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# *ALLOPHAIOMYS* OF THE SOUTHERN RUSSIAN PLAIN

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ABSTRACT

More than ten localities of different age with *Allophaiomys* remains have been discovered by the first author in the Dnieper, Don, Dniestr and Danube drainage basins and from the northern coastal regions of the Black and Azov Seas. These *Allophaiomys* sites are referred to different intervals of the Early Pleistocene. Morphological dental characteristics identify the earliest of these remnants as *A. deucalion* (Melekino and Khadzhimus /lower layer/ localities). Sediments with mammal bones from these localities display reversed paleomagnetic signatures. The fossiliferous layer of the Khadzhimus section is located below the Jaramillo paleomagnetic event.

More advanced *Allophaiomys* remains with positive enamel differentiation show different evolutionary stages. They were described earlier as *Allophaiomys pliocaenicus*. The earliest were found in sediments located just below the Jaramillo paleomagnetic event; the latest near the Brunhes-Matuyama boundary. A cluster analysis of these *Allophaiomys* remains was carried out on a number of m1 characters (size, enamel differentiation, length of anteroconid complex, degree of closure between AC 2 and T4-T5, shortest distance between BRA 3 and LRA 3) from various localities of the Russian Plain.

## INTRODUCTION

The last decades have produced a considerable amount of information on the Early Pleistocene small mammal localities in Eastern Europe with *Allophaiomys* remains. These localities are mostly concentrated in the southern part of the Russian Plain. They were examined by A. K. Agadjanian, L. P. Alexandrova, L. I. Rekovets, A. I. Shevchenko, A. F. Skorik, V. P. Sukhov, A. S. Tesakov, V. A. Topachevsky, and others. In the course of the Institute of Geography, Russian Academy of Sciences (RAS) expeditions the first author of this paper came across *Allophaiomys* fossils from about ten localities on the Russian Plain. Unfortunately, only a few remnants of *Allophaiomys* fossils were found.

All studied localities are dated between the middle Early and late Early Pleistocene. Their stratigraphic position was ascertained by direct geological and paleontological data and also by physical methods (TL and paleomagnetic). Detailed analysis of fossil small mammal dental morphology revealed important evolutionary progressions in many phyletic lineages of the arvicoline rodents, which in turn provided a basis for the establishment of small mammalian ages and subordinate phases.

Figure 1 shows the relative position of the localities with *Allophaiomys* remains discussed in this paper, and also some other localities previously investigated. The names of sites with *Allophaiomys* remains studied by the authors are underlined. The geological features of these localities were studied by different stratigraphers (Mikhailesku, 1990; Velichko et al., 1973, 1989; Chepalyga et al., 1989; Dodonov et al., in press).

## TERMINOLOGY

In this paper we use the terminology for the parts of occlusal surface of *Allophaiomys* molars introduced by van der Meulen (1973, 1974): L - length of molar; W, width of molar; AC 2, anterior cap; ACC, anteroconid complex; PL, posterior lobe; T1-T5, dentine fields of occlusial surface of molars; BRA, buccal re-entrant angle; LSA, lingual salient angle; B, shortest distance between AC 2 and T4 and T5; C, shortest distance between BRA 3 and LRA 3 angles; BRA, buccal re-entrant angle; BSA, buccal salient angle; LRA, lingual re-entrant angle; LSA, lingual salient angle. We also use the SDQ index after W. -D. Heinrich (1978), which shows the ratio between the enamel thickness on the posterior wall of molar salient angles and the anterior part of the salient angles. In this work we used the measurements of the enamel of three central angles of m1 (LSA2, LSA3, BSA2).

The first lower *Allophaiomys* molar is abbreviated as m1, the third upper molar as M3.

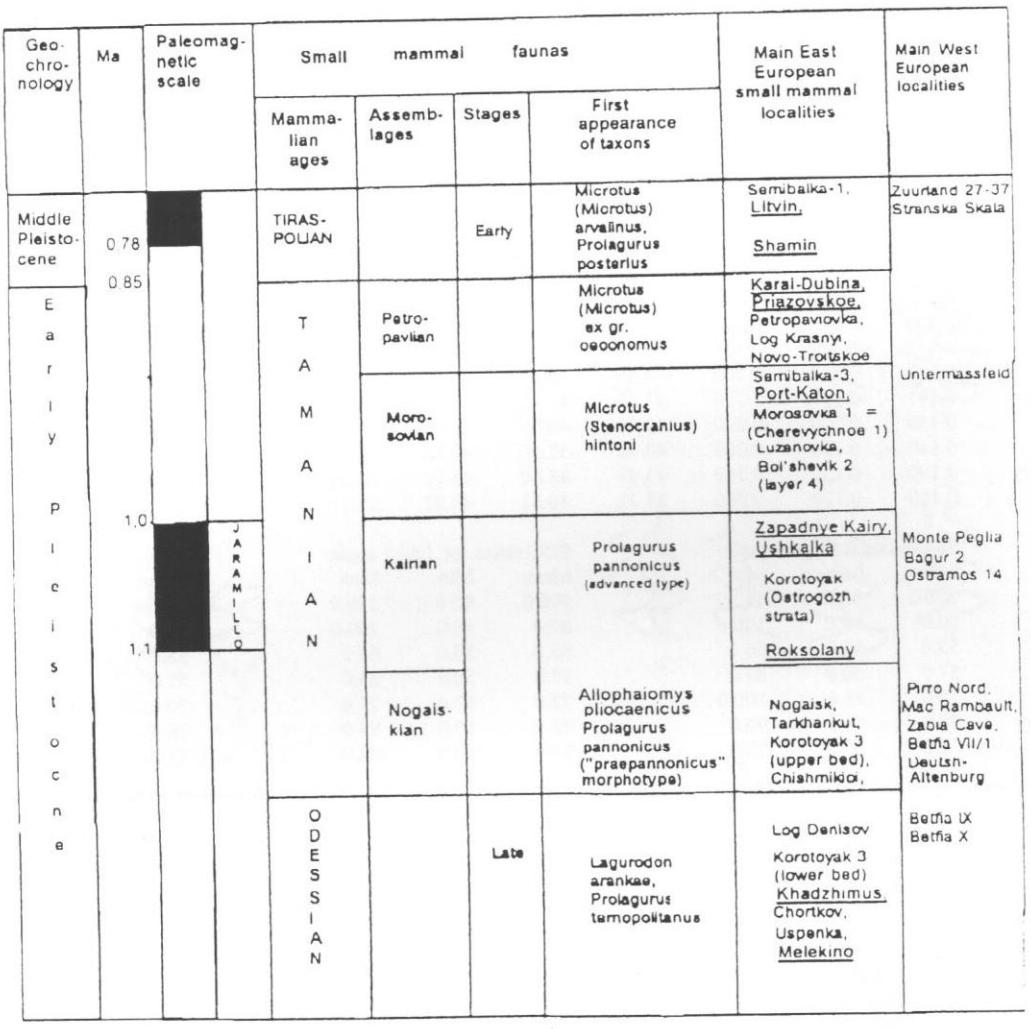


FIGURE 1. Stratigraphic position of Eastern European *Allophaiomys* localities.

## *ALLOPHAIOMYS DEUCALION* LOCALITIES

The earliest of investigated localities are Melekino (on the North Azov coastal region) and Khadzhimus (lower layer) (in the Dniestr lower drainage basin) (Mikhailesku, Markova, 1992; Markova, in press). The Khadzhimus locality was dated by TL to 1,300 +/- 350 ka BP (Kulikov, Chepalyga, 1985). The small mammal faunas from these localities were found under a loess-paleosol series of enormous thickness with numerous fossil soil horizons. The faunas include *Hypolagus* sp., *Ellobius* ex gr.*tancrei*, *Clethrionomys sokolovi*, *Pliomys episcopalis*, *Borsodia petenyii*, *B.fejervaryi*, *Prolagurus ternopolitanus*, *Lagurodon arankae*, *Mimomys savini*, *M.* ex gr.*reidi*, and *M. pitymyoides*. These localities fall into the Matuyama reversed polarity chron (Velichko et al., 1973). Khadzhimus fossiliferous deposits are located below the Jaramillo paleomagnetic event (Dodonov et al., in press; Figure 1).

The m1s of *Allophaiomys* from Khadzhimus (lower layer) and especially from Melekino have a rather simple structure and slightly negative enamel differentiation (Figure 2: 6-12; Table 1). An important feature of the species composition of these faunas is the presence of voles with arhizodont cementless molars such as *Prolagurus ternopolitanus* (Figure2.1) and *Lagurodon arankae* (Figure 2.2-4, 15-19). It should be also noted that the teeth of *Prolagurus ternopolitanus* were recovered from the upper layer of Khadzhimus locality.

*Allophaiomys* molars are characterized by SDQ values about 120-125, indicating negative enamel differentiation. The mean A/L ratio is about 42 (Table 1). The structure of the molars is rather simple. First

Table 1. Measurements (in mm) and indices of m1 for *Allophaiomys* from Russian Plain.

| Name | L | | | A | | | W | | | B | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max |
| Melekino | 2.594 | 2.520 | 2.700 | 1.126 | 1.100 | 1.180 | 0.870 | 0.800 | 0.950 | 0.240 | 0.200 | 0.250 |
| Port-Katon | 2.360 | 2.100 | 2.500 | 1.020 | 0.900 | 1.150 | 0.721 | 0.700 | 0.750 | 0.126 | 0.100 | 0.200 |
| Karai-Dubina | 2.610 | 2.500 | 2.750 | 1.140 | 1.050 | 1.200 | 0.880 | 0.800 | 0.950 | 0.183 | 0.100 | 0.300 |
| Ushakalka | 2.458 | 2.250 | 2.650 | 1.107 | 0.900 | 1.150 | 0.836 | 0.750 | 0.900 | 0.167 | 0.100 | 0.240 |
| Roksolany | 2.440 | 2.200 | 2.800 | 1.000 | 0.900 | 1.200 | 0.830 | 0.750 | 0.950 | 0.195 | 0.160 | 0.250 |
| Zapadnye Kairy | 2.500 | 2.450 | 2.650 | 1.137 | 1.100 | 1.150 | 0.910 | 0.900 | 0.950 | 0.197 | 0.150 | 0.260 |
| Nagornoe | 2.537 | 2.450 | 2.650 | 1.100 | 1.000 | 1.250 | 0.840 | 0.750 | 0.950 | 0.175 | 0.105 | 0.250 |

| Name | C | | | A/L | | | B/W | | | C/W | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max |
| Melekino | 0.152 | 0.120 | 0.180 | 42.37 | 40.20 | 44.02 | 27.66 | 23.53 | 31.25 | 21.42 | 12.63 | 22.50 |
| Port-Katon | 0.187 | 0.150 | 0.200 | 44.59 | 40.00 | 47.00 | 19.56 | 13.33 | 26.67 | 25.97 | 21.43 | 28.57 |
| Karai-Dubina | 0.191 | 0.100 | 0.270 | 43.65 | 41.82 | 46.00 | 17.38 | 11.76 | 37.50 | 18.92 | 11.11 | 30.00 |
| Ushakalka | 0.156 | 0.100 | 0.200 | 45.33 | 40.00 | 46.00 | 19.88 | 12.50 | 22.50 | 18.62 | 11.76 | 25.00 |
| Roksolany | 0.160 | 0.130 | 0.200 | 40.48 | 37.50 | 42.86 | 23.54 | 18.95 | 31.25 | 19.43 | 13.68 | 25.00 |
| Zapadnye Kairy | 0.190 | 0.150 | 0.250 | 45.07 | 43.40 | 46.00 | 21.68 | 16.67 | 28.89 | 21.02 | 16.67 | 26.32 |
| Nagornoe | 0.160 | 0.120 | 0.200 | 44.31 | 40.82 | 49.02 | 21.16 | 11.67 | 31.25 | 19.11 | 15.79 | 25.00 |

| Name | SDQ ratios for LSA3 angle | | | SDQ ratios for LSA2 angle | | | SDQ ratios for BSA2 angle | | |
|---|---|---|---|---|---|---|---|---|---|
| | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max |
| Melekino | 102.0 | 95.0 | 113.0 | 106.0 | 95.0 | 136.0 | 105.0 | 100.0 | 110.0 |
| Port-Katon | 80.0 | 50.0 | 100.0 | 80.0 | 50.0 | 100.0 | 78.0 | 50.0 | 105.0 |
| Karai-Dubina | 55.0 | 49.0 | 66.0 | 55.0 | 50.0 | 66.0 | 55.0 | 33.0 | 66.0 |
| Ushakalka | 57.0 | 50.0 | 83.0 | 57.0 | 50.0 | 83.0 | 57.0 | 50.0 | 83.0 |
| Roksolany | 75.0 | 66.0 | 100.0 | 72.0 | 67.0 | 77.0 | 70.0 | 67.0 | 75.0 |
| Zapadnye Kairy | 78.0 | 50.0 | 90.0 | 78.0 | 50.0 | 90.0 | 78.0 | 50.0 | 90.0 |
| Nagornoe | 71.0 | 50.0 | 83.0 | 71.0 | 50.0 | 83.0 | 71.0 | 50.0 | 83.0 |

lower molars have rounded a ACC with broadly confluent AC2, T4 and T5 (Figure 2). The C/W and B/W ratios are rather high (Table 1). These indices permit us to identify the *Allophaiomys* from Melekino and Khadzhimus sites as *A. deucalion*.

Species composition allows us to correlate Melekino and Khadzhimus (lower layer) faunas with the late phase of the Odessian faunal assemblage.

## *ALLOPHAIOMYS PLIOCAENICUS* LOCALITIES

More advanced *Allophaiomys*, *A.pliocaenicus*, were described from the Nogaisk section by W. Topachevski (1965). Specimens of *Prolagurus pannonicus* (morphotype "*praepannonicus*"), *Pliomys kretzoi* , *Borsodia fejervaryi* , *Lagurodon arankae*, *Eolagurus argiropuloi* , *Mimomys savini* and *M.reidi* were also found there. The Nogaiskian faunal assemblage was distinguished on the basis of this fauna (Topachevski, 1965).

The next stage in small mammal fauna evolution is marked by the appearance of a more progressive type of *Prolagurus pannonicus*. Faunas of this level are abundant on the Russian Plain. They have been found in the drainage basins of the Dnieper (the Zapadnye Kairy and Ushkalka localities), the Dniestr (the Roksolany locality) and the Don (the Korotoyak locality; Ostrogozh suite) (Markova, 1982; Mikhailesku, Markova, 1992; Iosifova, Krasnenkov, 1994; Rekovets, 1994). *Allophaiomys pliocaenicus* specimens from these localities are characterized by more advanced dental morphotypes (e.g., positevely differentiated enamel and shorter ACC: Figure 3; Table 1). *Eolagurus argyropuloi*, *Lagurodon arankae* and *Clethrionomys sokolovi* remain in existence. *Mimomys* is represented primarily by *M. savini* and *M. pusillus*.

By recent paleomagnetic data from the Roksolany locality (Dodonov et al., in press) these faunas are correlated with the interval just before the Jaramillo paleomagnetic event (1.0 -1.1 Ma). Based on paleontological materials the faunas of these levels can be referred directly to the Jaramillo paleomagnetic event (Iosifova et al., 1992). These faunas were described as the Kairian assemblage (Markova, in press). The *Allophaiomys* from Ushkalka and Zapadnye Kairy are characterized by an A/L index of about 45-46; a few m1s from Roksolany have a lower A/L ratio. All specimens have positive enamel differentiation with a mean SDQ index about 60-80 (Table 1). The Roksolany locality contains m1s of *Allophaiomys* with a rounded anterior cap lacking secondary complexity (Figure 3.1-3). The m1 of *Allophaiomys* from Ushkalka and Zapadnye Kairy, besides the analogous morphotypes (Figure 3.12, 13, 17, 18), include "praehintoni" and "ratticepoides"- like ones (Figure 3.14, 15, 16, 19-21). This reflects the process of divergence. Roksolany

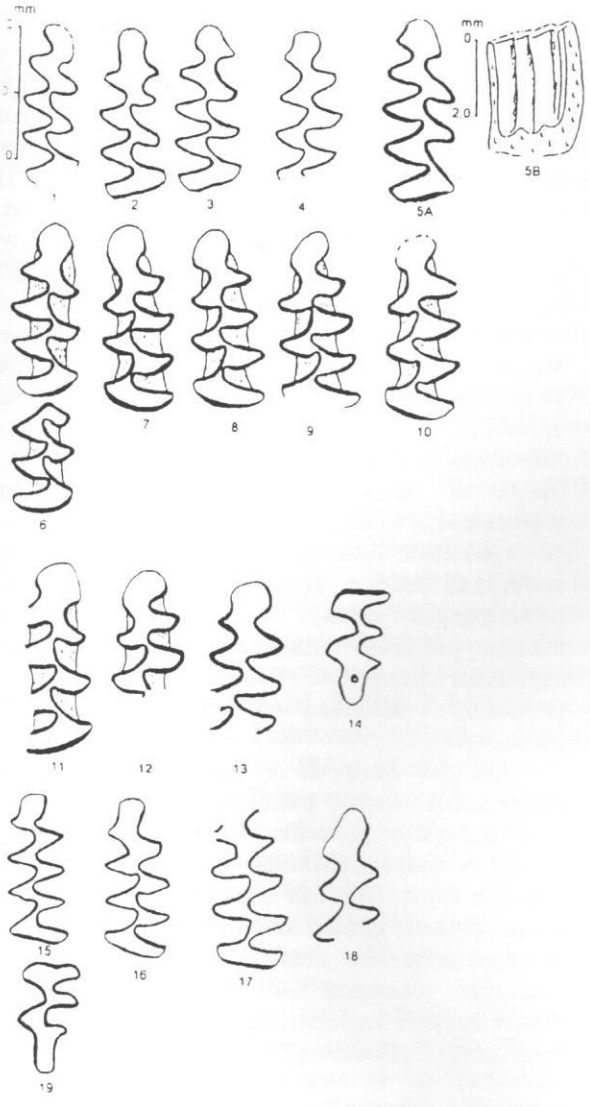

FIGURE 2. 1 - 10: molars of voles from Melekino locality. 1, m1 of *Prolagurus ternopolitanus*. 2-4, m1 of *Lagurodon arankae*. 5A, occlusial part; 5B, lateral part of m1 of *Pliomys episcopalis*. 6, m1 and m2 of *Allophaiomys deucalion*. 7-10, m1 of *Allophaiomys deucalion*. 11-18, molars of voles from the Khadzhimus locality (lower layer). 11, 12 , m1 of *Allophaiomys deucalion*. 13, m1 of *Borsodia petenyii*. 14, M3 of *Borsodia petenyii*. 15-18, m1 of *Lagurodon arankae*. 19, M3 of *Lagurodon arankae*.

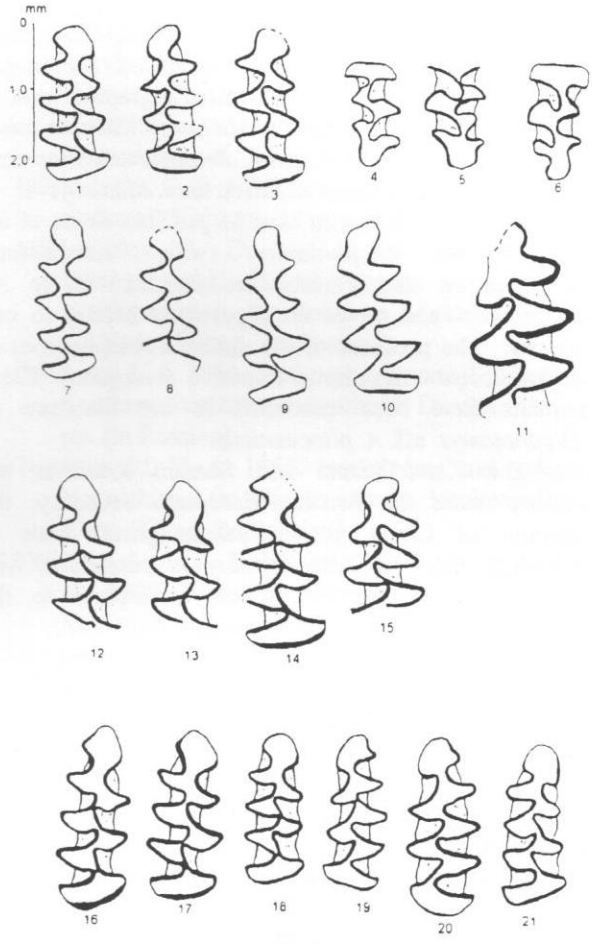

FIGURE 3. 1-11, molars of voles from Roksolany locality. 1-3, m1 of *Allophaiomys pliocaenicus*. 4-5, M3 of *Allophaiomys pliocaenicus*. 7, 8, m1 of *Prolagurus pannonicus*. 9, 10, m1 of *Lagurodon arankae*. 11, m1 of *Mimomys savini*. 12-15, m1 of *Allophaiomys pliocaenicus* from Zapadnye Kairy. 16-21, m1 of *Allophaiomys pliocaenicus* from Ushkalka.

*Allophaiomys* teeth have the most underived structure among the samples from the Kairian assemblage.

More advanced *Allophaiomys* with more complicated structure of the ACC ("praehintoni" and "praehenseli " morphotypes ) and A/L index about 45 were found in the Port Katon locality on Taman' Peninsula (Figure 4.5-8). A very extended anterior lobe characterized one m1 (Figure 4.4) (Markova, 1990). The SDQ index is about 80. Remains of the first *Terricola* appear here. The Nagornoe locality in the Danube drainage basin (excavations 9, 10) contains similar *Allophaiomys* remains ( Figure 4.11, 12, 14). One of the m1s from Nagornoe has "oeconomus" features (Figure 4.13). By species composition these faunas are referred to the so called "Morozovian" assemblage, described by L.P. Alexandrova (1976) and corresponding to a late stage of the Tamanian megafauna complex.

The most evolved *Allophaiomys* with "ratticepoides-oeconomus" (Figure 4.16, 17) and also "praehintoni" (Figure 4.18, 19) and "praehenseli" (Figure 4.20, 21) morphotypes of m1 were found in the Karai-Dubina locality (lower Dnieper basin), the Shamin locality (lower Don basin) and the Litvin locality on the Taman Peninsula ( Figure 4.16-21)(Markova, 1982, 1990). According to species composition, the first of them is referred to the Petropavlian assemblage. The Litvin and Shamin faunas were distinguished as early Tiraspolian (Markova, 1990). All the m1s feature rather

high values of the A/L ratio, and positively differentiated molar enamel with a mean SDQ ratio about 55 (Table 1). *Microtus* ex gr. *M. oeconomus* appeared for the first time at the stratigraphic level of the Karai-Dubina locality. *Mictotus (Stenocranius) hintoni*, *Eolagurus argiropuloi*, *Prolagurus pannonicus* (advanced type) are very abundant here. *Mimomys* is represented by *M. savini* and *M. pusillus*. Some of the remains of *Allophaiomys* (with "oeconomus" morphotypes) closely resemble *Microtus* ex gr. *M. oeconomus* and all of them probably belong to one species. The presence of the different morphotypes of *Allophaiomys* m1s shows intensive divergence. These remains have been described in the literature as *Allophaiomys* aff. *A. pliocaenicus*.

The Karai-Dubina and Shamin localities are located under the Brunhes-Matuyama boundary; the position of Litvin in the paleomagnetic scale is unknown. But the latter locality is connected with Chauda marine deposits, which correspond to the beginning of the Middle Pleistocene.

## DENDROGRAM ANALYSIS

An iterative procedure of cluster analysis allowed us to determine the basic groups of *Allophaiomys* remains from different localities, differing by the measured characteristics and morphological ratios of teeth (Figures 5, 6). The standardized value of Euclidian distance was used as a measure of similarity. Different combinations of the used attributes helped to reveal the most significant characters and to determine the degree of their information content. The most important characteristics are: ratios A/L, B/W and C/W (Figure 5), and also the SDQ indices (for LSA3, LSA2, BSA2 angles). Introduction of the measured characteristics: L, A, W, B, C as additional variables for the cluster analysis serves only to correct ratios (Figure 6). Structures of distinguished dendrograms are alike ( the maximum distances between characteristics are found for Melekino and Karai-Dubina materials). The differences in the dendrogram structures are connected with a scarcity of *Allophaiomys* materials from the localities described in this paper. The constructed dendrograms present a very general view.

## DISCUSSION

The above- discussed *Allophaiomys* materials from the southern Russian Plain covered the second half of the Early Pleistocene. Several small mammal assemblages correspond to this temporal interval and several types of *Allophaiomys* were revealed. The earliest of the fossils, from Melekino and Khadzhimus, are characterized by a simple structure of the anteroconid complex, with low values of A/L and negatively differentiated molar enamel. They were identified as *Allophaiomys deucalion*. In species composition of these localities *Mimomys pitymyoides*, *Mimomys savini*, *Mimomys reidi*, *Lagurodon arankae* and *Prolagurus ternopolitanus* are present. These localities are referred to the beginning of the second half of the Early Pleistocene. They are located below the Jaramillo paleomagnetic event, possibly about 1.3 Ma, by thermoluminescence (TL) data.

More advanced *Allophaiomys* were discovered in faunas with *Prolagurus pannonicus* of different evolutionary levels. Dental morphological features allow us to distinguish them as *Allophaiomys pliocaenicus*. The position of these localities is just below or directly equivalent to the Jaramillo paleomagnetic event (1.1- 1.0 Ma).

The latest localities with *Allophaiomys* remains correspond to the very end of the Matuyama paleomagnetic chron. The *Allophaiomys* molar morphotypes show considerable variation, suggesting significant divergence. These specimens have been previously described as *Allophaiomys* aff. *A. pliocaenicus*.

On the basis of a matrix of *Allophaiomys* characters the mostly parsimonious dendrograms have been elaborated. According to these dendrograms the Melekino and Karai-Dubina samples are placed on opposite sides. This fact substantiates our conclusion based on faunal species composition. The *Allophaiomys* materials from other sites fill an intermediate position. Indefinite placement of other samples in the dendrograms is explained by the scarcity of material from the studied localities.

## ACKNOWLEDGEMENTS

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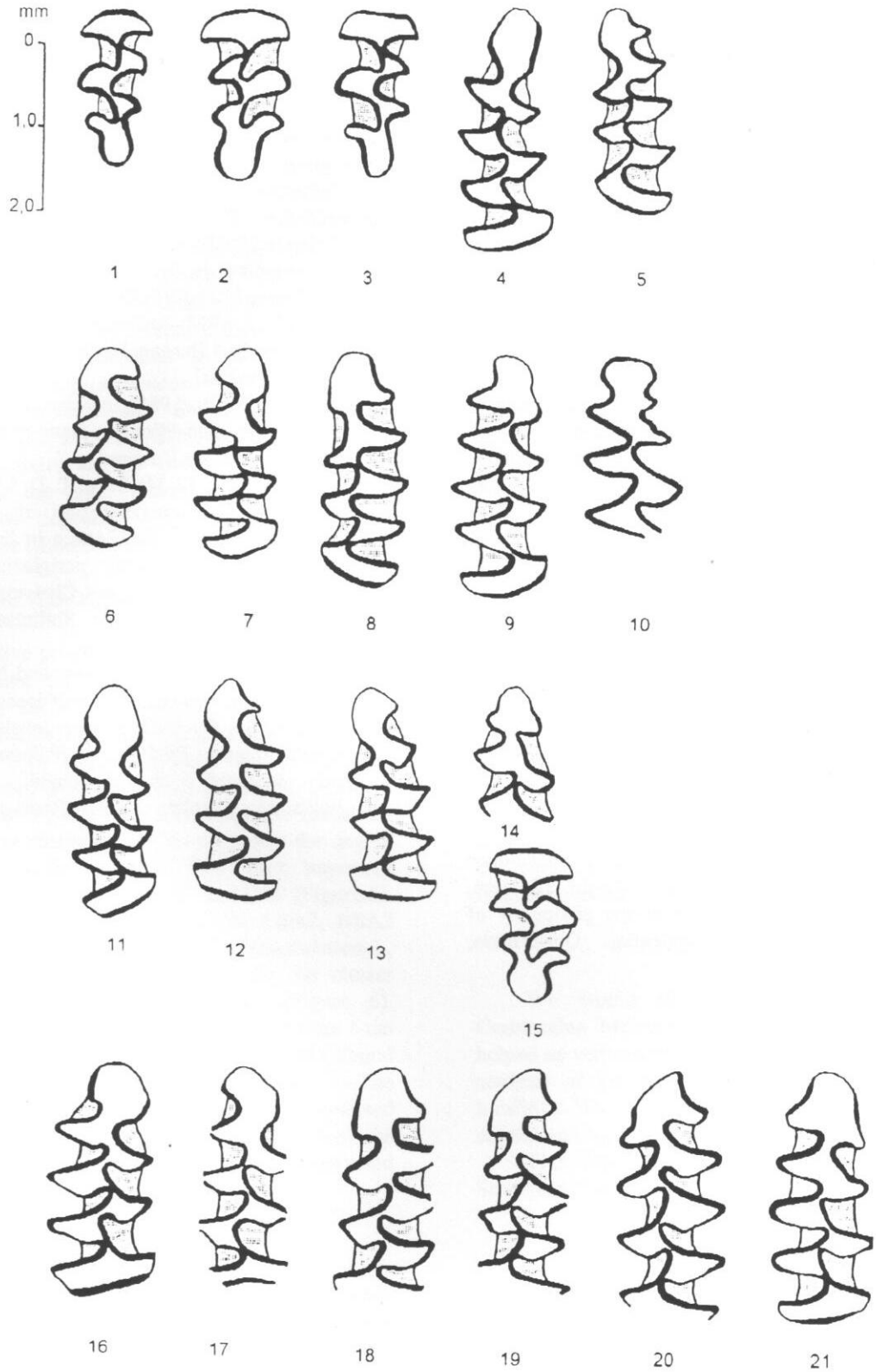


FIGURE 4. 1-10, molars of voles from Port-Katon locality. 1-3 , M3 of *Allophaiomys* aff. *A. pliocaenicus*. 4-8, m1 of *Allophaiomys pliocaenicus*. 9, m1 of *Microtus (Terricola )* sp. 10, m1 of *Borsodia petenyii*. 11-15, molars of *Allophaiomys* aff. *A. pliocaenicus* from N 11-14, m1. 15, M3. 16-21, m1 of *Allophaiomys* aff. *A. pliocaenicus* from Karai-Dubina.

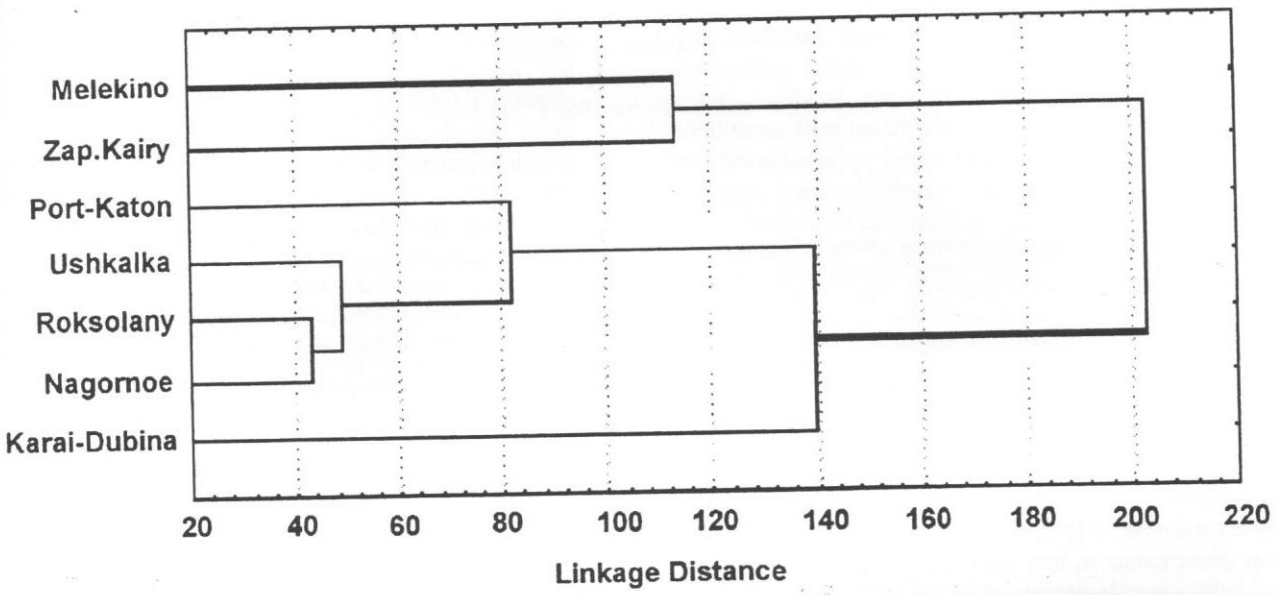


FIGURE 5. Dendrogram for the various *Allophaiomys* assemblages from the Russian Plain (based on A/L, B/W, C/W ratios) (Ward's method, Euclidean distances).

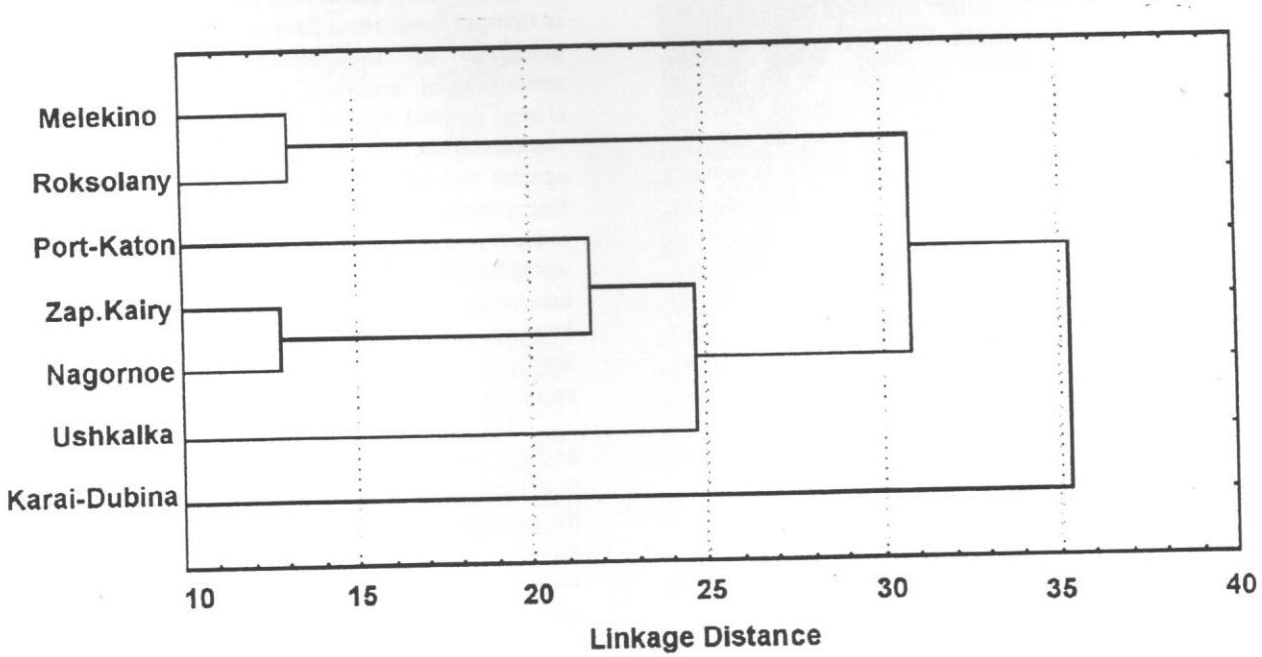


FIGURE 6. Dendrogram for the various *Allophaiomys* assemblages from the Russian Plain (based on L, A, W, B, C, A/L, B/W, C/W and SDQ ratios for LSA3, LSA2, BSA2) (Ward's method, Euclidean distances).