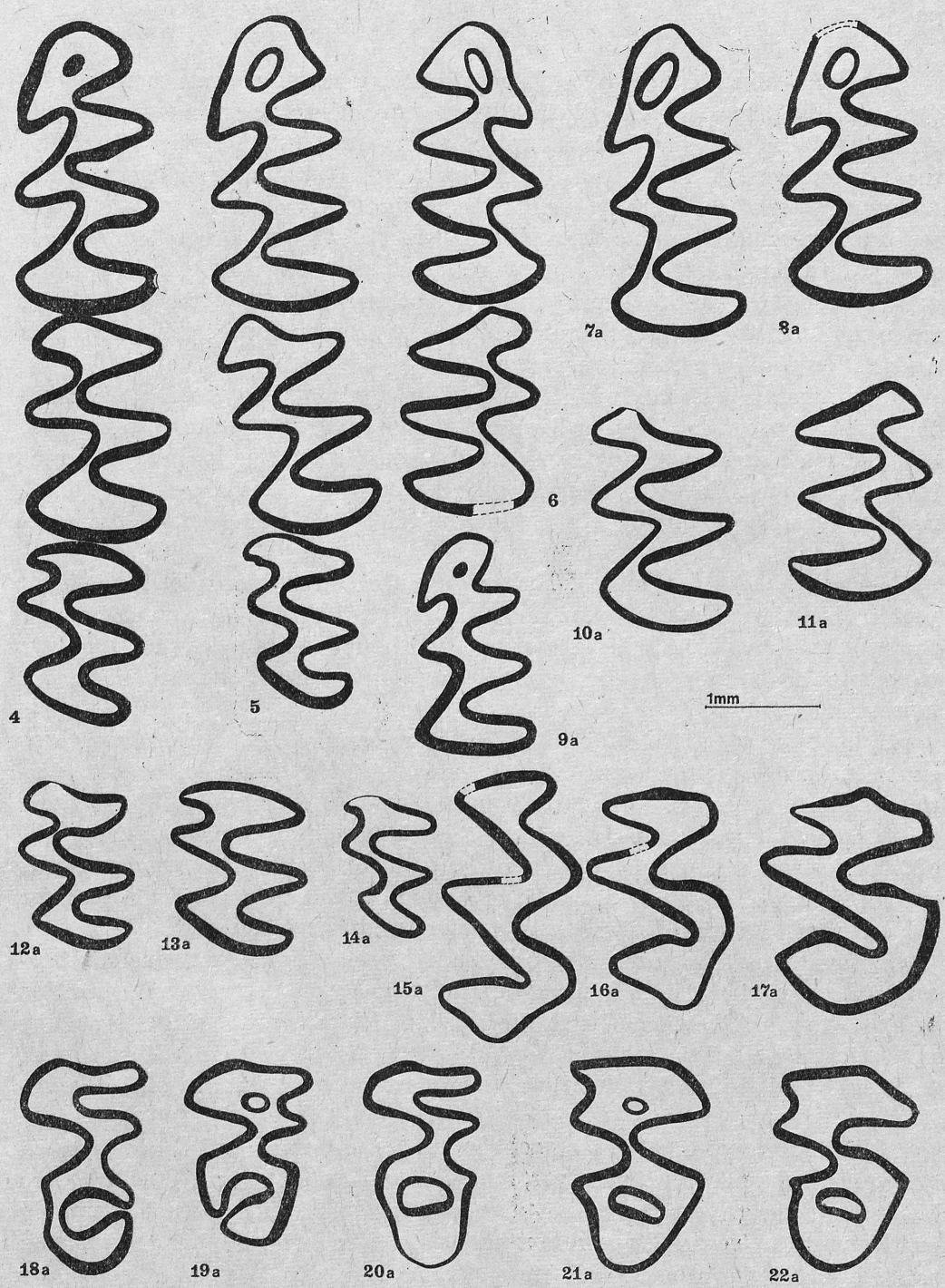
Podlesice. The material, preserved in the collections of the Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, in Kraków (No MF/22) contains the holotype, fragmentary left mandible with m_1—m_3 (MF /22/1), skull fragment with complete right tooth-row and with mandible (m_1—m_2 preserved) (MF/22/68), 2 mandibles with m_1—m_3, 5 mandibles with m_1—m_2,

1 mandible with m_1 (all mandibles more or less damaged), isolated molars: 8 m_1, 10 m_2, 9 m_3, 13 m^1, 9 m^2, 9 m^3. In the entire material particular molars are represented in the following numbers:

m_1	18
m_2	19
m_3	12
m^1	14
m^2	10
m^3	10



Figs. 1—3. *Prosomys insuliferus*, Podlesice, mandibles. 1 — MF /22/ 1 (holotype); 2a — MF /22/ 6; 2b — MF /22/ 5; 3a—3b — MF /22/ 2



Figs. 4—22a. *Prosomys insuliferus*, Podlesice, occlusal view of the molars. 4 — m_1—m_3, MF/22/1 (holotype); 5 — m_1—m_3, MF/22/6; 6 — m_1—m_2, MF/22/2; 7a—m_1, MF/22/11; 8a—m_1, MF/22/12; 9a—m_1, MF/22/9; 10a—m_2, MF/22/20; 11a—m_2, MF/22/19; 12a—m_3, MF/22/35; 13a—m_3, MF/22/31; 14a—m_3, MF/22/29; 15a—m^1, MF/22/47; 16a-m^2, MF/22/52; 17a—m^2, MF/22/54; 18a—m^3, MF/22/67; 19a—m^3, MF/22/61; 20a—m^3, MF/22/66; 21a—m^3, MF/22/62; 22a—m^3, MF/22/64

Mandible robust. On the buccal surface of the ascending ramus there is a depression situated posteroventrally from the anterior edge of this ramus and parallel to it ("Arvicoline groove" according to REPENNING, 1968). Lower masseteric crest prominent. Deep internal temporal fossa separates the row of lower molars from the ascending ramus. Diastema short. Arvicolid groove and lower masseteric crest meet at an acute angle. The end of processus coronoideus ascends nearly to the level of the upper margin of processus articularis. Processus angularis strongly developed, its end protruding behind the vertical line descending from the end of processus angularis. The constriction of processus articularis under its articular part unconspicuous.

Lower incisor massive. Its anterior part situated lingually from m_1 and from the anterior root of m_2. Further back the incisor passes below the posterior root of m_2, which is shortened and provided with a conspicuous incision, and then goes buccally from m_3. The proximal part of the incisor ascends far above the molar - row and forms a prominent protuberance on the lateral surface of the processus coronoideus.

Molars are mesodont, rooted. Their crowns are distinctly broader in the basal parts; when the molars are worn down, their grinding surface is much broader than it is in young teeth. The enamel thick, without dentine tracks, only slightly thinner in the anterior part of m_1 and in posterior part of m^3. No traces of cement in reentrant angles.

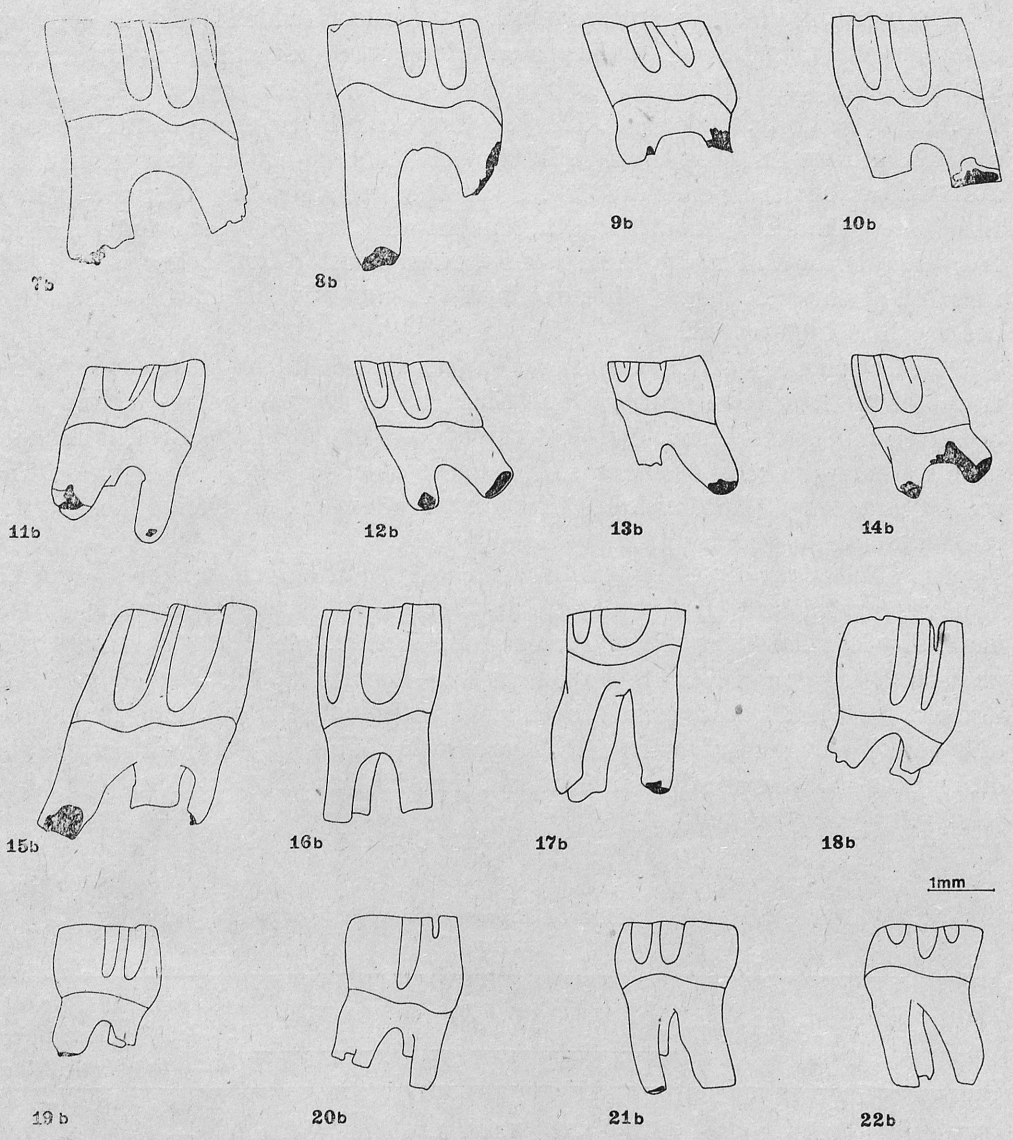
M_1 has two roots. Its grinding surface is composed of the anterior loop, three enamel triangles and the posterior loop. The anterior loop is simple, without additional re-entrant angles. On its surface, in all specimens except very old ones there is an enamel island. The enamel cone of this island reaches below half the height of the unworn tooth. The island is not formed by closing of a re-entrant angle. It is oval in shape, obliquely situated, and occupies a large part of the anterior loop. Second and third triangle are relatively broadly confluent.

M_2 two-rooted, the anterior root round in cross-section, slightly inclined buccally, the posterior one more massive, antero-posteriorly compressed, provided on its lower end with an incision for the incisor which passes below it. The grinding surface composed of the anterior loop (containing broadly confluent first enamel triangle), of two isolated or slightly confluent enamel triangles, and of the posterior loop.

M_3 with two roots. The anterior one is smaller, antero-posteriorly compressed and vertical, the posterior one larger, round in cross-section and directed obliquely backwards. The grinding surface composed of the anterior loop, which is broadly confluent with the small, antero-external enamel triangle, and of the internal triangle broadly confluent with the posterior loop.

The proximal end of the upper incisor meets the anterior end of m^1.

M^1 with three roots: the anterior and posterior one are round in cross-section, the middle root is laterally compressed, situated on the buccal side of the crown nearer its posterior end. The grinding surface of the crown composed of the anterior loop, which is distally concave, of three enamel triangles and of the



Figs. 7b—22b. *Prosomys insuliferus*, Podlesice, buccal view of the same molars as in Figs. 7a—22a

posterior loop. Two anterior triangles are confluent, the third one broadly connected with the posterior loop, which is proximally distinctly convex.

M^2 three-rooted. Posterior root is round, situated nearly on the long axis of the tooth. Of the two anterior roots the buccal one is slender and round, the lingual one large and laterally compressed. In two specimens on the proximal ridge of the anterior lingual root there is a small additional root, which is fused with the main root along nearly the whole of its length, but divided by a groove. Only its end is free. In another specimen there is an additional, entirely indepentetn fourth root on the postero-lingual part of the crown.

The grinding surface composed of the anterior loop (which is distally convex), of two enamel triangles and of the posterior loop, its proximal border also convex. The posterior enamel triangle is broadly confluent with posterior loop.

M^3 has, as a rule, three roots. The posterior one is large, the two anterior roots smaller, all round in cross-section. In two specimens the anterior roots are fused at the base, but their ends are free. In another specimen the anterior roots are fused along the whole of their length, and the only trace of their independence is a vertical groove. Finally, there is one specimen with its anterolingual root bifurcated at the end, and another one with this root divided into two, so that the tooth is four-rooted.

In all specimens of m^3 there is an enamel island on the posterior loop. No traces of the formation of this island through the closing of a re-entrant angle can be seen in our material. This posterior enamel island is large, oval, sometimes with its ends directed backwards. It persists even in deeply worn teeth. The second, anterior island developed through the closing of the end of the anterior re-entrant angle and is much more ephemeric.

The dimensions of the material from Podlesice are given in tables I and II.

Antipovka and Chugunovka. In the collection from these two localities, there are 69 isolated molars of *Prosomys insuliferus*. The material is very well preserved, only the roots are broken in some specimens. No morphological differences between materials from both localities could be found. The dimensions of specimens from Antipovka and Chugunovka (table III) are similar and the differences are statistically insignificant. The material is, therefore, described jointly.

Table I

Dimensions of mandibles of *Prosomys insuliferus* from Podlesice
(in mm)

No	M_1–M_3	M_1–M_2	M_1		M_2		M_3		Length of diastema	Height of mandible below m_1
			L	W	L	W	L	W		
MF/22/1	5.80	4.30	2.51	1.23	1.85	1.31	1.51	1.10	—	3.60
MF/22/10*	—	4.30	2.37	1.20	1.88	1.22	—	—	—	—
MF/22/11	—	4.15	2.37	1.18	1.78	1.22	—	—	3.55	3.45
MF/22/12	5.90	4.50	2.48	1.20	1.85	1.20	1.43	0.95	3.25	3.90
MF/22/13	—	4.47	2.59	1.31	1.90	1.32	—	—	—	3.58
MF/22/14	—	4.10	2.32	1.16	1.82	1.19	—	—	3.30	3.45
MF/22/15	—	—	—	—	1.85	1.10	—	—	3.16	3.60
MF/22/16	—	—	—	—	1.70	1.12	—	—	3.10	3.78
MF/22/17	—	—	2.49	1.20	—	—	—	—	—	3.80
MF/22/18	—	—	—	—	1.70	1.10	—	—	3.00	3.63
MF/22/22	6.00	4.50	2.62	1.30	1.85	1.30	1.55	1.12	3.50	3.65

* Dimensions of upper molars in the specimen MF/22/10: m^1—m^3 5.63, m^1 L 2.15, W 1,40, m^2 L 1.77, W 1.30, m^3 L 1.73, W 0.22.

Table II

Dimensions of molars of *Prosomys insuliferus* from Podlesice
(in mm)

	Length				Width			
	n	min	m	max	n	min	m	max
M^1	13	2.04	2.23	2.35	13	1.08	1.28	1.58
M^2	10	1.70	1.81	1.90	10	1.19	1.30	1.57
M^3	10	1.61	1.73	1.88	10	1.10	1.21	1.32
M_1	15	1.91	2.43	2.65	15	1.04	1.20	1.30
M_2	20	1.58	1.86	2.05	20	1.07	1.19	1.44
M_3	12	1.26	1.45	1.56	12	0.87	0.98	1.12

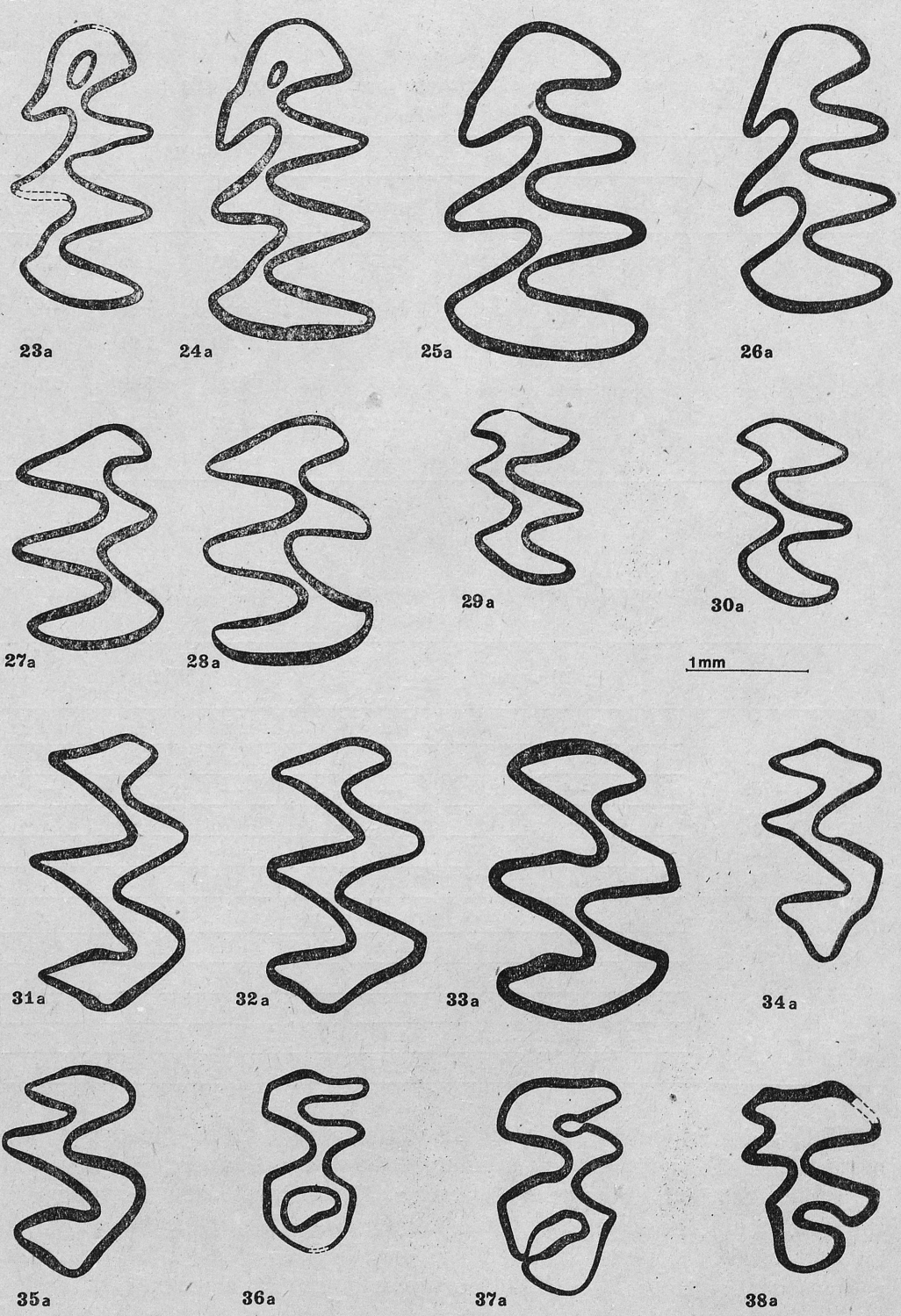
Table III

Dimensions of molars of *Prosomys insuliferus* from Antipovka and Chugunovka
(in mm)

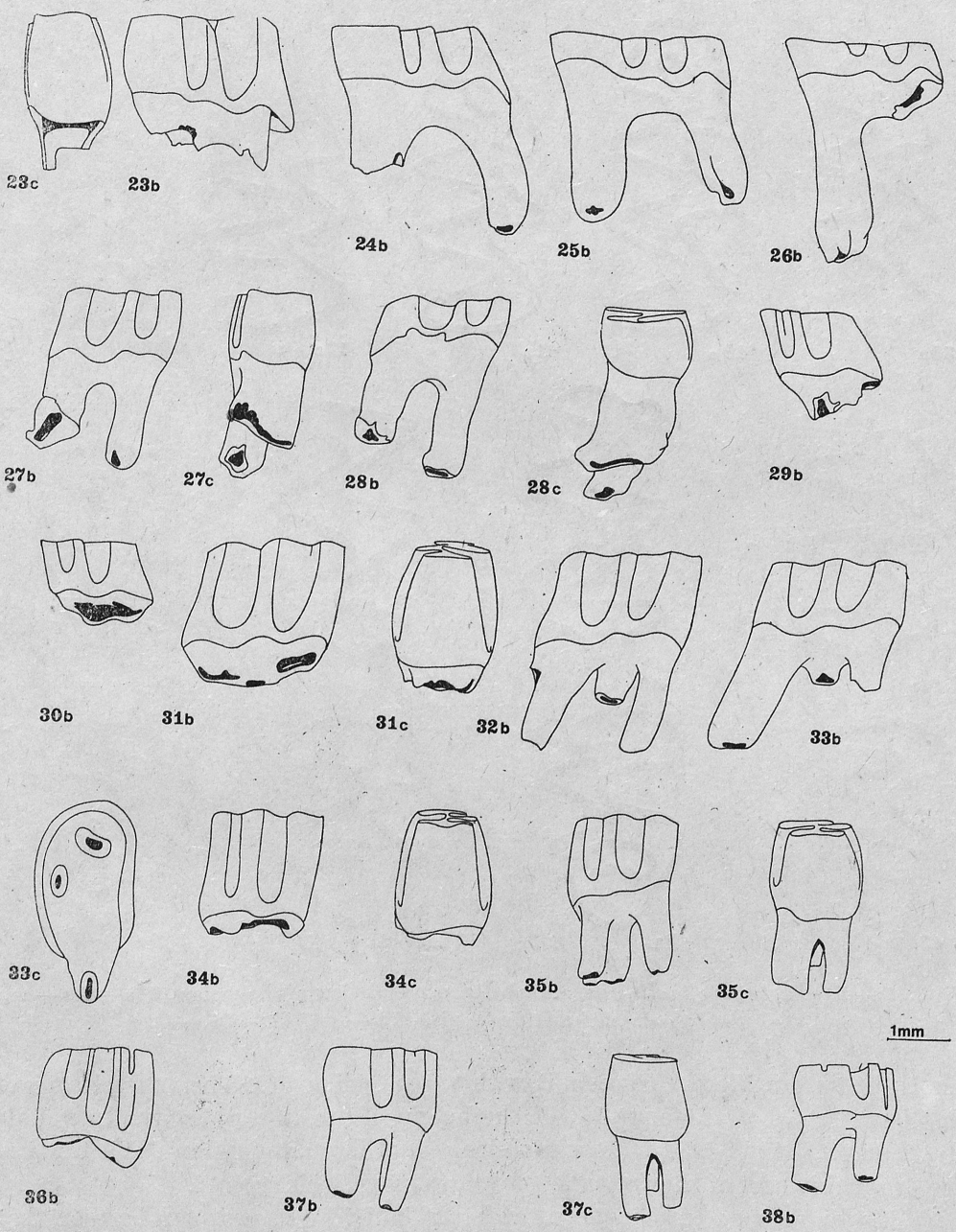
		Length				Width			
		n	min	m	max	n	min	m	max
Antipovka	M^1	8	2.0	2.18	2.4	13	1.1	1.28	1.4
	M^2	1	—	1.8	—	1	—	1.2	—
	M^3	4	1.6	1.67	1.7	4	1.0	1.18	1.25
	M_1	5	2.25	2.37	2.55	6	1.0	1.16	1.3
	M_2	4	1.65	1.77	1.85	4	0.95	1.07	1.2
Chugunovka	M^1	9	2.0	2.16	2.3	16	1.1	1.32	1.6
	M^2	7	1.7	1.76	1.8	8	1.0	1.12	1.25
	M^3	3	1.55	1.62	1.7	4	1.0	1.11	1.15
	M_1	5	2.2	2.35	2.5	5	1.1	1.37	1.6
	M_2	6	1.65	1.79	1.9	7	0.95	1.2	1.4
	M_3	2	1.45	—	1.5	2	0.95	—	1.0

Molars of mesodont type. The height of the crown even in youngest teeth is smaller than the length of their grinding surface exception made for m^2 where in young teeth both dimensions are similar. The thickness of enamel is nearly the same around the crown, only in the anterior parts of m_1 and m_2 and in posterior part of m^3 it is slightly thinner. The lower border of the enamel is smooth, without dentine-tracks. There are no traces of cement in re-entrant angles.

M_1. The crown is distinctly broader in the basal part. Two well developed roots are present. The grinding surface is slightly narrower in its anterior part.

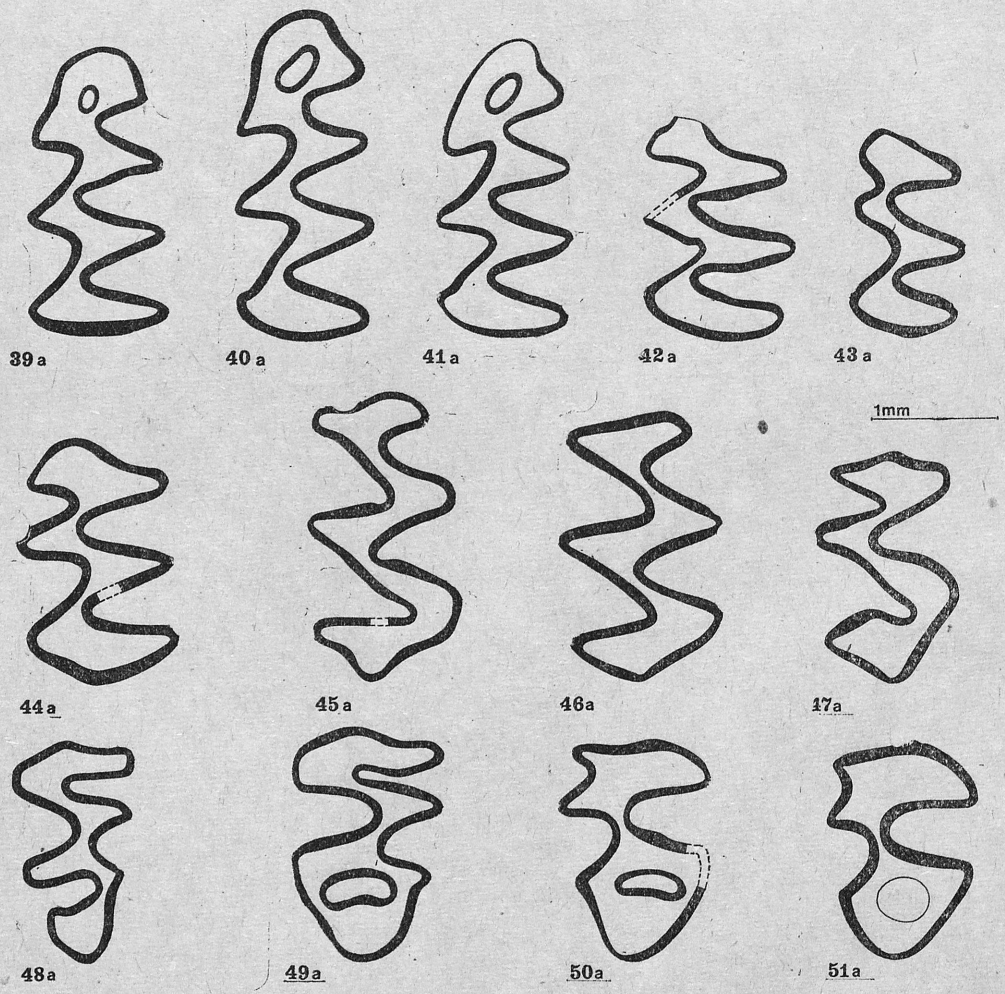


Figs. 23a—38a. *Prosomys insuliferus*, Chugunovka, occlusal view of the molars. 23a—26a — m_1; 27a—28a — m_2; 29a—30a — m_3; 31a—33a — m^1; 34a—35a — m^2; 36a—38a — m^3



Figs. 23b—38b. *Prosomys insuliferus*, Chugunovka, buccal view of the same molars as in Figs. 23a—38a. 23c, 27c,28c — posterior view; 31c, 34c, 35c, 37c — anterior view; 33c — view from the root-side

All the enamel fields are distinct but not completely isolated. The broader confluence exists between the second and third triangle (protoconid and endoconid) and also between the paraconid and metaconid. Two re-entrant angles are present on the both external and internal side of the crown. In all younger

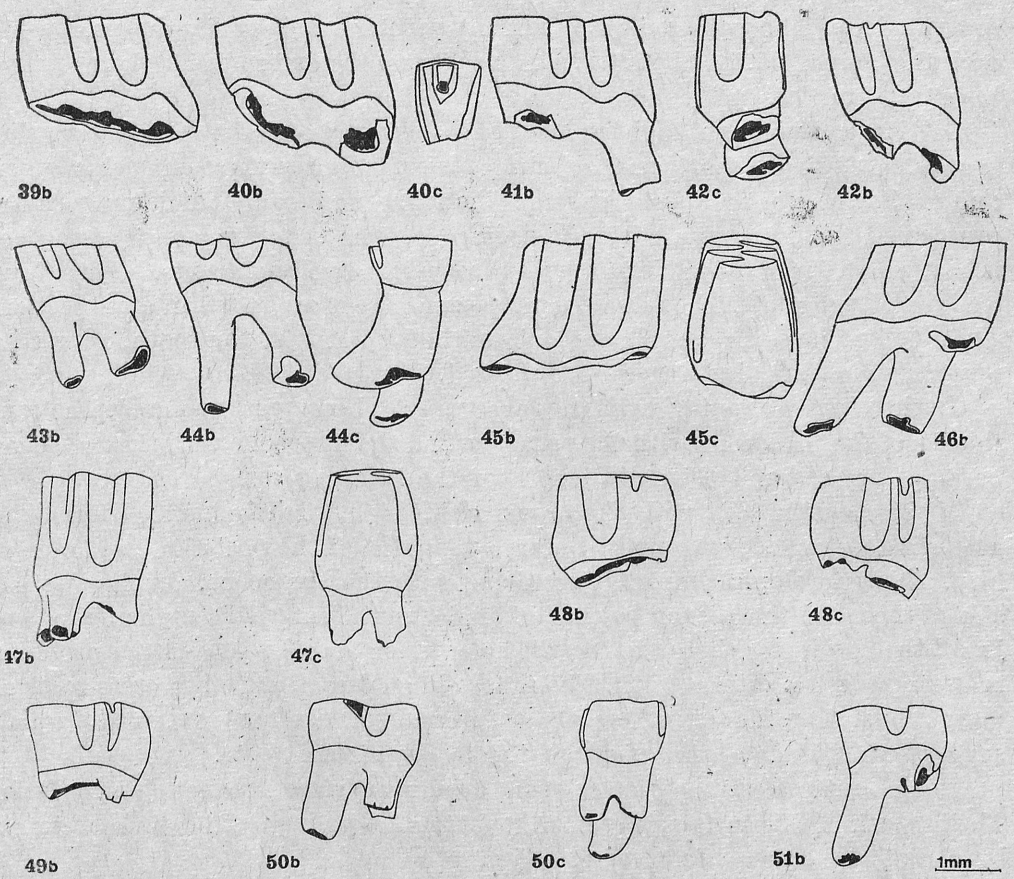


Figs. 39a—51a. *Prosomys insuliferus*, Antipovka, occlusal view of the molars. 39a—41a — m_1; 42a—44a — m_2; 45a—46a — m^1; 47a — m^2, 48a—51a — m^3

teeth the anterior loop (paraconid) with an enamel island. The enamel cone of this island reaches to about 1/3 of the height of the unworn crown. In middle stages of wear the island is oval in shape and of large dimensions. When 2/3 of the original height of the crown are worn, the island disappears.

When comparing specimens of different individual age it can be seen that in young teeth there is a shallow, additional re-entrant on the internal side of the paraconid. This re-entrant angle has no connection with the island and disappears when the teeth are worn more deeply. The length of the crown is greater in old than in young teeth, as a result of the greater length of the lower part of the crown. In very old teeth the roots are larger.

M_2 is of medium size. Its crown, distinctly inclined forwards, narrows in the upper part. It is composed of three triangles, of the paraconid and of posterior



Figs. 39b—51b. *Prosomys insuliferus*, Antipovka, buccal view of the same molars as in Figs. 39a—51a. 40c — fragment of m_1, the depth of the enamel island can be seen; 42c, 44a — posterior view; 45c, 47c, 50c — anterior view; 48c — lingual view

loop (hypoconid + posterolophid). The paraconid is confluent with the metaconid, the protoconid with the endoconid. The tooth has two re-entrants on each side. The roots are well developed. The anterior one is long, round in cross-section, its lower end inclined towards the buccal side of the mandible. Posterior root is massive, antero-posteriorly compressed and distinctly broader in the lower part. On older teeth it can be seen that it developed through the fusion of two roots. The form of m_2 proves that the lower incisor passes in the mandible lingually of the anterior root of this tooth and that the posterior root of m_2 is situated above the back of the incisor.

During the ontogenesis the pattern of the grinding surface of m_2 does not change much, only the breadth of this surface increases. With the development of m_2 the posterior root tightly embraces the back of the incisor. In very old teeth this root is somewhat reduced.

M_3 of small dimensions. The crown is distinctly inclined forward. The grinding surface is composed of three triangles, of the small paraconid and of the

anterior loop. The paraconid is confluent with the metaconif, the protoconid with the endoconid. On the internal as well as on the external side there are two re-entrant angles.

M^1 large, its crown slightly inclined backwards and distinctly narrowing towards the grinding surface. This surface is composed of three enamel triangles and of the anterior and posterior loop. The paracone broadly confluent with the protocone, the hypocone with the metacone. The anterior loop (anterocone) is best isolated. On each side of the tooth there are two re-entrants. M^1 has three well developed roots. The anterior and posterior root are round in cross-section. The middle one is situated buccally from the long axis of the tooth, nearer its posterior end, and is laterally compressed.

In the process of ontogenesis the salient angles become less pointed. The confluence of the protocone with the paracone and the hypocone with the metacone becomes greater and the total length of the grinding surface larger.

M^2 of medium size, with the crown quite high, slightly inclined forwards. The grinding surface is composed of two triangles, of the posterior and anterior loop. The anteroloph completely confluent with the protocone. On the internal side of the tooth there is one re-entrant angle, on the external size there are two. In all the specimens there are roots. The anterior buccal root and the posterior root are round in cross-section. The antero-lingual root is oval in cross-section, more robust than the two others. On its internal surface there is a groove, which suggests that it developed through the fusion of two roots.

During ontogenesis the pattern of the grinding surface does not change much. The breadth of this surface is greater in old than in young teeth and the anterior border of the crown becomes smoother.

M^3 small, its crown low, vertically situated. The pattern of the grinding surface is very complicated, particularly in adult specimens. In very young teeth the grinding surface is composed of two triangles and of the anterior and posterior loop. The anteroloph weakly developed and completely confluent with the paracone. The metacone originally well separated. Originally there are two re-entrants on each side of the tooth. Later, on the antero-internal and the postero-external re-entrant angles close, forming two enamel islands. M^3 has three well developed roots. The posterior root is largest, the two anterior ones small, with a tendency to fusion. However, in the studied material the tops of the anterior roots always remain free.

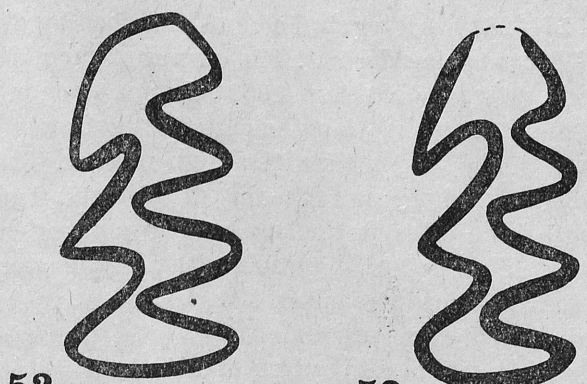
During ontogenesis the pattern of the grinding surface changes conspicuously. With the wear of one third of the original height of the crown the top of the postero-external re-entrant closes and forms an island. This large, oval island persists over a long period, nearly until the crown is quite worn down. The anterior island developes slightly later than the posterior one. It is formed by the closing of the end of the antero-internal re-rentrant angle. This anterior island is of short-duration and disappears when two-thirds of the original height of the crown is worn away. In our material a great variability in the pattern of the isolation of the islands can be seen, particularly of the posterior one. Sometimes

this island becomes closed very late, when two-thirds of the original height of the crown are already worn away, and when the anterior island has disappeared. Sometimes both islands close at the same time. In all specimens, however, the posterior island is larger and persists longer.

DISCUSSION

The material from Antipovka and Chugunovka shows no significant differences when compared with the typical series of *Prosomys insuliferus* from Podlesice, either in morphology, or in dimensions, and may be included in this species. Also the teeth of "*Promimomys insuliferus*" described by MICHAUX (1971, 1976) from Vendargues and from Canterrane in France have no characters pointing to a specific difference from the material from Poland and U.S.S.R. It is to be noted, that in Vendargues there were juvenile teeth present, which are absent from our collections.

For the determination of the systematic position of our materials it is necessary to discuss the genus *Promimomys* KRETZOI 1955, in which they were included by the majority of authors. This genus was set up by KRETZOI for the species



Figs. 52—53. Comparison of the occlusal view of m_1, of the holotype of *Promimomys cor* from Csarnóta (after KRETZOI 1955) (Fig. 52) with m_1 of a senile specimen of *Mimomys gracilis* from Węże, specimen MF/183/21 (Fig. 53)

Promimomys cor KRETZOI 1955, which was specified as its *typus generis*. *P. cor* is known from a unique specimen (small fragment of the mandible with m_1) which was found at the beginning of excavations in Csarnóta in Hungary on the surface of sediments accumulated during earlier diggings. The species was never found again and there is no material known besides the holotype. During later excavations in Csarnóta, executed after the description of *P. cor*, KRETZOI (1959, 1962) found in older layers a new, primitive form of the genus *Mimomys* F. MAJOR 1902, named by him *Cseria gracilis* KRETZOI 1959. The unique spec-

imen of *Promimomys cor* seems to be a senile specimen of *Cseria gracilis*. This is evident from the very low crown of m_1 and from the similarity of the morphology and dimensions *P. cor* to old specimens of *Cseria gracilis* e. g. from the locality of Węże in Poland (Fig. 52—53). This would make *Cseria gracilis* a junior synonym of *Promimomys cor* and the generic name *Cseria* KRETZOI 1959 (in general opinion a synonym of *Mimomys* or a valid name for its primitive subgenus) a junior synonym of *Promimomys*. If, however, the holotype of *Promimomys cor* is really a senile specimen, it is more advisable to put this name (and thus the generic name *Promimomys*) among the forms *incertae sedis*. The specific determination of the senile specimen of rooted *Arvicolidae* is uncertain, and the possibility that the holotype of *Promimomys cor* belongs to another small species of *Mimomys* cannot be excluded.

KRETZOI (1955) also included in the genus *Promimomys* another species, *Mimomys moldavicus* KORMOS 1932. The material of this form was collected by SIMIONESCU in Maluşteni in Roumania and first described by him (SIMIONESCU 1930) under the name *Arvicola pliocaenicus* MAJOR. SIMIONESCU (1930, p. 19—20, Figs. 26—28, Pl. III, Fig. 5) describes and illustrates two specimens: a mandible with m_1—m_2 (Fig. 26) and another one with m_1—m_3 (Figs. 27—28). They belong probably to two different species. The description and illustration of teeth represented in Fig. 26 are inadequate for exact determination. The second specimen, presented in Figs. 27—28, was later studied and described by KORMOS (1932) and is the holotype of *Mimomys moldavicus*. The crowns of the molars in it are very low, and, as already stated by KORMOS (1932), the specimen must be ontogenetically old. It is worth mentioning, that the older teeth of rooted *Arvicolidae* are more strongly fixed in the alveoli than the younger ones. That is why during earlier studies, when no washing and screening of sediments was used, mandibles with complete tooth-rows of senile molars were disproportionately numerous. *Mimomys moldavicus* has a robust mandible with short diastema, enamel fields strongly confluent, no cement in re-entrant angles and m_1 with a trace of an enamel island. Its dimensions are larger than those of *Prosomys insuliferus*. The exact determination of systematic position of *Mimomys moldavicus* is difficult, as stated already by KORMOS (1932).

In 1965 TOPACHEVSKY described from Kuchurgan in the Odessa region a mandible with a senile m_1 which, according to him, belongs to *Promimomys moldavicus*. M_1 of this specimen is strongly worn, its enamel is, however, rather thin and there is no trace of an enamel island on it. The anterior loop is slightly different from *M. moldavicus* from Maluşteni and in form approaches *Promimomys cor*. According to TOPACHEVSKY (1965) *P. cor* is a synonym of *P. moldavicus* and he erroneusly determines *P. moldavicus* as *typus generis* of the genus *Promimomys*.

Whatever the systematic position of specimens from Maluşteni and Kuchurgan (and this can be determined only when more material is available), it is of no significance on references to the validity of the genus *Promimomys*, because *P. cor* was explicitly determined by KRETZOI (1955) as its *typus generis*.

It is therefore clear, that the generic name *Promimomys* KRETZOI 1955 cannot

be used for the material from Podlesice, because the typical species of this genus is in all probability based on a senile specimen of a different systematic position. It should be remembered that *P. cor* was found in geologically much younger sediments than *Prosomys insuliferus*, in association with well differentiated typical *Arvicolidae*.

Table IV

Length of m_1 in different forms of *Prosomys* and *Promimomys* (in mm)

Species	Locality	Author	n	min	m	max
Prosomys insuliferus	Podlesice		15	1.91	2.43	2.65
„	Antipovka		5	2.25	2.37	2.55
„	Chugunovka		5	2.2	2.35	2.5
„	Vendargues	MICHAUX 1971	?	2.36	2.48	2.82
P. mimus	Mc Kay Reservoir	SHOTWELL 1956	1	—	1.9	—
„	Christmas Valley	REPENNING 1968	49	2.14	2.5	2.97
Promimomys microdon	Osztramos 9	JÁNOSSY 1974	1	—	±1.82	—
Promimomys cor	Csarnóta	KRETZOI 1955	1	—	2.9	—
Promimomys moldavicus	Maluşteni	KORMOS 1932	1	—	2.7	—
„	Kuchurgan	TOPACHEVSKY 1965	1	—	2.7	—

KRETZOI (1955), emphasizing the differences between the specimen from Csarnóta and those from Podlesice, created the generic name *Polonomys* for the latter. In 1968 REPENNING had the opportunity to compare directly the specimens from Podlesice with a rich material of *Prosomys minus* SHOTWELL 1956, known from two Hemphillian localities in Oregon, U.S.A. Thanks to the courtesy of Dr. C. REPENNING the authors were also able to compare the specimens of *P. mimus* from Christmas Valley in Oregon with their material. REPENNING (1968) found no generic differences between these materials and included both species in the genus *Promimomys*. As the name *Promimomys*, as stated above, cannot be used here, the generic name *Prosomys* SHOTWELL 1956 is the oldest available (*Polonomys* was described by KRETZOI in 1959 and is therefore its younger synonym) *.

The mandible of *Prosomys mimus* is, like the mandible of *P. insuliferus*, robust, with short diastema, but with typical characteristics of *Arvicolidae*. In both forms the height of the molar-crown is similar, the enamel in not differentiated, thick, without dentine tracks, cement is not present in re-entrant angles. Molars are rooted, the upper ones have three roots each, with identical localization and shape. There is an island on m_1, but in *P. mimus* it disappears

*One of the authors of the present paper (AGADJANIAN) is of the opinion that the differences between *Prosomys* and *Polonomys* are of generic order and prefers to use the designation *Polonomys insuliferus* for the European species.

earlier than in *P. insuliferus*. The proportions of particular teeth and the morphology of the grinding surface are similar in both species. In some specimens of m^2 in *P. mimus* the hypoconal complex is isolated from the anterior part of the crown (cf. REPENNING 1968, Fig. 9, no 7a), which was never stated in *P. insuliferus*. According to the description and in available specimens of *P. mimus* the anterior re-entrant angle of m^3 does not form an island, which developes as a rule in *P. insuliferus*. However, in both forms the posterior island on m^3 is large and long-lasting. It is hard to believe that so many common characters developed independently in these two species. *Prosomys mimus* and *P. insuliferus*, though specifically different, therefore undoubtedly belong to one genus.

JÁNOSSY (1974) described from the Middle Pliocene fauna of Osztramos Loc. 9 in Northern Hungary a new species, *Promimomys microdon* JÁNOSSY 1974. Only one damaged m_1 with a relatively high crown is known. The anterior loop, without enamel island, is slightly narrower than in *Prosomys insuliferus*. The dimensions of the tooth are also slightly smaller than those in *P. insuliferus*. *Promimomys microdon* is probably also a member of the genus *Prosomys*, but insufficient material makes the determination of its systematic position difficult. The faunal list of Osztramos Loc. 9 is similar to that of Podlesice but, according to JÁNOSSY (1974) it already includes a typical representative of the genus *Mimomys*, *M. silasensis* JÁNOSSY 1974.

From a fossil locality of similar age, Osztramos Loc. 1, two upper teeth of "*Polonomys* sp." were described.

In Chirgis-Nur in Mongolia DEVIATKIN and LISKUN (1966) note the presence of "*Promimomys* (?) sp.", but any description is lacking. From Ostraia Sopka in Siberia "*Promimomys* aut *Villanyia*" was mentioned by VANGENGEIM and ZAZHIGIN (1974). In another part of their paper the authors write about "*Promimomys (Cseria) gracilis*", which would suggest that they recognize *Promimomys* as a valid name for the forms generally included in the subgenus *Cseria*.

"*Promimomys*" without specific determinanation and description was mentioned from the Pliocene of Turkey: from Çalta (GINSBURG, HEINTZ, SEN 1974, SEN, HEINZT, GINSBURG 1974) and from Dinar-Akcaköy (TOBIEN 1973, 1974, BECKER-PLATEN et al. 1975). The authors of the present paper were able, thanks to the courtesy of Prof. Dr. H. TOBIEN, to study the material from Akcaköy. It represents undoubtedly a new species, different and maybe slightly more advanced than *Prosomys insuliferus*, but belonging to the same genus.

At the beginning of the Pliocene there appear among *Cricetidae* many forms with hypsodont teeth and a tendency to the formation of enamel loops on the grinding surface of the molars. Among these forms *Baranomys* KORMOS 1933 and *Microtodon* MILLER 1927 approach the genus *Prosomys* in their molar pattern. Of two better known species of *Baranomys* (maybe representing two genera), *B. kowalskii* KRETZOI 1962, which is known form the fauna of Podlesice, has a very short and simple m_3 and therefore is very different from *Prosomys insuliferus*. *B. loczyi* KORMOS 1933 from Late Pliocene and Earliest Pleistocene is more similar in its tooth pattern to *Prosomys*. Both forms of *Baranomys*, how-

ever, have mandibles without characteristics typical of *Arvicolidae* (REPENNING 1968) and are of very small dimensions. Finally, *Microtodon atavus* (SCHLOSSER 1924) from Ertemte in China (SCHAUB 1934) is also small (L m_1 1.9 mm) and its m_3 is similar to that of *Baranomys kowalskii*. For the determination of the systematic position of *Microtodon* further studies, especially concerning its mandibular structure, are essential.

In 1965 KRETZOI described two isolated molars discovered in Upper Pannonian during a boring in Jaszladany in Hungary and created for them a new species and genus *Pannonicola brevidens* KRETZOI 1965. According to KRETZOI this is the oldest representative of *Arvicolidae*. The teeth are deeply worn and evidently senile. If the teeth, as determined by KRETZOI, really represent m_2 and m_3, than their pattern is very different from that of *Promimomys*. The opinion expressed by KRETZOI (1955, 1965) that the most primitive *Arvicolidae* (*Promimomys* and *Pannonicola)* were brachyodont does not seem justified. Arvicolids developed from Cricetids through the adaptation to grinding of large amounts of the green parts of plants, which are hard and of low nutritive value. Therefore, already the Cricetids which were the ancestors of oldest Arvicolids were relatively hypsodont, as were the first forms of Arvicolids.

It is evident that the genus *Prosomys* existed as early as in the Lower and Middle Pliocene, before the appearance of diversified lines of true *Arvicolidae* (*Mimomys*, *Dolomys*, *Pliomys* etc.) over extensive territories of Europe, Asia Minor (and probably also central and northern Asia) as well as western part of North America. Its mandibular structure and molar pattern were typically arvicoline, but at the same time it had many primitive characteristics. Its origin and its role in the development of younger groups of *Arvicolidae* are not known. Opinions on these problems concern the genus *Promimomys*, but were based mainly on the material of *Prosomys insuliferus*, this being the best known. REPENNING (1968) was of the opinion that it may be ancestral to many evolutionary lines of *Arvicolidae*. According to CHALINE (1975) *Promimomys* (= *Prosomys)* is a direct ancestor of the genera *Dolomys* NEHRING 1898, *Pliomys* MÉHELY 1914 and *Mimomys* F. MAJOR 1902. In KRETZOI's opinion (1969) *Polonomys*, *Prosomys* and *Promimomys* are distinct genera and represent successive stages in the development of primitive *Arvicolidae*. MEIN (1975) described from Upper Vallesien in France a new species of *Cricetidae*, *Rotundomys bressanus* MEIN 1975 which has a tendency to the formation of enamel loops and to hypsodonty. It is MEIN's opinion that this form may be ancestral to *Promimomys* (= *Prosomys*). As usually with transient forms it is a matter of controversy whether they belong to an ancestral or a descendant group. The authors of this paper are of the opinion that *Prosomys*, with its numerous arvicolid characteristics, is best placed in the family *Arvicolidae*.

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STRESZCZENIE

W r. 1958 opisany został z Podlesic w Polsce nowy gatunek prymitywnych przedstawicieli *Arvicolidae*, *Promimomys insuliferus* KOWALSKI. Forma ta znaleziona została następnie w plioceńskich faunach Vendargues i Canterrane we Francji (MICHAUX, 1971, 1976). W ostatnich latach gryzoń ten został także znaleziony w miejscowościach Antipowka i Czugunowka w rejonie woroneżskim w europejskiej części ZSRR. Autorzy opisują materiał z Podlesic, Antipowki i Czugunowki. Podają również spisy fauny tych miejscowości (s. 30).

Prosomys insuliferus ma zęby trzonowe mezodontyczne, z grubą i słabo zróżnicowaną warstwą szkliwa, nie wykazującą przerw. W zatokach tych zębów brak cementu. Dolne zęby trzonowe mają po dwa, górne po trzy korzenie. M_1 ma jedną, m^3 zwykle dwie wysepki szkliwa. Morfologia żuchwy jest typowa dla *Arvicolidae*. Wymiary podano w tabelach I—III.

Materiały z Podlesic, Antipowki i Czugunowki, podobnie jak z Vendargues nie wykazują żadnych różnic i mogą być zaliczone do jednego gatunku. Autorzy wykazują, że rodzaj *Promimomys* KRETZOI 1955 należy uważać za *incertae sedis*. Jako *typus generis* tego rodzaju wyznaczony został przez KRETZOIA *Promimomys cor* KRETZOI 1955 z Csarnóta na Węgrzech. Holotyp i zarazem jedyny znany okaz tego gatunku jest według wszelkiego prawdopodobieństwa senilnym okazem m_1 jednego z pierwotnych gatunków z rodzaju *Mimomys* FORSYTH MAJOR 1902.

Materiał opisany z Podlesic i innych stanowisk nie wykazuje różnic rodzajowych w stosunku do gatunku *Promimomys mimus* SHOTWELL 1956 z Oregonu, chociaż zaznaczają się między nimi różnice gatunkowe. Ze względu na to forma europejska powinna nosić nazwę *Prosomys insuliferus* (KOWALSKI 1958). Do tego samego rodzaju należą także materiały opisane z Turcji pod nazwą „*Promimomys* sp.".

Stanowisko systematyczne prymitywnych *Arvicolidae*, opisanych pod nazwami *Mimomys moldavicus* KORMOS 1932, *Promimomys microtodon* JÁNOSSY 1974 i *Pannonicola brevidens* KRETZOI 1965, nie może być określone z pewnością, ponieważ ich znajomość opiera się na nielicznym i fragmentarycznym materiale.

Rodzaj *Prosomys* SHOTWELL 1956 był szeroko rozmieszczony w środkowym i zapewne dolnym pliocenie Europy, Azji i zachodniej części Ameryki Północnej. Przedstawia on najdawniejszą dobrze poznaną formę *Arvicolidae*, noszącą cechy pośrednie między typowymi rodzajami tej rodziny i wyspecjalizowanymi w podobnym jak *Arvicolidae* kierunku przedstawicielami *Cricetidae*.

РЕЗЮМЕ

В 1958 г. был описан новый вид примитивного арвиколида, *Promimomys insuliferus* KOWALSKI. Эта форма была позднее открыта в плиоценовых фаунах Вен-

держё и Контерране во Франции (Мишо 1971, 1976). В последние годы этот грызун был также найден в местонахождениях Антиповка и Чугуновка в Воронежской области Европейской части СССР. Авторы описывают материал из Подлесице, а также из Антиповки и Чугуновки. Приведены фаунистические списки упомянутых местонахождений (стр. 30).

Prosomys insuliferus имеет мезодонтные моляры, эмаль которых толстая и слабо дифференцированная, без перерывов. Цемент в наружных бухтах отсутствует. Зубы с корнями, нижние имеют по два, верхние — по три корня, M_1 имеет один, M^3 — обычно два эмалевых островка. Морфология нижней челюсти типично арвиколидная. Размеры см. в таблицах I, II, III.

Материал Подлесиц, Антиповки и Чугуновки также как Вендержё не показывает каких-либо видовых различий и может быть отнесен к одному виду. Авторы полагают, что род *Promimomys* Kretzoi 1955 следует считать как *genus incertae sedis*. Как *typus generis* этого рода был выбран Кретцоем *Promimomys cor* Kretzoi 1955 из Чарнота Венгрии. Голотип и одновременно единственный известный экземпляр этого вида представляет вероятнее всего старый M_1 одного из примитивных видов рода *Mimomys* Forsyth Major 1902.

Материал, описанный из Подлесиц и других местонахождений не имеет родовых отличий от вида *Prosomys mimus* Shotwell 1956 из Орегоны, хотя имеет отличия видового ранга. Поэтому европейская форма должна называться *Prosomys insuliferus* (Kowalski 1958). К этому роду относится также материал, который был описан из Турции под именем „*Promimomys* sp.".

Систематическое положение примитивных арвиколид, которые были описаны под названиями *Mimomys moldavicus* Kormos 1932, *Promimomys microtodon* Jánossy 1974, *Pannonicola brevidens* Kretzoi 1965 не может быть удовлетворительно определено, так как знание этих форм опирается на малочисленные и очень фрагментарные остатки.

Род *Prosomys* Shotwell 1956 был широко распространен в среднем и вероятно в нижнем плиоцене Европы, Азии и западной части Северной Америки. Он представляет древнейшую хорошо изученную форму арвиколид, которая занимает промежуточное положение между родами этого семейства и специализированными полевковидными хомяками.

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