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TAXONOMIC HIERARCHY AND EVOLUTIONARY SCENARIO OF THE GENUS GROUP *APODEMUS* S. L. (MURIDAE) OF THE PALAEARCTIC BASED ON GENETIC DIFFERENTIATION IN THE cyt-b GENE

S. V. Mezhzherin[1] & V. O. Tereshchenko[2]

Schmalhausen Institute of Zoology NAS of Ukraine,vul. B. Khmelnytskogo, 15, Kyiv, 01054 Ukraine
[1] *E-mail: smezhzherin@gmail.com*
[2] *E-mail: valeriiaschool@gmail.com*

S. V. Mezhzherin (http://orcid.org/0000-0003-2905-5235)
V. O. Tereshchenko (http://orcid.org /0000-0001-6671-0265)

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Taxonomic Hierarchy and Evolutionary Scenario of the Genus Group *Apodemus* s. l. (Muridae) of the Palaearctic based on Genetic Differentiation in the cyt-b Gene. Mezhzherin, S. V. & Tereshchenko, V. O. — Characters of taxonomy and evolutionary scenario based on genetic differentiation of generic groups of forest and field mice *Apodemus* s. l. were established by analyzing the variability of the cyt-b (cytochrome-1, cytb) gene. For this purpose, 124 sequences of *Apodemus* s. l. and other Palearctic Muridae genera (*Mus*, *Micromys*, *Rattus*) were downloaded from GenBank. The adequacy of the categories of semispecies, allospecies, species, whose genetic differentiation corresponds to GD ranges of 0.03–0.06, 0.06–0.1 and 0.1–0.15, has been proven. Within the genus *Sylvaemus* the following species are recognised: *S.* (*Sylvaemus*) *alpicola*, *S.* (*S.*) *arianus* (= *witherbyi*), *S.* (*S.*) *flavicollis*, *S.* (*S.*) *hyrcanicus*, *S.* (*S.*) *ponticus*, *S.* (*S.*) (superspecies) *sylvaticus*, *S.* (*S.*) (superspecies) *uralensis*, *S.* (*Karstomys*) *epimelas*, *S.* (*K.*) *mystacinus*, *S.* (?) *rusiges*: within *Apodemus*: *A. agrarius*, *A. chevrieri*, within *Alsomys*: *Al. argenteus*, *Al. ilex, Al. Latronum, Al.* (superspecies) *major* (= *peninsulae*), *Al. nigrus*, *Al. semotus*, *Al. speciosus*. Generic taxonomy remains ambiguous, which is caused not only by different scales of differentiation of most species of Western and Eastern Palaearctic lineages, but also by the lack of information on key genus-specific characters: the number of roots on upper molars and number of mammary glands for most East Asian species.

Key words: *Apodemus*, cyt-b, genetic differentiation, taxonomy, phylogeny.

Introduction

Questions of taxonomy, phylogeny and evolution of Palaearctic mice group of genera *Alsomys*, *Apodemus*, *Sylvaemus*, traditionally included in the extensive genus *Apodemus* s. l., are of particular interest in modern mammalian taxonomy. In virtue of using genetic methods of taxonomic analysis, the number of investigated species in this group has more than doubled over the past decades and, according to various estimates, is in the range of 22–24 (Filippucci et al., 1989; Mezhzherin & Zagorodnyuk, 1989; Vogel et al., 1991; Vorontzov et al., 1992; Mezhzherin, 1997; Musser & Carleton 2005; Wilson et al., 2016; Ge et al., 2019). An unprecedented increase in size of the genus inclines to a necessity for its transformation in accordance with the data of genetic

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studies (Mezhzherin & Zykov, 1992; Mezhzherin et al., 1992; Orlov et al., 1996; Chelomina et al., 1998; Bellinvia et al., 1999; Filippucci et al., 2002; Michaux et al., 2002; Reutter et al., 2003; Suzuki et al., 2003; Bellinvia, 2004; Fan et al., 2012; Krystufek et al., 2012; Darvish et al., 2015; Mohammadi et al., 2021).

The initial revision based on the results of multilocus allozyme analysis and involving 13 species from Northern Eurasia (Mezhzherin, 1997), is currently hardly acceptable due to the large number of uncovered species living in the south of the Eastern Palaearctic. Their comprehensive studies conducted during the last two decades (Serizawa et al., 2002; Suzuki et al., 2003, 2004, 2008; Fan et al., 2012; Liu et al., 2004, 2012, 2018; Ge et al., 2019) have largely determined a number of questions, the answers to which are relevant. The first question concerns the lower limit of taxonomically meaningful differentiation. In other words, whether there is a hiatus in the values of genetic distances between separate geographical populations and taxonomically significant entities. The second problem is the systemic organization of a species (Vavilov, 1931). According to this concept, numerous wide-range species are actually hierarchically ordered evolutionary genetic entities (Amadon, 1966; Mallet, 2007; Vinarsky, 2015). The third aspect concerns the characters of genetic differentiation of lineage of Western and Eastern Palaearctic origin. The fourth question is related to the essential revision at the genus/subgenus level. The latter circumstance is connected not only with what is considered a genus and what a subgenus, but likewise with the species composition of these groups.

To answer these questions, it is indispensable to generalize the results of studies of the genetic differentiation of *Apodemus* s. l., both within and between species levels. An appropriate marker for such research is the cyt-b (cytochrome-1, cytb) gene, which is widely used in mammalian taxonomy (Irwin et al., 1991; Tobe et al., 2010) and in particular the *Apodemus* s. l. group (Filippucci et al., 2002; Michaux et al., 2001, 2002; Liu et al., 2004, 2018; Suzuki et al., 2008; Fan et al., 2012; Krystufek et al., 2012; Darvish et al., 2015; Ge et al., 2019; Mohamadi et al., 2021).

Material and methods

The actual basis of the work were 124 sequences of the cytochrome-1 (cyt-b) gene retrieved from GenBank. Within *Apodemus* s. l., 25 taxa of species or intraspecies ranks were analysed. The work also includes 10 Palaearctic taxa of mice of the genera *Mus*, *Micromys*, *Rattus* and, as outgroups, two species of the families Arvicolidae and Cricetidae. These sequences were primarily presented in the following major works (Michaux et al., 2003, 2004, 2005; Yasuda et al., 2005; Suzuki et al., 1990; 2008; Darvish et al., 2015; Kim & Park, 2016; Ge et al., 2019). For the selection of sequences, full sequences were selected to cover the species ranges as fully as possible. The quantity of sequences used was determined not only by their presence in the database, but also by taxonomic characters and size of the distribution of the certain species.

The article applies the system of genus and nomenclature in accordance with the previous revision (Mezhzherin 1997).

Family Muridae Illiger, 1811. Genus *Sylvaemus* Ognev, 1924: *S. sylvaticus sylvaticus* (Linnaeus, 1758), *S. s. dichrurus* (Rafinesque, 1814), *S. s. stankovici* (Martino, 1937), *S. flavicollis* (Melchior, 1834), *S. ponticus* (Sviridenko, 1936), *S. alpicola* (Heinrich, 1952), *S. hyrcanicus* (Vorontsov, Boyeskorov & Mezhzherin, 1992), *S. uralensis uralensis* (Pallas, 1811) (= *Apodemus microps* Kratochvil & Rosicky 1952), *S. u. tokmak* (Severtzov, 1873), *S. pallipes* (Barrett-Hamilton, 1900), *S. arianus* (Blanford, 1881) (= *A. witherbyi* (Thomas, 1902)); *A. fulvipectus* Ognev, 1924; *A. hermonensis*, Filippucci, Simson & Nevo, 1989; *A. falzfeini* Mezhzherin & Zagorodnyuk, 1989; *A. avicennicus* Darvish, Javidkar & Siahsarvie, 2006). Subgenus *Karstomys* Martino, 1939: *S.* (*K.*) *epimelas* (Nehring, 1902); *S.* (*K.*) *mystacinus* (Danford & Alston, 1877).

Genus *Apodemus* Kaup, 1829: *A. agrarius* (Pallas, 1771), *A. chevrieri* (Milne-Edwards, 1868).

Genus *Alsomys* Dukelskii, 1928 s. l.: *Al. major* (Radde, 1862) (= *Al. peninsulae* (Thomas, 1907)), *Al. speciosus* (Temminck, 1844), *Al. argenteus* (Temminck, 1844), *Al. gurkha* (Thomas, 1924), *Al. draco* (Barrett-Hamilton, 1900), *Al. ilex* (Thomas, 1922), *Al. latronum* (Thomas, 1911), *Al. nigrus* (Ge, Feijó & Yang, 2019), *Al. semotus* (Thomas, 1908).

As outgroups for the group of genera *Alsomys*, *Apodemus*, *Sylvaemus* the following representatives of Palaearctic mice genera were taken.

Genus *Mus*. *Mus musculus* (Linnaeus, 1758), *M. musculus domesticus* Schwarz & Schwarz, 1943, *M. m. castaneus* Waterhouse, 1843, *M. spicilegus* Petényi, 1882, *M. tataricus* Satunin, 1908 (= *Mus macedonicus* Petrov & Ruzic, 1983), *M. spretus* Lataste, 1883.

Genus *Micromys* Dehne, 1841: *Mic. minutus* (Pallas, 1771), *Mic.* cf. *erithrotis* (Blyth, 1856).

Genus *Rattus* Fischer de Waldheim, 1803: *R. rattus* (Linnaeus, 1758), *R. norvegicus* (Berkenhout, 1769).

In addition, representatives of the families Cricetidae Fischer-Waldheim, 1817 *Cricetus cricetus* (Linnaeus, 1758) and Arvicolidae Gray, 1821 *Microtus arvalis* (Linnaeus, 1758) were used as outgroups.

Analysis was conducted using the Tamura-Nei model (Tamura & Nei, 1993). Evolutionary analysis was conducted in MEGA11 (Tamura et al., 2021). Since the emphasis of this article is genetic differentiation estimated by pairwise distances, we used a phenogram constructed by the standart UPGMA algorithm as a graphic illustration for genetic relationships.

Results

The phenograms were formed based on a matrix for pairwise values of genetic distances, obtained from the nucleotide sequences of the cyt-b gene (figs 1, 2), and reflect the hierarchi-

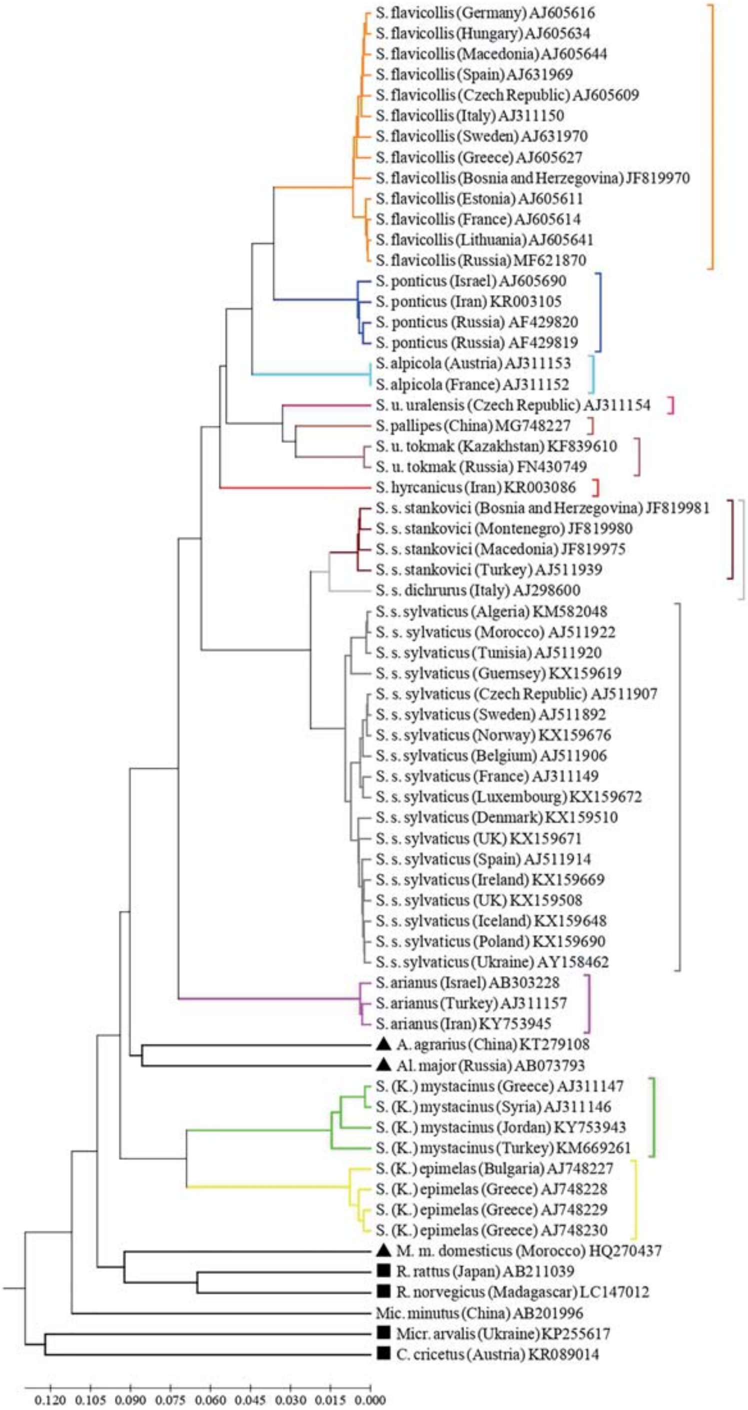

Fig. 1. Phenogram of genetic distances calculated from cytb sequences amongst representatives of the genera *Sylvaemus*, *Rattus*, constructed using the UPGMA algorithm, as mentioned above. *Microtus arvalis* (Arvicolidae) and *Cricetus cricetus* (Cricetidae) are used as outgroups.

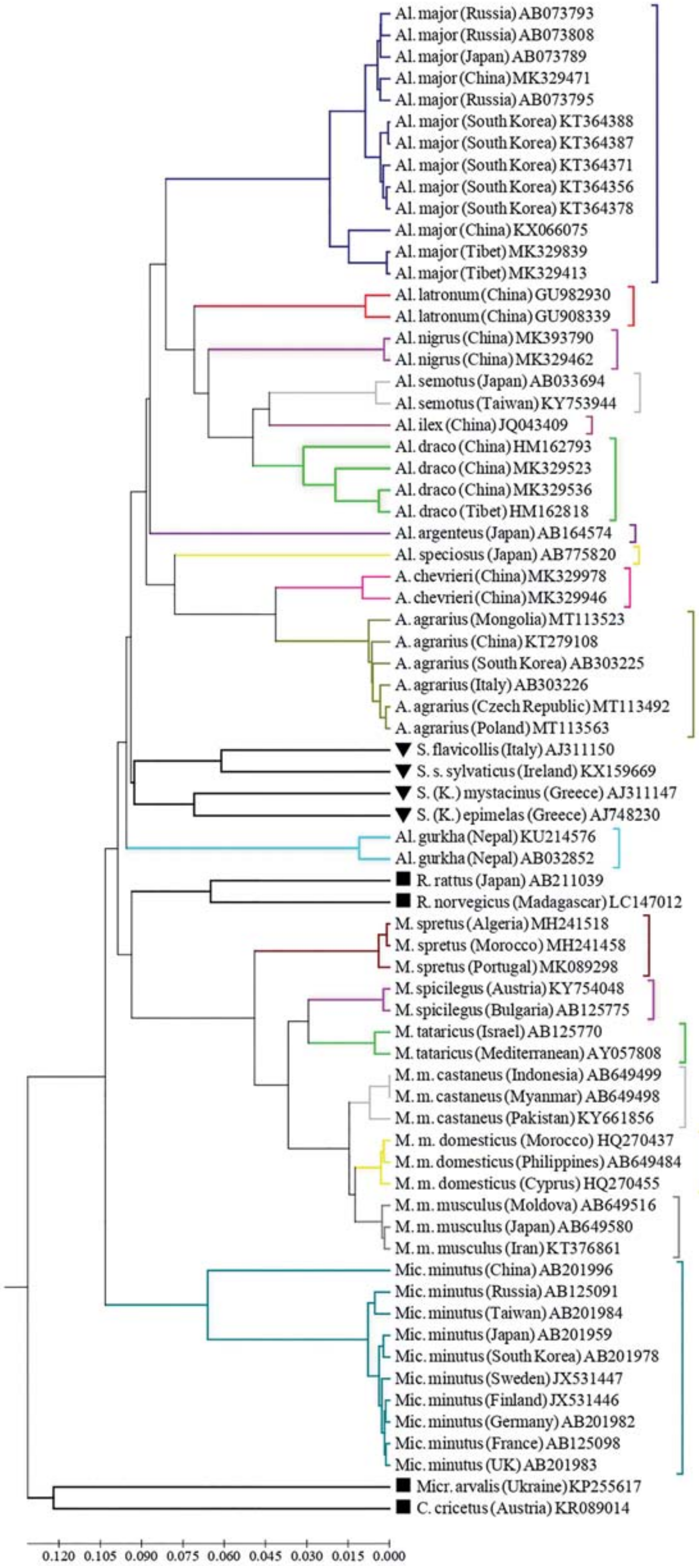

Fig. 2. Phenogram of genetic distances (Tamura, Nei, 1993) calculated from cytb sequences amongst representatives of the genera/subgenera *Alsomys*, *Apodemus* and genera *Micromys*, *Mus*, *Rattus*, constructed using the UPGMA algorithm. Representatives of the Arvicolidae and Cricetidae as well as *S. s. dichrurus*, *S. flavicollis*, *S.* (*K.*) *mystacinus* and *S.* (*K.*) *epimelas* were taken as outgroups.

Table 1. Mean values (M) and limits (Min–max) of genetic distances (GD) at the intraspecies and species levels of comparisons

Genera	Populations		Semispecies		Allospecies		Species	
	M	Min–max	M	Min–max	M	Min–max	M	Min–max
Sylvaemus	0.012	0–0.024	0.045	0.032–0.068	0.079	0.063–0.099	0.128	0.09–0.161
Karstomys	0.019	0.006–0.03	–	–	0.132	0.121–0.138*	–	–
Apodemus	0.012	0.003–0.02	–	–	0.083	0.076–0.09	–	–
Alsomys	0.013	0.002–0.022	0.045	0.03–0.066	0.097	0.08–0.114	0.166	0.124–0.220
Mus	0.007	0–0.014	0.028	0.022–0.031	0.082	0.057–0.101	0.085	0.074–0.107
Micromys	0.010	0.003–0.019	–	–	0.132	0.13–0.135*	0.130	–

cal organization of this group of genera. In addition to the three main levels of genetic differentiation (intraspecies, species and genera), there are sublevels that intergrade.

Intraspecies differentiation. Represented by two sublevels (table 1). The first is intra- and inter-population differences reflecting individual and/or geographic variability. Genetic distances (GD) in this case are in the range of 0–0.02. The second sublevel takes place between vicarious geographic forms (semispecies), between the populations where gene flow is limited and morphological characters fitting into the geographic variability. Genetic distances in this case vary from 0.04 to 0.06 (fig. 3). There is a dip in values in the range of GD from 0.02 to 0.04.

Mean values of genetic distances for the species at population level vary within 0–0.027 (table 1). The maximum intraspecies GD was noted in *S.* (*K.*) *mystacinus* (GD_M = 0.027; $GD_{Min\text{-}max}$ = 0.023–0.03). Minimal GD_M from 0 to 0.01 was found in *S. alpicola*, *S. ponticus*, *S. u. uralensis*, *Al. nigrus*. At the same level, differentiation also takes place within species of the genus *Mus* (table 1). Interestingly the genetic distances between the populations of the transpalaearctic species *A. agrarius* and *Mic. minutus* are quite insignificant (GD_M = 0.012; $GD_{Min\text{-}max}$ = 0.003–0.016 and GD_M = 0.01; $GD_{Min\text{-}max}$ = 0.003–0.019, respectively). This indicates a relatively rapid and recent expansion of the ranges of these species.

Within the genus *Sylvaemus*, semispecies distinction occurs between *S. s. sylvaticus* and *S. u. uralensis*. In the first case the differentiation of the subspecies *S. s. sylvaticus* and *S. s. dichrurus* (GD_M = 0.044), originating from the Western and Eastern Mediterranean refugia (Michaux et al., 2004). The second case concerns somewhat more differentiated intraspecies forms of *S. u. uralensis*, *S. u. tokmak* and a controversial related species

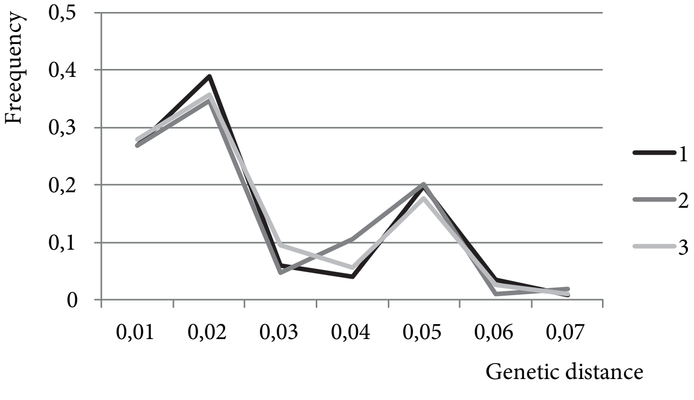

Fig. 3. Distribution of pairwise intraspecies genetic distances within: 1 — the Western Palearctic genus *Sylvaemus*; 2 — the Eastern Palearctic genera *Apodemus* and *Alsomys*; 3 — in general for the Palearctic Muridae, including *Micromys* and *Mus*.

S. pallipes. When comparing the first two subspecies, the mean GD is 0.066; when comparing *S. pallipes* and *S. uralensis*, it turns out to be 0.059.

Gaps in the values of genetic distances were also obtained when comparing the South Siberian and Korean populations of *Al. major* with Tibetan populations of the same species. The GD between populations within the indicated regions varies from 0.001 to 0.022 (M = 0.012), but comparing them the range was 0.03–0.048 (M = 0.042). Similarly, *Al. draco* obtains $GD_{\text{Min-max}}$ = 0.037–0.064 between distant populations.

Among the semispecies *Mus musculus* l. GD values are significantly lower than between semispecies within *Sylvaemus* and *Alsomys* (table 1). Nevertheless, a clear hiatus between population and taxonomically significant GDs persists within house mice as well.

Interspecies differentiation. In regards of divergence of the species within the same genus GD ranges from 0.063 to 0.220 (table 1). Apparently, in such a wide range, several sublevels of genetic differentiation can be distinguished.

For the first sublevel, GD ranges from 0.063–0.135 (fig. 4). It is associated with the divergence of allospecies — allopatric cryptic forms, between which there are no gene flows and whose evolutionary genetic discreteness is maintained due to spatial isolation. Within *Sylvaemus*, it is a group of three species — *S. flavicollis*, *S. alpicola*, *S. ponticus*, previously considered as a single species. GD parameters are M = 0.082, Min–max = 0.063–0.095. A similar observation takes place within a group of species *Al. draco* s. l., which along with *Al. draco* s. str., also evidently includes *Al. ilex*, *Al. nigrus*, *Al. semotus* (GD_M = 0.114; $GD_{\text{Min-max}}$ = 0.08–0.144). Formally, the Southwest Asian *S.* (*K.*) *mystacinus* and the Balkan *S.* (*K.*) *epimelas*, whose genetic differentiation is at a significantly higher level (GD_M = 0.133; $GD_{\text{Min-max}}$ = 0.121–0.138), should formally be considered as allospecies.

In the genus *Mus*, the allospecies group is formed by *M. spicilegus*–*M. tataricus*–*M. spretus* (GD_M = 0.084; $GD_{\text{Min-max}}$ = 0.057–0.101). An allospecies structure is also possible within *Micromys*, but there is no information about the contact zone of *Mic. minutus* and *Mic.* cf. *erithrotis* does not allow a definitive conclusion about their vicarious status.

Sympatric species of the same genus have a reliable reproductive isolation due to ethological characters, a clear morphological diagnosis, and GD in the range from 0.09 to 0.22. The differentiation within the Western Palaearctic genus *Sylvaemus* is significantly lower (GD_M = 0.128; $GD_{\text{Min-max}}$ = 0.09–0.161) than between the Eastern Palaearctic *Alsomys*

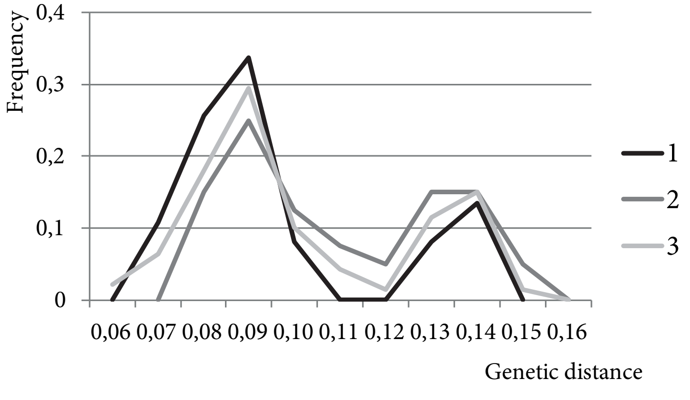

Fig. 4. Distribution of pairwise values of genetic distances amongst species with allopatric areas: 1 — for the Western Palearctic genus *Sylvaemus*; 2 — for the Eastern Palearctic genera *Apodemus* and *Alsomys*; 3 — for the Palearctic Muridae as a whole, including species of genera *Micromys* and *Mus*.

Table 2. Mean values (M) and limits (Min–max) of genetic distances at the level of subgeneric/generic comparisons

Compared taxa	M	Min–max
Alsomys ↔ *Apodemus*	0.178	0.152–0.197
Alsomys ↔ *Karstomys*	0.182	0.149–0.218
Alsomys ↔ *Sylvaemus*	0.187	0.114–0.223
Apodemus ↔ *Karstomys*	0.175	0.160–0.189
Apodemus ↔ *Sylvaemus*	0.183	0.153–0.204
Karstomys ↔ *Sylvaemus*	0.176	0.160–0.196
Karstomys + *Sylvaemus* ↔ *Alsomys* + *Apodemus*	0.186	0.152–0.223
Mus ↔ *Sylvaemus*	0.192	0.157–0.215
Mus ↔ *Alsomys*	0.193	0.162–0.211
Mus ↔ *Apodemus*	0.206	0.186–0.223
Mus ↔ *Karstomys*	0.208	0.181–0.230
Mus ↔ *Alsomys* + *Apodemus* + *Karstomys* + *Sylvaemus*	0.194	0.157–0.230
Rattus ↔ *Alsomys* + *Apodemus* + *Karstomys* + *Mus* + *Sylvaemus*	0.203	0.180–0.229
Micromys ↔ *Alsomys* + *Apodemus* + *Karstomys* + *Mus* + *Sylvaemus*	0.206	0.180–0.243
Cricetus ↔ Muridae	0.256	0.231–0.288
Microtus ↔ Muridae	0.265	0.233–0.297

(GD_M = 0.166; $GD_{Min\text{-}max}$ = 0.124–0.220).

In house mice, the GD is significantly lower (M = 0.085; Min–max = 0.074–0.107) between sympatric reproductively reliably isolated groups of *Mus musculus* s. l. and *Mus spicilegus* s. l., compared to *Apodemus* s. l.

Subgenus/genus differentiation. It covers GD values from 0.152 to 0.243 (table 2). Within *Apodemus* s. l. differences between *Alsomys*, *Apodemus* s. str., *Karstomys*, *Sylvaemus* are approximately the same ($GD_{Min\text{-}max}$ = 0.178–0.187). Simultaneously, the mean value of GD between the Western is 0.186. Differentiation of the genus *Mus* from *Apodemus* s. l. is relatively larger than within *Apodemus* s. l. (GD_M = 0.194). The apartness of the genera *Rattus* and *Micromys* is even greater (GD_M = 0.203 and 0.206, respectively). Significantly higher are the interfamily differences (GD = 0.231–0.297).

Comparative analysis of *Apodemus* s. l. divergence. Genetic divergence within the suprageneric *Apodemus* s. l., is a sequential and synchronous process leading to

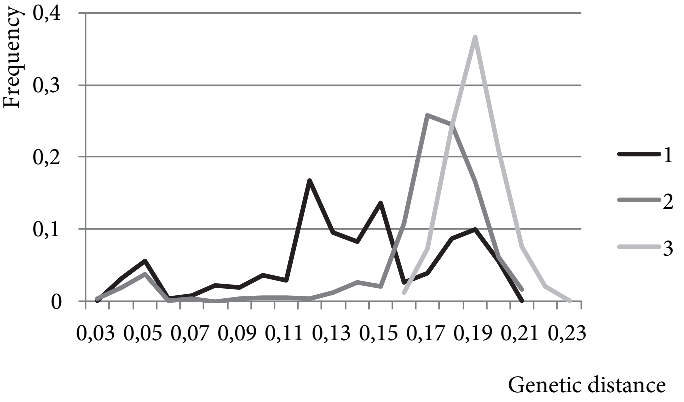

Fig. 5. Distribution of pairwise genetic distances amongst taxa: 1 — Western Palearctic genus *Sylvaemus*, 2 — Eastern Palearctic genera *Apodemus*, *Alsomys*, 3 — Western Palearctic genus *Sylvaemus* and contrarily Eastern Palearctic genera *Apodemus*, *Alsomys*.

the formation of taxa with different levels of genetic differentiation (fig. 5). The divergence of the Western Palaearctic lineage *Sylvaemus–Karstomys* and the Eastern Palaearctic genera *Alsomys* and *Apodemus* (GD_M = 0.186) should be considered as primary. Secondary and close in time is the radiation of species *Al. major*, *Al. speciosus*, *Al. argenteus, Al. gurkha* and *Al. draco* s. l. (GD_M = 0.166), divergence of *Alsomys* and *Apodemus* (GD_M = 0.178) and subgenera *Sylvaemus–Karstomys* (GD_M = 0.176). The third level is the radiation of sympatric species within the subgenus *Sylvaemus* (GD_M = 0.128), divergence of *Al. latronum–Al. draco* s. l. (GD_M = 0.142), *S.* (*K.*) *mystacinus–S.* (*K.*) *epimelas* (GD_M = 0.132). The fourth and fifth levels are the divergence of allospecies (GD_M = 0.79–0.097) and semi-species (GD_M = 0.045).

In general, within the Eastern Palaearctic complex the scale of genetic differences is significantly higher (GD_M = 0.163) than within the Western complex (GD_M = 0.132). These differences are conditioned by the fact that the intensive formation of modern species in the Western group occurred later than in the Eastern group. In the first case, this concerns the radiation of *Sylvaemus* s. str., in the second — *Alsomys*.

Discussion

The identified characters of the genetic differentiation of Palaearctic *Apodemus* s. l. using cyt-b sequences coincide with the results obtained by multilocus allozyme analysis (Mezhzherin, 1997 Filippucci et al., 2002). This applies not only to the confirmation of new taxa of species rank, but also proves the complex multilevel organization of the species. The fact of greater antiquity of the species of the Eastern Palaearctic group *Apodemus–Alsomys*, as compared to the West Palaearctic lineage *Sylvaemus–Karstomys*, was also confirmed. The only exception concerns the divergence of *Sylvaemus–Karstomys*. According to the cyt-b gene sequences, these two groups are no less distant from each other than *Sylvaemus–Alsomys–Apodemus* are from each other. Whereas, according to the allozyme data (Mezhzherin, 1997 Filippucci et al., 2002), the divergence level of *Karstomys* fits completely into *Sylvaemus* at subgenus level. The latter circumstance confirms the sequencing of other genes (Michaux et al., 2002), as well as analysis of key morphological characters of the generic level. This concerns the number of roots on the upper molars, which for *A. mystacinus* ($M^1 : M^2 : M^3 = 4 : 4 : 3$) is the same as for other species of the genus *Sylvaemus*. Additionally, for representatives of the subgenus *Karstomys*, as well as for the species *Sylvaemus* s. str., three pairs of mammary glands are characteristic. The Eastern Asian mice of the genera *Alsomys* and *Apodemus* have 4 pairs of mammary glands, and the number of roots of upper molars in *A. agrarius* is ($M^1 : M^2 : M^3 = 4 : 4 : 2$), while in those studied for this trait *Al. major* and *Al. speciosus* ($M^1 : M^2 : M^3 = 3 : 3 : 3$). Apparently such a significant scale of divergence of *Karstomys* and *Sylvaemus* obtained with cyt-b sequencing is a special case of the evolution of this gene and does not fully reflect the history of the species.

At the present stage of research, the taxonomic composition of *Apodemus* s. l. can already be considered well established, and its structure is as follows. The genus group *Sylvaemus* s. l. includes the subgenus *Sylvaemus* s. str. and *Karstomys*. The first subgenus consists of species groups, superspecies and monotypic species. The species group *S. flavicollis* s. l. includes three allopatric species (*S. flavicollis* s. str., *S. alpicola*, *S. ponticus*). The superspecies S. (superspecies) *sylvaticus* is represented by two vicarious taxonomic units of the semispecies level *S.* (*sylvaticus*) *sylvaticus* and *S.* (*sylvaticus*) *dichrurus*. The *S.* (superspecies) *uralensis* complex consists of three taxa *S. (uralensis) uralensis*, *S. (uralensis) tokmak*, and *S. (uralensis) pallipes*. Monotypic species are *S. arianus* and *S. hyrcanicus*.

The subgenus *Karstomys* is represented by two geographically isolated and significantly divergent species *S. epimelas* and *S. mystacinus*.

The question of the generic and subgeneric position of *Apodemus rusiges* Miller, 1913 remains opened. Exterior characters, three pairs of mammaries and nucleotide composition of Fv1 gene (Young et al., 2018) give a reason to believe that this is a representative *Sylvaemus* s. l. At the same time, it is a member of the subgenus *Karstomys* based on the significant level of divergence for this Fv1 from European representatives of the subgenus *Sylvaemus* s. l. However, the color of the fur, small length as for *Karstomys* subgenus species of the row of upper molars in the range of 3.8–4.2 mm (Musser & Carleton, 2005; Wilson et al., 2016) does not allow it to be unambiguously attributed to that subgenus. Therefore, three options are possible: a distant species within the subgenus *Sylvaemus* s. str., a representative of the subgenus *Karstomys* or a separate subgenus.

The genus group *Apodemus* s. str. includes two allospecies *A. agrarius* and *A. chevrieri*.

The *Alsomys* genus group is presumably based on five ancient phyletic lineages. *Al. speciosus*, *Al. argenteus* and *Al. gurkha* are monotypic. The *Al. major* species should be considered as *Al.* (superspecies) *major*. It includes Northeastern *Al.* (*major*) *major* semi-species, whose range covers the South of Siberia and Far East, Sakhalin, Hokkaido and the Korean Peninsula. The habitat of *Al.* (superspecies) *major* is the Southwestern part of *Al.* (*major*) *major* range. *Al. draco* s. l. was proved to be difficult for systematic constructions, together with *Al. latronum* forming a poorly studied group of mice in extratropical Southeast Asia. In the composition of *Al. draco* s. l. it is logical to include *Al. draco* s. str., *Al. ilex*, *Al. nigrus* and *Al. semotus*. At the same time *Al. draco* s. str. obviously should be considered as *Al.* (superspecies) *draco*, whose structure at the level of semispecies is yet to be elucidated.

Evolutionary-genetic and taxonomic boundaries between semispecies, allospecies and sympatric species are rather conditional. This is due to the relative subjectivity of criteria based on the characteristics of their distribution areals, morphological differences and reproductive relations. The formal use of genetic distances also has limitations, since they often form a uniform row, division of which is not always based on unambiguous hiatuses. At the same time, such a large range of genetic distances from 0.04 to 0.12 within *Sylvaemus* and *Alsomys* and even up to 0.16 within *Apodemus* s. l. is an objective situation reflecting different stages of evolution and settlement of the members of this suprageneric grouping. As a result, taking into account the arealogical, reproductive and morphological characteristics within *Sylvaemus* and *Alsomys*, it would be appropriate to distinguish three, and within *Apodemus* s. l. four intrageneric taxonomic levels.

The issue of generic structure remains debatable. Several solutions are possible: 1) one genus *Apodemus* s. l.; 2) two genera (West Palaearctic *Sylvaemus* and Eastern Palaearctic *Apodemus*); 3) two genera (*Alsomys*, *Apodemus*), or possibly more genera within the Eastern Palaearctic group and two subgenera (*Sylvaemus* and *Karstomys*) within the Western Palaearctic genus *Sylvaemus* s. l. The concept of one genus should be recognised as the least adequate and impractical, firstly, due to large-scale genetic distances corresponding to the lower generic level of division within Muridae (Pages et al., 2012), and secondly, due to the lack of a clear generic diagnosis based on morphological characters. The division into Western Sylvaemus and Eastern *Apodemus* also looks artificial due to significant divergence within the latter and the impossibility of creating a single diagnosis for *Apodemus* genus, which includes Eastern Asian mice. The advantage of identifying three and possibly even more genera is the ability to generate reliable genera diagnoses based on characters such as number of roots on upper molars and number of mammary glands. The first character is key in the taxonomy of fossil forms of mice (Knitlova & Horaček, 2017), the second character also can be considered as genus-species (Gilbert, 1986). On this basis, *Apodemus* s. l. can be divided at least into *Sylvaemus* (3 pairs of mammary glands and the number of roots per $M^1 : M^2 : M^3 = 4 : 4 : 3$, respectively), *Apodemus* s. str. (4 pairs of mammary glands and $M^1 : M^2 : M^3 = 4 : 4 : 2$) and *Alsomys* (4 pairs of mammary glands, $M^1 : M^2 : M^3 = 3 : 3 : 3$). However, the lack of information on the number of roots and mammary glands in *Al. argenteus*, *Al. gurkha*, *Al. draco* s. l., *Al. latronum* do not provide an opportunity to put this concept into practice.

The evolutionary scenario for *Apodemus* s. l. looks in the following way. The initial divergence into lineage, which gave rise to the modern genera *Sylvaemus*, *Alsomys* and *Apodemus*, apparently took place in the South of the Eastern Palaearctic during the Early Pliocene or Late Miocene period. Immediately after the primary divergence in the same region, a secondary divergence of the Eastern lineage occurred, leading to the separation of the phyletic branches of *Apodemus* and *Alsomys* and radiation within the latter. As a result, five phyletic lineages corresponding to modern species *Al. major, Al. speciosus*, *A. argenteus*, *A. gurkha* and species group *Al. draco* s. l. were formed. A secondary divergence within the western lineage apparently occurred in the Southwestern borders of the Western Palaearctic and resulted in the formation of *Sylvaemus* s. s. and *Karstomys*. Further evolutionary events are associated with the end of the Late Pliocene–the Early Pleistocene. At this time, the divergence of *Al. latronum* from *Al. draco* s. l. occurred in the Eastern lineage, *S. mystacinus* and *S. epimelas* separated within the *Karstomys*, radiation began within the *Sylvaemus*. Further events took place in the Pleistocene and are associated with synchronous peaks of speciation activity within the Eastern and Western lineages. Then vicarious forms of allospecies and semispecies ranks were formed.

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