

PHENETIC STUDIES OF THE SPECIES *TALPA EUROPAEA* L. IN LITHUANIA

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Summary. Seventeen non-metric features of the mole skull with 40 variants of these features have been determined. Dependence of non-metric features of the mole skulls on age and sex has been established: three features (No2; No4; No5) are related to age and five features (No3; No7; No10; No14; No17) depend on sex. Nine working phenetic features of the mole skull with 20 variants have been determined. It has been elucidated that the phenetic structure of moles is determined by natural factors. The impact of river barriers and the Nemunas glacier on the formation of the population-phenetic structure of Lithuanian moles has been established. Having studied the phenetic structure of the mole subpopulations, the earliest origin of Puvočiai No1 subpopulation was established. The results obtained by means of the phenetic research method showed that phenetic distances were determined by the development of the historic changes in a landscape. No reliable correlation between a geographical distance among the samples and phenetic similarity of moles in a geochronological space were established ($p > 0.05$). It was elucidated that the population structure of the moles (*Talpa europaea*) was determined by a complex of natural factors in Lithuania.

Keywords: *Talpa europaea*, mole, skull, phenetic structure, population.

FENETINIAI RŪŠIES *TALPA EUROPAEA* L. TYRIMAI LIETUVOJE

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Santrauka. Išskirta 17 nemetrinių kurmių kaukolės 40 požymių variantų. Nustatyta kurmių kaukolių nemetrinių požymių priklausomybė nuo amžiaus ir lyties: trys požymiai (№2; №4; №5) susiję su amžiumi, o penki požymiai (№3; №7; №10; №14; №17) priklauso nuo lyties. Nustatyti 9 darbiniai 20 variantų fenetiniai kurmių kaukolės požymiai. Išaiškinta, kad kurmių fenetinę struktūrą apsprendžia skirtingi gamtiniai veiksniai. Nustatyta upių barjerų bei Nemuno ledyno įtaka Lietuvos kurmių populiacinės-fenetinės struktūros formavimuisi. Ištyrus fenetinę kurmių subpopuliacijų struktūrą, nustatyta ankstyviausia Puvočių №1 subpopuliacijos kilmė. Rezultatai, gauti fenetiniu tyrimo metodu parodė, jog fenetines distancijas apsprendžia istorinių kraštovaizdžio pokyčių raida. Patikimos geografinio atstumo koreliacijos tarp imčių ir fenetinio kurmių panašumo geochronologinėje erdvėje nustatyta nebuvo ($p > 0,05$). Išaiškinta, jog kurmių (*Talpa europaea*) populiacinę struktūrą Lietuvoje apsprendžia gamtinių veiksnių kompleksas.

Raktažodžiai: *Talpa europaea*, kurmis, kaukolė, fenetinė struktūra, populiacija.

Introduction. Close populations are similar according to a larger number of features, and they differ in a smaller number of features. Similar features can intermittently differ in different parts of the natural habitat of the species but then they are most often of an independent origin, and have appeared in a common gene pool of the species due to different mutations (Яблоков, Ларина, 1985). Shubin and Sedakova investigate frequency of phene variants of the Siberian mole in Tomsk and Krasnojarsk regions in the article “Epigenetic polymorphism of the skull of the Siberian mole (*Talpa altaica*)”. They distinguish two features: the number of premolar teeth in the upper jaw and the number of openings on the palatine bone. The asymmetric phenetic research method is used in this work: the variants of the same feature of the left and right sides of the skull are compared (Шубин, Седокова, 1980). Having investigated 466 common moles a wide morphometric geographical variety of the jaw (mandibulare) was established and four phenetic clusters were distinguished: France-Spain, Central Europe, Italy and England. They

state that appearance of these phenetic groups has been influenced by the geographical position and climate, and they relate the formation of the populations to the withdrawal of ice fields of the last icing. All these investigations form a constituent part of larger biogeographical investigations carried out with various species of vertebrates spread in Europe. Moles are especially popular in the said investigations because components of their skeleton are noted for conservatism (Loy, Corti, 1996). The statement that geographically close populations are also related phylogenetically should not be treated as a rule. The process of evolution is so diverse that sometimes geographically close groups of individuals can form due to different micro-evolutionary processes inside the species. Having thoroughly studied and selected the phenes it is possible to distinguish not only one but also entire groups (complexes) of populations of a different rank. The phenogeographical diversity of the species can be influenced by biotic and abiotic factors (Berry, 1964). Phenetic differentiation of common moles in Lithuania

has not been studied yet.

The aim of the work is to establish the spatial – phenetic structure of moles (*Talpa europaea*) in Lithuania.

Materials and methods. Non-metrical features and their variants (phenes) were distinguished by means of the A. Ulevičius (1993) method, which the author applied in his work “The formation of the beaver (*Castor fiber*) population and the spatial-phenetic structure in Lithuania”. First of all, a search for features was conducted randomly choosing from 12 to 21 skulls from the total samples. This number was taken because a too large number

of skulls would overload and burden the visual memory of a researcher, and a too small number of them would fail to reveal a large part of the range of a change in the feature. A total of 281 specimens (12 – 33 specimens in each site) of the *Talpa europaea* from 14 ecologically different localities (Kamajai, Šilutė, Salantai, Vilūnai, Pašvinė, Joniškis, Rusnė, Šeškinės ozas, Puvociiai №1, Kairėnai, Žuvintas, Kupiškis, Puvociiai №2, Šakiai) were taken. Moles were investigated from April to August. The specimens were caught with cone traps. Traps were checked once a day. Only undamaged skulls with clearly visible structures were analysed (Fig.1).

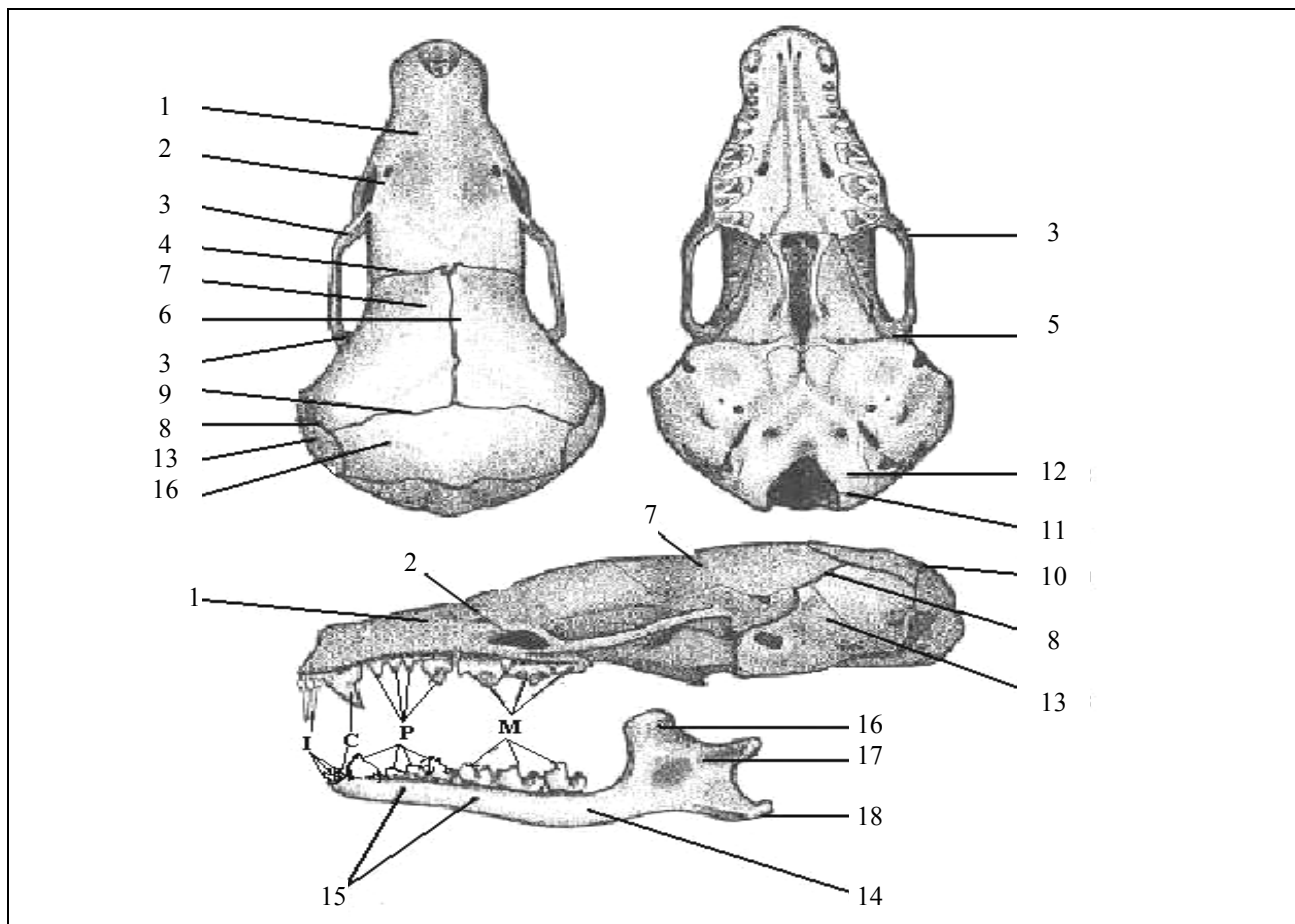


Fig. 1. The skull of a mole (*Talpa europaea*) (The Fauna of Lithuania, 1988):

1. the upper jaw (*maxillare*); 2. the suborbital opening (*foramen infraorbitale*); 3. the cheekbone (*jugale*); 4. the seam of the frontal bone of the upper jaw (*sutura maxillae frontalis*); 5. the lower jaw bone squamosum (*squamosum*); 6. the frontal bone seam (*sutura frontalis*); 7. the frontal bone (*frontale*); 8. the seam of the ear-drum of the frontal bone (*sutura fronto tympanicum*); 9. the seam of the parietal bone of the frontal bone (*sutura fronto parietalis*); 10. the side bone of the skull (*parietale*); 11. the great hole of the occiput (*foramen magnum*); 12. knuckles of the occiput (*condyli basioccipitale*); 13. the ear-drum (*tympanicum*); 14. the lower jaw (*dentale*); 15. genial holes (*foramen mentale*); 16. the coronary appendix (*processus coronoideus*); 17. the articular appendix (*processus articularis*); 18. the angular appendix (*processus angularis*); I – the incisors (*incisivi*); C – the canine teeth (*canini*); P – the premolar teeth (*praemolares*); M – the molar teeth (*molares*).

After that some structure of the skull is chosen and checked whether it is the same in all the skulls. If the structure has at least a couple of alternative variants, these variants are treated as variants of the working feature. Then all the skulls are reviewed and it is checked whether

there are no any other alternative variants. If there are some, these variants of the features are also included in a further analysis. Now we have a distinguished feature with all its variants and can review the distribution of the variants in all the samples. Each sample from different

regions is reviewed several times and it is counted how many skulls in these samples have one or another variant of the feature.

The non-metric dependence on the skulls on age and sex is checked by means of the Životovski test. The test of dependence of the features on age is carried out only between adult individuals because sexual dimorphism reveals itself in the groups of older age. The features that depend on sex and age are not included in a further analysis. The test by Životovski is used to determine the phenetic distance of the value when comparing two samples. This method is based on the values of the similarity indicator (r) and the identity criterion (I). The similarity indicator shows the phenetic similarity between two samples and is calculated according to the following formula:

$$r = \sqrt{p_1q_1} + \sqrt{p_2q_2} + \dots + \sqrt{p_mq_m},$$

where p_1, p_2, \dots, p_m is the m phene frequencies in i – the first sample of non-metric parameters ($p_i < 1$), and q_1, q_2, \dots, q_m is frequencies of the same m phene in i – the second sample of non-metric parameters ($q_i < 1$). If samples are compared according to the k complex of non-metric features, r is calculated in the following way:

$$r = (r_1 + r_2 + \dots + r_k)/k.$$

The identity criterion is used to assess statistical reliability of phenetic distances. It is calculated as follows:

$$I = 8n_1n_2(1 - r - (p_0 + q_0)/4)/n_1 + n_2,$$

where n_1 and n_2 are values of the samples being compared; p_0 is the sum of frequencies of those phenes, which are expressed in the first sample, and q_0 – analogously – is the sum of frequencies of those phenes, which are expressed in the second sample only. The identity criterion I is distributed as χ^2 criterion with degrees of freedom $df = m - 1$. If I is used for a pair comparison of the samples according to the k complex of features, I is defined as:

$$I = I_1 + I_2 + \dots + I_k$$

Then the degrees of freedom are calculated in the following way:

$$df = m_1 + m_2 + \dots + m_k - k$$

Phenetic distances between the samples are determined according to both the individual features and according to a complex of features. The r values obtained according to the complex of features show the similarity between the samples, and the values of the identity criterion – I – indicates phenetic distances between the samples under study.

The programme STATISTICA is used to compare the samples.

Results and discussion. *Non-metric features of the mole skull.* A total of 17 non-metric features of the mole skull with 40 variants of these features (phenes) were distinguished. The majority of features (13) have two alternative variants, two features have three phenes and two features have four phenes. The greatest number of features was distinguished on the basis of differences in the bones, their joints, the relief and the form of openings (9

features). On the basis of the position of some structures of the skull with respect to others, seven features were distinguished, and only one feature was distinguished on the basis of the presence-absence of the openings. The majority of these features are localised in the upper part of the skull and on the lower jaw.

Localisation of the distinguished non-metric skull features and their variants is represented in figures 2 and 3.

The following non-metric skull features and their variants were distinguished and analysed:

1. The form of the protrusion on the front part of the upper jaw (*os maxillare*) (the view from above):

1.1. The protrusion is bent obliquely forward; 1.2. The protrusion is turned down backwards.

2. The form of the protrusion on the back part of the upper jaw (*os maxillare*) (the view from above):

2.1. “The diamond”; 2.2. “The triangle”; 2.3. “A small diamond-shaped arrow”; 2.4. “A large arrow”.

3. Position of the protrusion on the back part of the upper jaw (*os maxillare*) with respect to the seam (*sutura maxillae frontalis*) (the view from above):

3.1. Does not reach the seam; 3.2. Reaches the seam.

4. The form of the median seam (*sutura maxillae frontalis*) of the upper jaw and the frontal bone (the view from above):

4.1. The seam is straight; 4.2. The seam is bent in the direction of the upper jaw; 4.3. The seam is bent in the direction of the frontal bone.

5. The position of the protrusion on the frontal bone (*os frontale*) with respect to the seam (*sutura frontalis*) of the frontal bones. The point of the protrusion divides the seam into two parts (the view from above):

5.1. The back one is shorter than the front one; 5.2. Both parts are almost equal.

6. The form of the part of the median seam (*sutura fronto parietalis*) of the frontal bone (*os frontale*) and the parietal bone (*os parietale*) (the view from above):

6.1. The seam is straight; 6.2. The seam is with a round distal bend; 6.3 The seam is with a sharp distal bend; 6.4 The seam with the “M-letter-shaped” distal bend.

7. The position of the protrusion on the frontal bone (*os frontale*) with respect to the seam of the parietal bone of the frontal bone (*sutura fronto parietalis*) (the view from above):

7.1 The protrusion does not adjoin the seam; 7.2. The protrusion adjoins the seam.

8. The seam of the frontal-parietal bone (*sutura fronto parietalis*) joins the seam of the ear-drum of the frontal bone (*sutura fronto tympanicum*) (the view from above):

8.1. The joining point has moved behind the turn of the seam of the parietal bone of the frontal bone (*sutura fronto parietalis*); 8.2. The joining point is at the turn of the seam of the parietal bone of the frontal bone (*sutura fronto parietalis*).

9. The position of the additional suborbital opening with respect to the main suborbital opening (*infraorbitale*) (the view from above):

9.1. The additional opening is above the main suborbital opening (*infraorbitale*); 9.2. The additional opening is

in front of the main suborbital opening (*infraorbitale*).

10. The form of the upper edge of the great hole of the occiput (*foramen magnum*) (the view from below):

10.1. The edge is even; 10.2. The edge is with a bend.

11. The form of the bottom edge of the great hole of the occiput (*foramen magnum*) (the view from below):

11.1. The edge is even; 11.2. The edge is with a bend.

12. The position of the frontal genial hole (*foramen mentale*) with respect to the front of the premolar (pm_1) tooth (the view from below):

12.1. In front; 12.2. At the back.

13. The number of the genial holes (*foramen mentale*) (the view from the side):

13.1. Two; 13.2. Three and more.

14. The position of the back genial hole (*foramen*

mentale) with respect to the first molar tooth (M_1) (the view from the side):

14.1. Near the middle of the tooth; 14.2. At the front of the tooth; 14.3. At the back of the tooth.

15. The form of the top of the coronary appendix (*processus coronoideus*) (the view from the side):

15.1 There is a hook-shaped protrusion; 15.2. There is no protrusion.

16. The form of the upper edge of the angular appendix (the view from the side):

16.1. With a bend; 16.2. Without a bend.

17. A socket on the proximal part of the lower jaw (*os mandibulare*) (the view from the side):

17.1. A socket consists of two parts; 17.2. An integral socket.

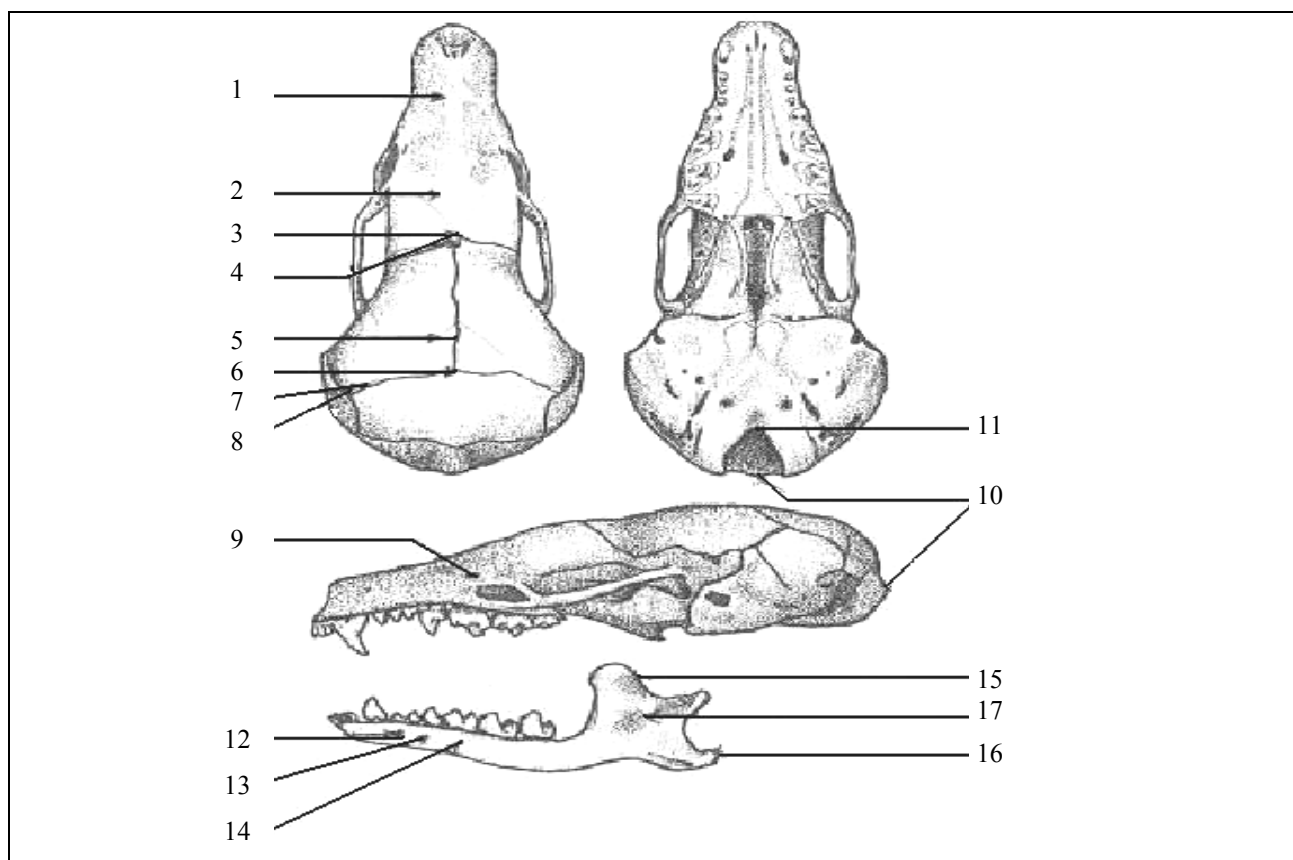


Fig. 2. Localisation of non-metrical features in the mole (*Talpa europaea*) skull:

1. The form of the protrusion on the front part of the upper jaw (*os maxillare*); 2. The form of the protrusion on the back part of the upper jaw (*os maxillare*); 3. Arrangement of the back part of the upper jaw (*os maxillare*) with respect to the seam (*sutura maxillae frontalis*); 4. The form of the median seam of the upper jaw and the frontal bone (*sutura maxillae frontalis*); 5. The position of the protrusion on the frontal bone (*os frontale*) with respect to the frontal bone seams (*sutura frontalis*). The point of the protrusion divides the seam into two parts; 6. The form of the median seam (*sutura fronto parietalis*) of the frontal bone (*os frontale*) and the parietal bone (*os parietale*); 7. The position of the protrusion on the frontal bone (*os frontale*) with respect to the seam of the parietal frontal bone (*sutura fronto parietalis*); 8. Joining of the frontal-parietal bone seam (*sutura fronto parietalis*) with the ear-drum of the frontal bone (*sutura fronto tympanicum*); 9. The position of the additional suborbital opening with respect to the main suborbital opening (*infraorbitale*); 10. The form of the upper edge of the great hole of the occiput (*foramen magnum*); 11. The form of the lower edge of the great hole of the occiput (*foramen magnum*); 12. The position of the front genial hole (*foramen mentale*) with respect to the front of the second premolar (pm_1) tooth; 13. The number of genial holes (*foramen mentale*); 14. The position of the back genial hole (*foramen mentale*) with respect to the first molar tooth (M_1); 15. The form of the point of the coronary appendix (*processus coronoideus*); 16. The form of the upper edge of the angular appendix (*processus angularis*); 17. A socket on the proximal part of the lower jaw (*os mandibulare*).

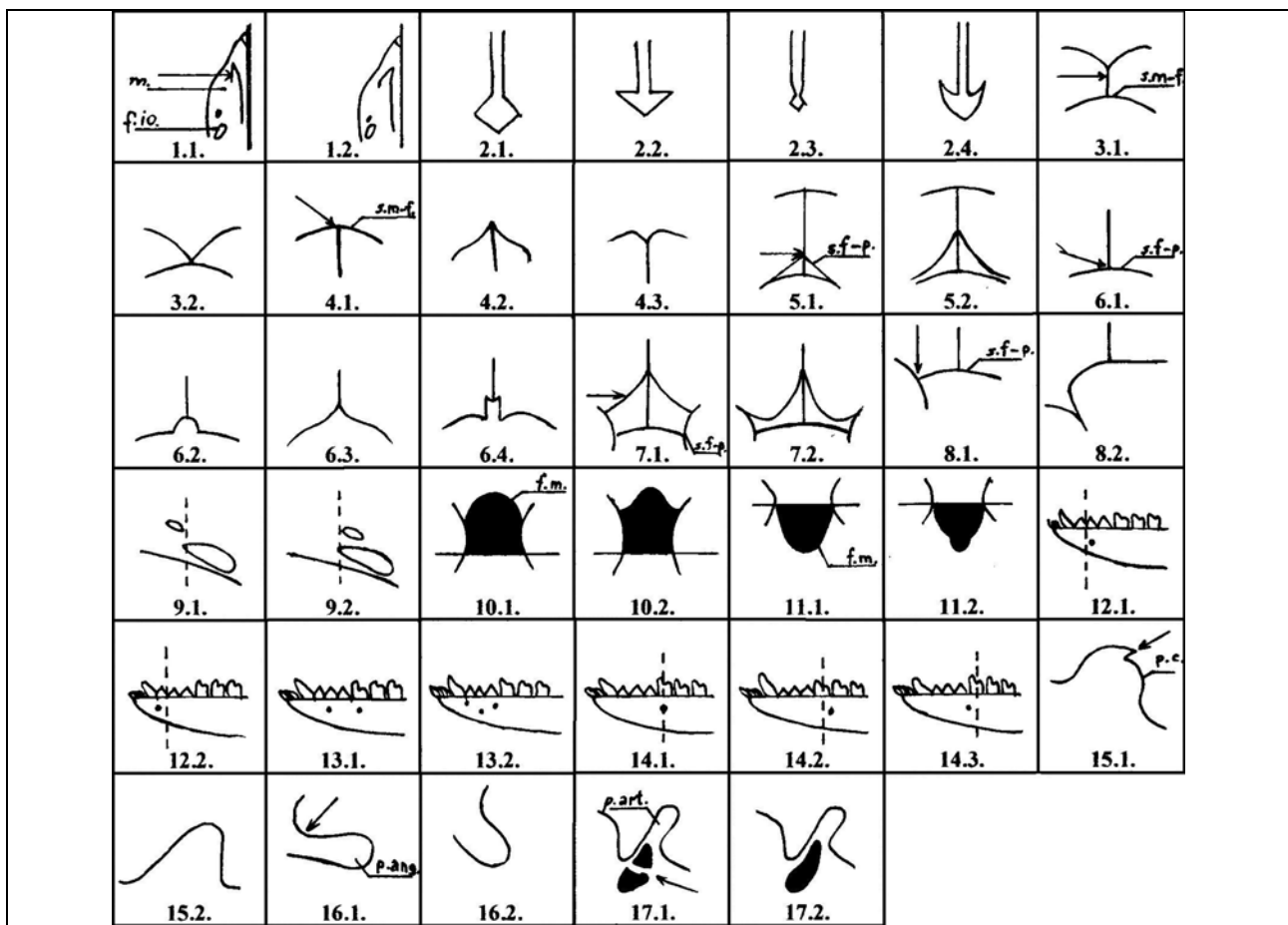


Fig. 3. Variants of non-metrical features of the mole (*Talpa europaea*) skull:

m. – os maxillare; f. io. – foramen infraorbitale; s. m – f. – sutura maxillo – frontalis; s. f – p. – sutura fronto – parietalis; s. f – t. – sutura fronto – temporalis; f. m. – foramen magnum; p. c. – processus coronoideus; p. ang. – processus angularis; p. art. – processus articularis

Dependence of a non-metric change on age and sex.

Dependence of non-metric features of the mole skull on age and sex was established.

It was established that features No. 2; No. 4; No. 5 are related to age therefore these features are not included in a further analysis (Table 1).

It was established that features No.3; No.7; No.10; No.14; No.17 are related to sex therefore they were not included in a further analysis (Table 2).

8 out of 17 features depend on age or sex therefore a further analysis was carried out on the basis of the remaining 9 features.

Frequencies of the variants of non-metric features in the locations studied. Thus nine features were established (No.1; No.6; No.8; No.9; No.11; No.12; No.13; No.15; No.16) that do not depend on age and sex, and are considered to be working ones. All these features, with the exception of No. 6, have two alternative states of the feature each, and feature No. 6 has four alternative states of the feature. On the basis of these features the samples are compared. The distribution of variants of working features in the samples is presented in Table 3.

It was established that variant 2 (No.1(2) phene) of

feature No.1 was most rare and it was not discovered in seven (50.0 % of the studied samples) samples that have been studied: in Salantai, Pašvinė, Joniškis, Šakiai, Vilūnai, Šeškinės Ozas and Puvočiai No.2. Phene No.11(1) was also quite rare and it was not found in the individuals of six (42.9 %) studied samples (Salantai, Pašvinė, Joniškis, Šakiai, Vilūnai and Kamajai). Phene No.9(1) was not discovered in three (21.4 %) samples (Salantai, Joniškis and Puvočiai No.2). Phenes No.6(3) and No.11(2), No.12(1), No.16(2) were not discovered respectively in the samples of Puvočiai No.2, Kamajai and Joniškis. Phenes of features No.8, No.13 and No.15 were discovered in all three samples. It should be noted that populations of Puvočiai No.1, Žuvintas, Kupiškis, Šilutė and Rusnė are quite closed and they have been affected by a long-term isolation because frequency of rare morphs, as compared with those in other samples, is smallest. The smallest number of phenes (16 out of 20 possible variants) was found in the samples of Joniškis, which is most probably related to a drift of the genes, which determined inheritance of the above-mentioned phenotype features or to a small density of the population. The samples of Salantai and Joniškis are most similar by the frequencies

of three features (No.1, No.9, No.11), and those of Pašvinė, Šakiai and Vilūnai – by features No.1 and No.11 (Table 3). The sample of Puvočiai No.2 corresponds to the samples of Salantai and Joniškis according to the frequencies of two features (No.1, No.9), Pašvinė, Šakiai, Vilūnai and Šeškinės Ozas – according to the frequencies of feature No.1, the sample of Kamajai corresponds to the samples of Salantai, Joniškis, Pašvinė, Šakiai and Vilūnai

according to the frequencies of feature No.11. The results obtained allow the conclusion to be drawn that the samples of Salantai and Joniškis are closest according to the largest number of features and are closely related because close populations are similar in a larger number of features (Berry, 1964). The geographical distance between them is not great (126 km) and there are no more distinct natural barriers there (large rivers, etc.).

Table 1. Differences between young and adult individuals according to non-metric features of mole skulls

| Feature No | n (young) ^b | n (adults) | r | I | df | p |
|------------|------------------------|------------|-------|--------|----|--------|
| 1 | 14 | 78 | 0.998 | 0.190 | 1 | >0.300 |
| 2* | 14 | 78 | 0.834 | 10.540 | 3 | <0.025 |
| 3 | 14 | 78 | 0.985 | 1.424 | 1 | >0.200 |
| 4* | 14 | 78 | 0.917 | 7.881 | 2 | <0.025 |
| 5* | 14 | 78 | 0.933 | 6.362 | 1 | <0.025 |
| 6 | 14 | 78 | 0.933 | 6.362 | 3 | >0.050 |
| 7 | 14 | 78 | 0.961 | 3.703 | 1 | >0.050 |
| 8 | 13 | 78 | 0.977 | 2.407 | 1 | >0.100 |
| 9 | 14 | 78 | 0.927 | 3.608 | 1 | >0.050 |
| 10 | 13 | 78 | 0.999 | 2.050 | 1 | >0.050 |
| 11 | 13 | 78 | 0.997 | 0.267 | 1 | >0.300 |
| 12 | 14 | 78 | 0.996 | 0.380 | 1 | >0.300 |
| 13 | 14 | 78 | 1.0 | 0.000 | 1 | 0.999 |
| 14 | 14 | 78 | 0.988 | 1.139 | 2 | >0.200 |
| 15 | 14 | 78 | 1.0 | 0.000 | 1 | 0.999 |
| 16 | 14 | 78 | 0.992 | 0.760 | 1 | >0.300 |
| 17 | 14 | 78 | 1.0 | 0.000 | 1 | 0.999 |

Note: *- features related to age

Table 2. Differences between sexes according to non-metric features of mole skulls

| Feature No. | n males (♂♂) | n females (♀♀) | r | I | df | p |
|-------------|--------------|----------------|-------|-------|----|--------|
| 1 | 50 | 28 | 1.0 | 0.000 | 1 | 0.999 |
| 2 | 50 | 28 | 0.985 | 1.775 | 3 | >0.300 |
| 3* | 50 | 28 | 0.962 | 4.496 | 1 | <0.050 |
| 4 | 50 | 28 | 0.995 | 0.592 | 2 | >0.300 |
| 5 | 50 | 28 | 0.982 | 2.130 | 1 | >0.100 |
| 6 | 50 | 28 | 0.995 | 0.592 | 3 | >0.300 |
| 7* | 50 | 28 | 0.956 | 5.206 | 1 | <0.025 |
| 8 | 50 | 28 | 0.990 | 1.183 | 1 | >0.200 |
| 9 | 50 | 28 | 0.985 | 1.775 | 1 | >0.100 |
| 10* | 50 | 28 | 0.965 | 4.141 | 1 | <0.025 |
| 11 | 50 | 28 | 0.999 | 0.118 | 1 | >0.300 |
| 12 | 50 | 28 | 0.985 | 1.775 | 1 | >0.100 |
| 13 | 50 | 28 | 0.998 | 0.237 | 1 | >0.300 |
| 14* | 50 | 28 | 0.947 | 6.270 | 2 | <0.050 |
| 15 | 50 | 28 | 0.988 | 1.420 | 1 | >0.200 |
| 16 | 50 | 28 | 1.0 | 0.000 | 1 | 0.999 |
| 17* | 50 | 28 | 0.943 | 6.744 | 1 | <0.001 |

Note: *- features related to sex

Table 3. Frequencies of the variants of non-metric features of the mole skull in samples

| Feature | Variantas | Sample | | | | | | | | | | | | | |
|-----------|-----------|--------------|--------------|----------|----------|----------|--------|-------|----------|----------|----------|----------|----------|----------|----------|
| | | Puvočiai (1) | Puvočiai (2) | Žuvintas | Kairėnai | Kupiškis | Šilutė | Rusnė | Kamajai | Ozas | Salantai | Joniškis | Šakiai | Pašvinė | Vilūnai |
| | | n=27 | n=17 | n=23 | n=21 | n=21 | n=17 | n=24 | n=20 | n=21 | n=21 | n=12 | n=18 | n=18 | n=21 |
| 1 | 1 | 0.59 | 1 | 0.43 | 0.62 | 0.48 | 0.06 | 0.58 | 0.95 | 1 | 1 | 1 | 1 | 1 | 1 |
| | 2 | 0.41 | 0 | 0.57 | 0.38 | 0.52 | 0.94 | 0.42 | 0.05 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6 | 1 | 0.52 | 0.35 | 0.13 | 0.38 | 0.33 | 0.50 | 0.42 | 0.35 | 0.47 | 0.24 | 0.30 | 0.39 | 0.28 | 0.33 |
| | 2 | 0.30 | 0.47 | 0.35 | 0.33 | 0.14 | 0.20 | 0.37 | 0.25 | 0.10 | 0.33 | 0.30 | 0.28 | 0.22 | 0.48 |
| | 3 | 0.15 | 0 | 0.30 | 0.29 | 0.20 | 0.20 | 0.12 | 0.15 | 0.10 | 0.14 | 0.10 | 0.06 | 0.17 | 0.05 |
| | 4 | 0.03 | 0.18 | 0.22 | 0 | 0.33 | 0.10 | 0.09 | 0.25 | 0.33 | 0.29 | 0.30 | 0.28 | 0.33 | 0.14 |
| 8 | 1 | 0.26 | 0.53 | 0.22 | 0.48 | 0.62 | 0.59 | 0.67 | 0.80 | 0.91 | 0.52 | 0.50 | 0.72 | 0.56 | 0.48 |
| | 2 | 0.74 | 0.47 | 0.78 | 0.52 | 0.38 | 0.41 | 0.33 | 0.20 | 0.09 | 0.48 | 0.50 | 0.28 | 0.44 | 0.52 |
| 9 | 1 | 0.93 | 0 | 0.91 | 0.90 | 0.95 | 0.82 | 0.88 | 0.05 | 0.24 | 0 | 0 | 0.11 | 0.39 | 0.33 |
| | 2 | 0.07 | 1 | 0.09 | 0.10 | 0.05 | 0.18 | 0.12 | 0.95 | 0.76 | 1 | 1 | 0.89 | 0.61 | 0.67 |
| 11 | 1 | 0.74 | 1 | 0.96 | 0.90 | 0.76 | 0.35 | 0.71 | 0 | 0.09 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0.26 | 0 | 0.04 | 0.10 | 0.24 | 0.65 | 0.29 | 1 | 0.91 | 1 | 1 | 1 | 1 | 1 |
| 12 | 1 | 0.70 | 0.29 | 0.22 | 0.67 | 0.86 | 0.35 | 0.54 | 0 | 0.10 | 0.10 | 0.25 | 0.11 | 0.22 | 0.24 |
| | 2 | 0.30 | 0.71 | 0.78 | 0.33 | 0.14 | 0.65 | 0.46 | 1 | 0.90 | 0.90 | 0.75 | 0.89 | 0.78 | 0.76 |
| 13 | 1 | 0.93 | 0.82 | 0.87 | 0.71 | 0.81 | 0.71 | 0.96 | 0.95 | 0.91 | 0.90 | 0.83 | 0.78 | 0.83 | 0.81 |
| | 2 | 0.07 | 0.18 | 0.13 | 0.29 | 0.19 | 0.29 | 0.04 | 0.05 | 0.09 | 0.10 | 0.17 | 0.22 | 0.17 | 0.19 |
| 15 | 1 | 0.81 | 0.76 | 0.61 | 0.71 | 0.29 | 0.82 | 0.50 | 0.15 | 0.29 | 0.52 | 0.42 | 0.39 | 0.78 | 0.76 |
| | 2 | 0.19 | 0.24 | 0.39 | 0.29 | 0.71 | 0.18 | 0.50 | 0.85 | 0.71 | 0.48 | 0.58 | 0.61 | 0.22 | 0.24 |
| 16 | 1 | 0.59 | 0.94 | 0.57 | 0.48 | 0.71 | 0.65 | 0.67 | 0.65 | 0.62 | 0.86 | 1 | 0.28 | 0.89 | 0.95 |
| | 2 | 0.41 | 0.06 | 0.43 | 0.52 | 0.29 | 0.35 | 0.33 | 0.35 | 0.38 | 0.14 | 0 | 0.72 | 0.11 | 0.05 |

The most frequent (85.1 %) phene in all the samples studied is phene No.13(1) (Table 4) whose greatest frequency (0.96) is in the sample of Rusnė (Table 3). This most probably was influenced by a long-term isolation of this territory, the phenomena of the gene drift and a complex of other natural factors, as well as epigenetic processes related to that. A similar distribution of phenes is observed in the samples of Šilutė, which could have been determined by a close relationship of these two groups of moles. The lowest frequency (15 %) as compared with frequency in other samples, is that of features No. 6(3) and No.13(2). Values of phene frequencies in all samples ranged from 0 to 1.

We think that a greater frequency of phenes in the sample of Puvočiai No.1 has been influenced by longer reproduction isolation. The largest value (0.96) of phene frequency has been noticed in Rusnė (Table 3).

Phenetic distances between the mole samples studied have been determined (Table 5).

It was established that according to the largest number of features (according to I criterion) the sample of Salantai differed from the samples of Žuvintas (200.84), Kupiškis (190.98), Puvočiai No.2 (190.95), Kairėnai (173.95) and Puvočiai No.1 (169.13), and according to the smallest number of features, the samples of Salantai differed from those of Kamajai (19.10), and the samples of Joniškis – from the samples of Šeškinės Ozas (21.71), Pašvinė (25.70) and Vilūnai (29.70).

Table 4. Frequency of features in all samples studied

| Feature No. | Number of variant (phene) of the feature | Number of individuals (n) | Feature frequency (%) |
|-------------|--|---------------------------|-----------------------|
| 1 | 1 | 211 | 75.1 |
| | 2 | 70 | 24.9 |
| 6 | 1 | 94 | 33.5 |
| | 2 | 84 | 29.9 |
| | 3 | 42 | 15.0 |
| | 4 | 54 | 19.2 |
| 8 | 1 | 155 | 55.2 |
| | 2 | 126 | 44.8 |
| 9 | 1 | 142 | 50.5 |
| | 2 | 139 | 49.5 |
| 11 | 1 | 119 | 42.4 |
| | 2 | 163 | 58.0 |
| 12 | 1 | 99 | 35.2 |
| | 2 | 182 | 64.8 |
| 13 | 1 | 239 | 85.1 |
| | 2 | 42 | 15.0 |
| 15 | 1 | 168 | 59.8 |
| | 2 | 123 | 43.8 |
| 16 | 1 | 194 | 69.0 |
| | 2 | 87 | 31.0 |

Table 5. Phenetic differences in the studied mole skulls according to a complex of non-metric features when comparing the samples in pairs (values of the similarity indicator (r) – above the diagonal, values of the identity criterion (I) – under the diagonal)

| | Kamajai | Šilutė | Salantai | Vilūnai | Pašvinė | Joniškis | Rusnė | Šeškinės ozas | Puvočiai №1 | Kairėnai | Žuvintas | Kupiškis | Puvočiai №2 | Šakiai |
|---------------|--------------|--------|---------------|--------------|--------------|--------------|--------|---------------|-------------|--------------|--------------|----------|-------------|--------|
| Kamajai | *** | 0.809 | 0.968 | 0.934 | 0.934 | 0.943 | 0.838 | 0.939 | 0.772 | 0.763 | 0.774 | 0.785 | 0.810 | 0.972 |
| Šilutė | 115.99 | *** | 0.792 | 0.865 | 0.864 | 0.787 | 0.930 | 0.806 | 0.944 | 0.941 | 0.933 | 0.949 | 0.762 | 0.825 |
| Salantai | 19.10 | 142.64 | *** | 0.966 | 0.962 | 0.977 | 0.822 | 0.912 | 0.807 | 0.742 | 0.725 | 0.769 | 0.754 | 0.961 |
| Vilūnai | 36.85 | 178.03 | 55.91 | *** | 0.990 | 0.961 | 0.883 | 0.904 | 0.867 | 0.839 | 0.820 | 0.830 | 0.885 | 0.938 |
| Pašvinė | 39.28 | 105.82 | 52.84 | 61.02 | *** | 0.980 | 0.879 | 0.913 | 0.845 | 0.832 | 0.821 | 0.825 | 0.847 | 0.952 |
| Joniškis | 30.74 | 113.48 | 34.67 | 29.70 | 25.70 | *** | 0.816 | 0.928 | 0.777 | 0.753 | 0.744 | 0.775 | 0.876 | 0.938 |
| Rusnė | 126.03 | 76.97 | 149.37 | 104.30 | 163.04 | 116.21 | *** | 0.853 | 0.763 | 0.957 | 0.956 | 0.977 | 0.853 | 0.823 |
| Šeškinės ozas | 40.34 | 98.44 | 59.30 | 59.82 | 53.01 | 21.71 | 81.32 | *** | 0.800 | 0.794 | 0.778 | 0.813 | 0.807 | 0.952 |
| Puvočiai №1 | 163.99 | 79.82 | 169.13 | 162.57 | 155.94 | 115.63 | 100.32 | 139.68 | *** | 0.822 | 0.941 | 0.958 | 0.804 | 0.814 |
| Kairėnai | 144.42 | 75.28 | 173.95 | 128.25 | 112.20 | 108.29 | 75.11 | 102.12 | 85.003 | *** | 0.959 | 0.953 | 0.838 | 0.802 |
| Žuvintas | 148.98 | 70.29 | 200.84 | 153.75 | 127.49 | 152.10 | 96.69 | 140.86 | 85.99 | 83.91 | *** | 0.936 | 0.836 | 0.786 |
| Kupiškis | 170.78 | 79.03 | 190.98 | 163.84 | 106.75 | 126.90 | 78.27 | 120.86 | 86.04 | 167.01 | 75.75 | *** | 0.805 | 0.803 |
| Puvočiai №2 | 111.46 | 146.63 | 190.95 | 127.69 | 124.45 | 91.42 | 110.75 | 106.86 | 142.71 | 125.48 | 125.13 | 118.76 | *** | 0.829 |
| Šakiai | 33.35 | 112.65 | 119.94 | 41.08 | 42.48 | 44.20 | 123.71 | 43.72 | 128.43 | 150.22 | 157.50 | 140.64 | 116.32 | *** |

The highest similarity between the samples studied (according to the indicator R) has been established between the samples of Pašvinė and Vilūnai (0.990) and Joniškis (0.980), and the lowest similarity has been observed between the samples of Salantai and Kairėnai (0.742) and Joniškis and Žuvintas (0.744) (Table 5).

Having carried out a cluster analysis (Table 5, Fig. 4) according to a complex of non-metric features (according to I values), it has been established that the sample of Puvočiai No.1 is most distant from other samples. This territory is attributed to the boundaries of the formations of the edge of the last Nemunas glaciations that covered Lithuania – Grūda Stadial. Apart from the earlier deglaciated Medininkai hill, Eišiškių plateau and a part of Švenčionys hill, the latter area freed itself from the glacier approximately 19 thousand years ago (Česnulevičius, 1993). Hence, the greatest phenetic peculiarity of the individuals of the sample of Puvočiai No.1 most likely was influenced by their formation, which was the earliest to have started (it can be stated that this is the population of moles that formed in the highest place of the territory of Lithuania), and also by natural factors that are operating at the present time: peculiarity of soil (a small amount of humus, the greatest depth of congelation of soil), the largest annual radiation balance (Basalykas, 1981; Lietuvos dirvožemiai, 2001); besides, three large Lithuanian rivers (Nemunas, Neris and Merkys) separate this territory from all other studied localities.

The phenetic difference is also considerable between the individuals of Vilūnai and Puvočiai No.2 samples. This reflects the chronology of Lithuania's deglaciation quite clearly. Grūda stage was immediately followed by the Žiogeliai phase (stage) covering the territory of Puvočiai No.2, which deglaciated approximately 18 thousand years ago. However, morenic formations that it created

are not so distinct as those of Grūda. Vilūnai is attributed to the first East Lithuanian phase of the Aukštaičių (Baltic) stage that followed the Žiogeliai stage and that started 17 thousand years ago and created the relief of the Baltic highlands and started the formation of the surface of Žemaičių highlands. The deglaciation phenomena, most probably, reflects itself in the formation of the structure of the population of the *Talpa europaea* species and determined the beginning of migration in the territory of Lithuania. The samples of Puvočiai No.1 and Puvočiai No.2 are not close phonetically though the geographical distance between them is the smallest of all the samples (3 km). These localities are separated not only by the development of glacial chronology but also by the Merkys River, which, most likely, limits migration of animals between these two territories. Quite a considerable phenetic distance from the studied samples has been noticed in Salantai samples of moles. This locality is attributed to the glacial phase of Middle Lithuania, which started 15 thousand years ago. This is the last but one Nemunas glacial phase, which was preceded by the phase of South Lithuania. Alongside the historical geomorphological development the peculiarity of Salantai sample could have been influenced by the most humusous soils in this locality of Lithuania and the largest concentration of radionuclides and heavy metals in soil (Lietuvos dirvožemiai, 2001).

Other studied samples formed a block of rather similar phenetic groups (Fig.4), in which two obvious phenetic groups distinguished themselves. One of them is made of the samples of Žuvintas, Kairėnai, Kupiškis, Rusnė, Šilutė and Joniškis, and the other is formed from the samples of Kamajai, Pašvinė, Šeškinės Ozas and Šakiai. The most similar are Žuvintas – Kairėnai, there is somewhat less phonetic similarity between the samples of Šeškinės Ozas

– Šakiai and Kamajai – Pašvinė could have been influenced by a diverse action of natural selection based on the formation of various abiotic and biotic peculiarities. Since even a small flow of genes (several per cent per groups) can determined genetic differences maintained by isolation for a long time (Berry, 1964). Furthermore, phenetic similarity between these samples, most probably, reflects the directions of mole migration during the time of deglaciation of the Nemunas glacier.

Samples of Šilutė and Rusnė are quite close, which is

likely to have been influenced by a rather late formation of the Nemunas River Delta because the present Nemunas River Delta formed only about 6 thousand years ago – from transgression of the Littoral Sea (Gudelis, Klimavičienė, 1993). Since that time the phenomena of gene drift, the “founder effect” (Berry, 1964), etc. could have had a great impact on the later territory due its isolation. Pollution with heavy metals and radionuclides is rather high in these localities (Lietuvos dirvožemiai, 2001).

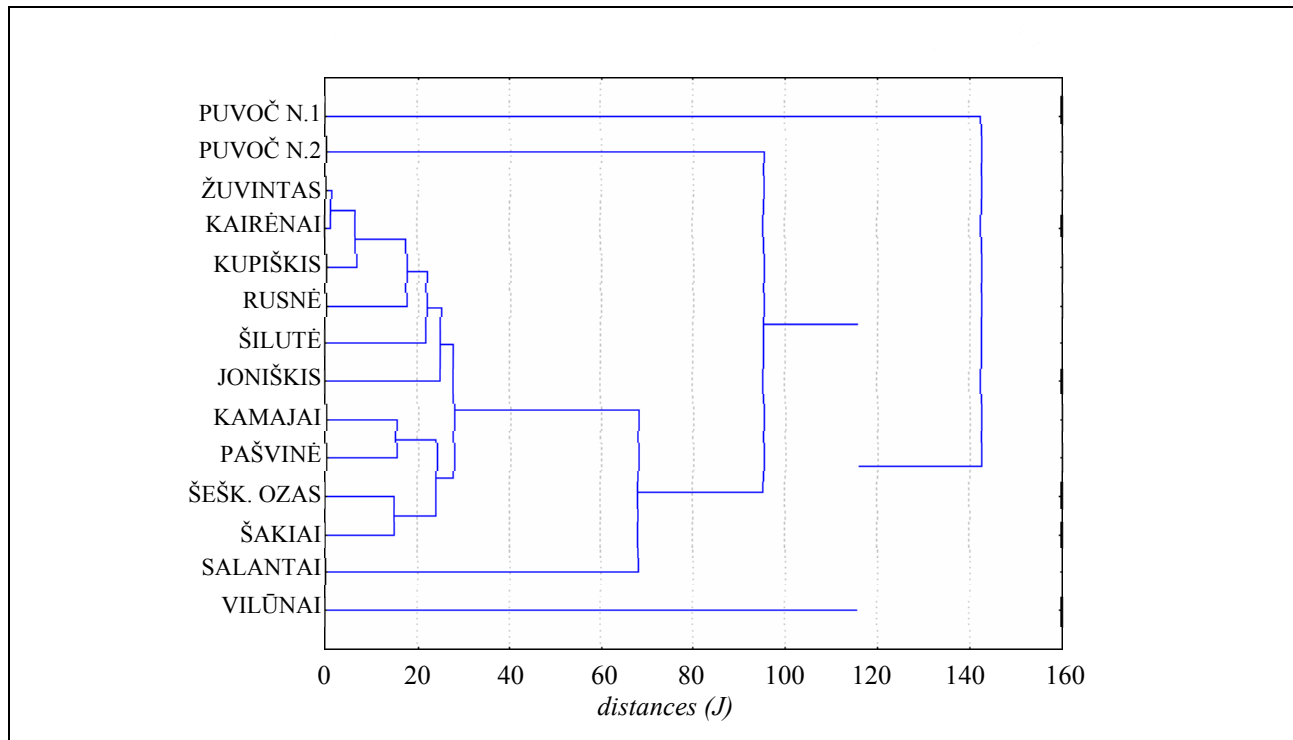


Fig. 4. Phenetic distances between samples according to the identity criterion I

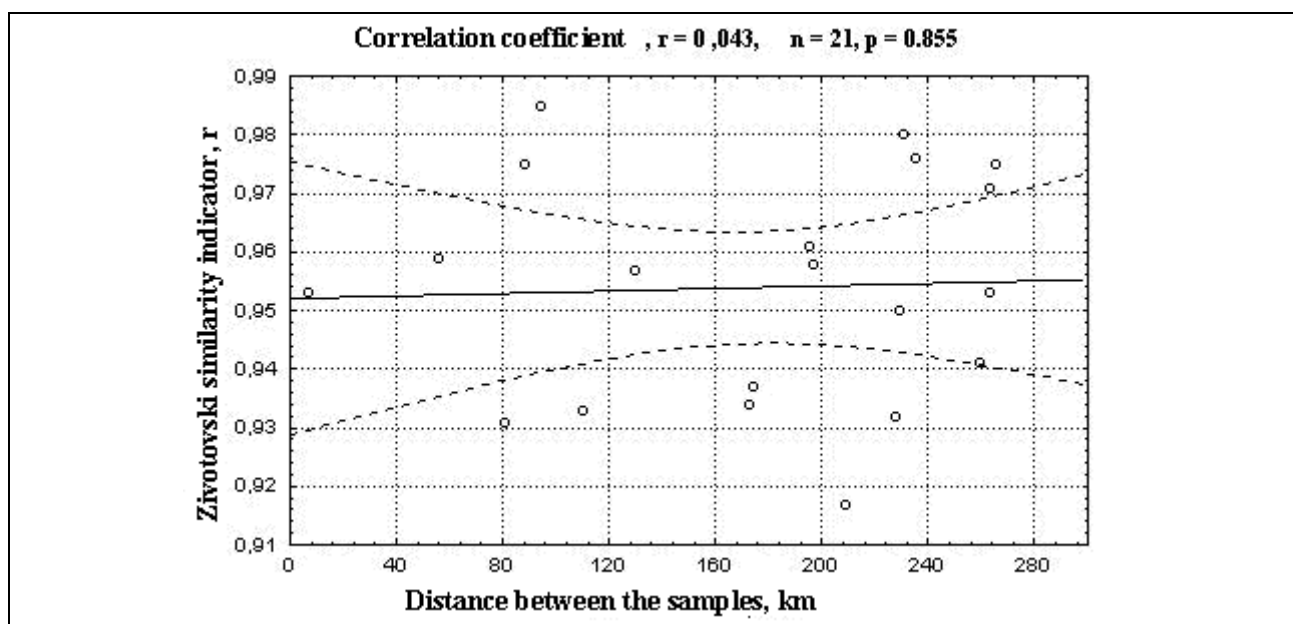


Fig. 5. Correlation between phenetic similarity and the geographical distance between the studied local mole groups

Having checked correlation between the values of the similarity indicator (r) and geographical distances between the studied samples, no reliable correlation was obtained (Fig.5). The samples that are geographically remote from one another at a larger distance can be phenetically more similar than those between which the distance separating them is relatively small. Hence, phenetic distances between the samples do not depend on geographical distances between them. Geographically near populations are not always related phylogenetically (Berry, 1964). Natural barriers (for example, rivers) or other forms of isolation can have a much greater influence. The phenomena of the gene drift cannot be ignored either, which in local (small) groups can be especially clearly felt.

Hence, the results obtained show an obvious impact of the glacier on the phenetic differentiation of moles. However, the contribution of other above-mentioned natural factors is also undisputable. The results obtained allow us to state that the glacier, as far back as in the quaternary, determined the peculiarities of the formation of the phenetic structure of moles. 10 thousand years ago, in the Holocene, after the glaciers melted completely, the formation of the population-phenetic structure of moles was in essence determined by a complex of abiotic and biotic natural factors.

Conclusions.

1. Seventeen non-metric features of the mole skull with 40 variants of these features and nine working phenetic features of the mole skull with 20 variants have been determined.

2. The impact of natural factors such as river barriers and the Nemunas glacier on the formation of the population-phenetic structure of Lithuanian moles has been established.

3. Having studied the phenetic structure of the mole subpopulations, the earliest origin of Puvočiai No1 subpopulation was established.

4. Phenetic distances were determined by the development of the historic changes in a landscape.

5. No reliable correlation between a geographical distance among the samples and phenetic similarity of moles in a geochronological space were established ($p > 0.05$).

6. It was elucidated that the population structure of the moles (*Talpa europaea*) was determined by a complex of natural factors in Lithuania.

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