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Evolutionary classification of European wood mice of the subgenus *Sylvaemus* based on allozyme and chromosome data

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Abstract. A review is given of the European species in the subgenus *Sylvaemus* of genus *Apodemus*. Based on biochemical markers (protein electrophoresis) and, in particular, karyotypic differences of banding patterns, up to eight taxa of presumable species or semispecies rank can be distinguished now in Europe, including the Caucasus. They form four superspecies. In western Europe two superspecies, *A. flavicollis* and *A. sylvaticus*, occur sympatrically, in central Europe a third one, *A. uralensis*, and in eastern Europe a fourth one, *A. fulvipectus*. Thus, species diversity of wood mice is increasing eastward.
Key words. Systematics, superspecies, semispecies, chromosome banding analysis, Europe, Caucasus, wood mice, *Apodemus*, *Sylvaemus*.

Introduction

The systematics of wood mice (*Apodemus*) of the subgenus *Sylvaemus* has remained in the focus of scientific interest of Jochen Niethammer for a long time. Particularly, he inspired genetic studies of the most common Eurasian species, *Apodemus sylvaticus* (Martens & Niethammer 1972; Gemmeke & Niethammer 1982; Gemmeke 1980, 1981, 1983).

Until recently three species were assigned to the subgenus *Sylvaemus* in Europe: *A. sylvaticus* (Linnaeus, 1758), *A. flavicollis* (Melchior, 1834) and *A. microps* Kratochvil & Rosicky, 1952 (Niethammer & Krapp 1978). Species such as *A. sylvaticus* and *A. flavicollis* are polytypic but easily separated in some regions, mainly in northern Europe, while identification may be difficult in other regions, particularly in southern and eastern Europe. One of the many "subspecies", *A. flavicollis alpicola* (Heinrich, 1952), has recently been elevated to species rank due to morphological peculiarities and sympatry with *A. flavicollis* and *A. sylvaticus* (Storch & Lütt 1989).

Together with electrophoretic studies, the first data on the striking karyological differentiation of the subgenus *Sylvaemus* were gathered in Germany (Engel et al. 1973), and later in Austria (Gamperl et al. 1982), Azerbaijan (Nadjafova 1989; Kozlovsky et al. 1990; Bulatova et al. 1991) and Bulgaria (Nadjafova et al. 1993).

Half a century ago, the morphological variability of mice of the subgenus *Sylvaemus* in the Caucasus was interpreted as representing a complete series of intermediate forms resulting from natural hybridization between *A. sylvaticus* and *A. flavicollis* (Heptner 1940). This hypothesis appeared to be supported by

laboratory crosses of "*A. sylvaticus*" and "*A. flavicollis*" from the Caucasus (Larina 1961). However, the first electrophoretic studies showed that four valid sympatric species are found in this region. They differ genetically and are obviously reproductively isolated in nature. According to the electrophoretic differences and correlated morphological features they were classified as "form 1", "form 2 of Talysh", "form 3-1" and "form 3-2 of Dzegam" by Vorontsov et al. (1989). At the same time they were classified as "*A. microps*", "*Apodemus* sp. 2", "*Apodemus* sp. 1" and "*A. sylvaticus* 1 — *A. sylvaticus* 2", respectively, by Nadjafova (1989) in the course of a taxonomic study of wood mice of Azerbaijan based on allozymic differences established by O. P. Likhnova.

A recent systematic revision of wood mice of the Caucasus (Vorontsov et al. 1992) on the basis of electrophoretic studies of *Sylvaemus* in the Caucasus and Ukraine (Mezhzherin & Zagorodnyuk 1989; Mezhzherin 1990; Mezhzherin & Zykov 1991; Mezhzherin et al. 1992) clearly demonstrated the need of a systematic revision of the entire subgenus *Sylvaemus*, including chromosome analyses.

We hold that a reliable species definition as to size, coat colour and cranial characters will only be possible on the basis of multivariate analyses (Lavrenchenko & Likhnova 1995). Morphological diagnoses of some species of *Sylvaemus* recently published by Vorontsov et al. (1992) and Zagorodnyuk (1993) must therefore be considered as preliminary. In this review we limit ourselves to allozyme and particularly to chromosome diagnoses.

Systematics of the wood mice of the subgenus *Sylvaemus*

Superspecies *Apodemus flavicollis*

Two species recognized in this group replace each other geographically and are similar in allozymes and morphology (large size, great chest spot, etc.), but differ in chromosome structure. Perhaps *A. alpicola* should be included in this group; unfortunately we have no sufficient information on this taxon.

1. *Apodemus (S.) flavicollis* (Melchior, 1834) — Yellow necked wood mouse.

Type locality: Denmark, Seeland Is.

Diagnosis: Centromeric heterochromatin is uniformly distributed between all 23 pairs of autosomes. Additional heterochromatic regions in the X-chromosome, including increased pericentromeric block and interstitial C-banding. NORs, or nucleolar-organizing regions, are exclusively of telomeric location in each or only one homologue of 9 pairs. Intra- or interpopulation polymorphism is due to variation in a few B-chromosomes (1 to 3), usually entirely heterochromatic (Fig. 1-1).

Differs in 2 to 12 loci from *sylvaticus*-like and *microps*-like wood mice in W, C and E Europe (Engel et al. 1973; Csaikl et al. 1980; Gemmeke 1980, 1981, 1983) and from *A. alpicola* (Vogel et al. 1991). 9 and 2 diagnostic loci were found between *A. flavicollis* and *A. ponticus* Sviridenko, 1936 from Ukraine and Georgia and C Russia and Daghestan, respectively (Mezhzherin et al. 1992; Lavrenchenko & Likhnova 1995).

Morphologically this species is well distinguished from small *Apodemus* specimens of northern Europe and less well from larger *sylvaticus*-like mice of

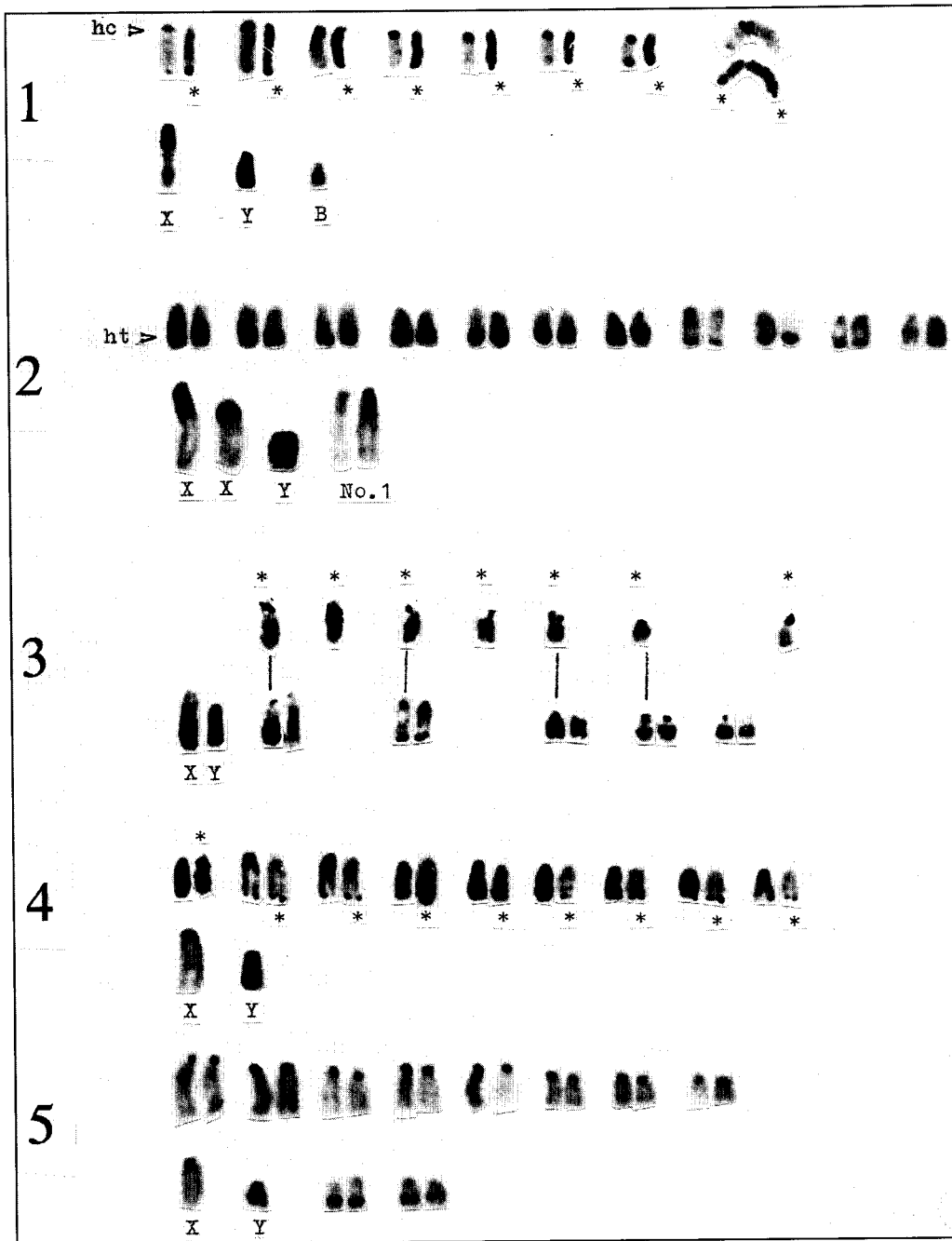


Fig. 1: Species-specific chromosome markers in the subgenus *Sylvaemus*: 1 *A. flavicollis* (Tver, NW Russia); 2 *A. vohlynensis* (Brjansk, C Russia); 3 *A. fulvipectus* (Khunsah, E Daghestan); 4 *A. mosquensis* (Samara, E Russia); 5 *A. ciscaucasicus* (Nalchik, N Caucasus). Chromosomes with NOR and/or heterochromatic markers were cut out from all acrocentric karyotypes. hc = centromeric heterochromatin, ht = telomeric heterochromatin. NORs are marked by an asterisk.

southern Europe. Here the morphological diagnosis requires support by karyological or electrophoretical data. For instance, among karyologically tested specimens of *A. flavicollis* from Bulgaria we found a specimen without a yellow chest spot (Nadjafova et al. 1993), as also reported by Britton-Davidian et al. (1991).

Distribution: Specimens tested by C- or NOR chromosome banding were reported from Germany, vicinity of Freiburg (Engel et al. 1973), Ulm (Hirning et al. 1989), Halle/Saale (our data); from Austria, vicinity of Graz (Gamperl et al. 1982); from Bulgaria, vicinity of Sofia (Nadjafova et al. 1993) and Plovdiv (our data); from the Leningrad region of Russia (Sablina et al. 1985) as well as from Finland, Tver, Tula, Voronezh, Brjansk regions of Russia and from Crimea (our data). Sympatric occurrence with the karyotypically different *A. vohlynensis* Migulin, 1938 is known in montane Bulgaria (Nadjafova et al. 1993), Russia (Brjansk region), and with *A. mosquensis* (Ognev, 1913) in the Tver region (our data). Electrophoretical data are available from W and S Europe (for references see Britton-Davidian et al. 1991) and from E Europe (Ukraine, Gomel region in Belorussia, Volgograd region in Russia) (Mezhzherin 1990; Mezhzherin et al. 1992). The southern limit of this species in E Europe is open to question. In the Caucasus the proper yellow-necked mouse was so far not found among specimens studied karyologically and electrophoretically. However, an extension of the range of *A. flavicollis* into the E Caucasus in the course of natural progression or as a result of human transportation seems possible.

2. *Apodemus (S.) ponticus* Sviridenko, 1936 — Caucasian wood mouse

Type locality: W Ciscaucasia, vicinity of Tuapse, Olginka village.

Diagnosis: Centromeric heterochromatin in many but small autosomes. A marker pair (approximately no. 14) carries both centromeric and telomeric heterochromatin, the latter covering no less than half of the chromosome length. Small telomeric blocks present in two small pairs without centromeric heterochromatin. The X-chromosome has a distinct centromeric block and distal interstitial heterochromatin. NORs of telomeric location are identified by restaining in 9 chromosome pairs (approx. nos. 11–17, 20, 21) bearing centromeric as well as telomeric heterochromatin, including the marker pair 14 (Kozlovsky et al. 1990).

Genetically (allozymes) well separated from the Caucasian *A. fulvipectus* (Ognev, 1924) and *A. ciscaucasicus* (Ognev, 1924) and from *A. flavicollis* of Kiev and Tula regions (Mezhzherin 1990; Mezhzherin et al. 1992; Lavrenchenko & Likhnova 1995).

In some morphological features the Caucasian wood mouse is intermediate between *A. flavicollis* and *A. fulvipectus*. From the last species it can reliably be separated by multivariate analysis only (Lavrenchenko & Likhnova 1995).

Nomenclatural remarks: Formerly a karyological and electrophoretical form "*Apodemus* sp. 1" from Azerbaijan (Nadjafova 1989), an electrophoretical "form 3-1" from Adzharia and E Georgia (Vorontsov et al. 1989) or "*A. ponticus*" from Batumi (Mezhzherin 1990) were described. The last name was fixed after electrophoretical and morphological analyses of populations from near the type locality (Vorontsov et al. 1992).

Distribution: Karyological (banding chromosome analysis) evidence was obtained from several sites in north-east Azerbaijan (Nadjafova 1989; Kozlovsky et al. 1990; Bulatova et al. 1991; our data). Electrophoretical markers were found in neighbour-

ing Daghestan (Lavrenchenko & Likhnova 1995) and in Transcaucasia, from Alazan valley west to the Black Sea coast (Mezhzherin 1990; Mezhzherin & Zykov 1991; Vorontsov et al. 1989, 1992). As far as we know, the northern limit of the range is in north-eastern Caucasus. The southern limits need to be re-examined biochemically and karyologically.

Superspecies *Apodemus sylvaticus*

Two allopatric species in this group are similar to each other electrophoretically and morphologically, but differ sharply in their chromosome structure.

3. *Apodemus (S.) sylvaticus* (Linnaeus, 1758) — West European wood mouse.

Type locality: Sweden, Uppsala.

Diagnosis: All 23 pairs of autosomes carry centromeric heterochromatin; 5 pairs show distinct telomeric blocks. A weak differentiation of heterochromatin is found along the X-chromosome (Engel et al. 1973). After restaining proper telomeric blocks are visible in pairs 17 and 21, while in pairs 15, 16 and 22 they are interstitial; NORs are observed in a telomeric position in a number of unidentified chromosomes only (Hirning et al. 1989).

The species is reliably distinguished by allozymes from *A. flavicollis* s.l. in W, C and S-E Europe, and from *A. uralensis* s.l. (including microps) in C and E Europe (Engel et al. 1973; Csaikl et al. 1980; Gemmeke 1980, 1981, 1983; Mezhzherin 1990; Britton-Davidian et al. 1991). Electrophoretic differences on the subspecies level were found in populations from France and Italy compared with populations from Greece and Spain (Britton-Davidian et al. 1991). A similar degree of differentiation was found by Vogel et al. (1991) between populations from Switzerland/Italy and Austria.

Nomenclatural remarks: This form is provisionally assigned to *A. sylvaticus* of Linnaeus on the basis of the general morphological similarity of wood mice from the Rhine basin (biochemically and karyologically studied) and Sweden (biochemically not yet examined). In the case that any other form will be found in southern Scandinavia, one of the junior European synonyms of *A. sylvaticus* has to be applied.

Distribution: Only three populations from Germany, Freiburg (Engel et al. 1973), Ulm (Hirning et al. 1989) and Bonn (Kozlovsky, unpubl. data), were karyologically tested so far. Electrophoretic data appear to be insufficient for the definition of the distribution of this species.

4. *Apodemus (S.) vohlynensis* Migulin, 1938 — South European wood mouse

Type locality: Ukraine west to the Dnepr river, Zhitomir Polesye.

Diagnosis: Centromeric heterochromatin is practically lacking in the autosomes, except sometimes for the 1st pair. On the contrary, telomeric heterochromatin is accumulated to a great extent in 5 to 6 pairs and less in at least 5 other pairs. The X-chromosome is extremely variable due to changes in the amount of pericentromeric heterochromatin (Fig. 1-2). NORs are located centromeric in a few autosome pairs (1 to 3) and telomeric in several others (up to 8) (Nadjajfova et al. 1993).

Allozyme markers for this species are unknown. We assume that the allozyme characteristics reported for “*sylvaticus*” of the right river bank of the Dnepr in Ukraine and Belorussia (Mezhzherin 1990) refer to this species. If so, then *A. vohlynensis* is electrophoretically close to *A. sylvaticus*. In the light of sharp karyological differences the subspecific electrophoretic differences between populations of *A. sylvaticus* of W Europe reported previously (Britton-Davidian et al. 1991; Vogel et al. 1991) are worth of further study.

Nomenclatural remarks: Differentially stained chromosomes of this species from Austria were first published under the name *A. sylvaticus* (Gamperl et al. 1982) and from Bulgaria as “E2-*sylvaticus* cytotype” (Nadjafova et al. 1993). As the valid scientific name for this species we suggest *Sylvimus* (sic!) *sylvaticus vohlynensis* Migulin, 1938, the first valid use of *Sylvimus* (sic!) *sylvaticus vohlynensis* Charlemagn, 1936 (nomen nudum). Future nomenclatural changes cannot be excluded. In his original description Migulin (1938) noted the large size of *vohlynensis* (larger than *mosquensis* Ognev, 1913 and *charkovenski* Migulin, 1936) and the often well expressed yellow neck spot. Therefore, the proposed synonymy of *vohlynensis* with *A. uralensis* (Vorontsov et al. 1992) seems to be erroneous. The inclusion of “*sylvaticus*” under this name (Zagorodnyuk 1993) requires karyological evidence which unfortunately is not yet available.

Distribution: The species definition is based only on karyological data. These indicate the occurrence of *A. vohlynensis* in Austria, environs of Graz (Gamperl et al. 1982), in Bulgaria, Stara Planina Mts and Pazardjik valley (Nadjafova et al. 1993), in the Ukraine, vicinity of Kiev, and in the neighbouring Brjansk region of Russia (our data). Very likely the electrophoretically studied “*sylvaticus*” from the vicinities of Kishinev and Gomel, Kiev, Sumy and Nikolaev regions (Mezhzherin 1990; Mezhzherin & Zykov 1991) also belong to this species. This would define the known area as Central Europe, the Balkans and East of Europe to the Dnepr basin.

Superspecies *Apodemus fulvipectus*

Steppe wood mice differ markedly from *A. sylvaticus* s.l. in electrophoretic and morphological features. Geographically this species replaces *A. vohlynensis* on the northern coast of the Black Sea and in eastern Ukraine, and on this basis could even be attributed to the superspecies *A. sylvaticus*.

5. *Apodemus* (*S.*) *fulvipectus* (Ognev, 1924) — Steppe wood mouse

Synonym: *A. (S.) falzfeini* Mezhzherin & Zagorodnyuk, 1989.

Type locality: Georgia, Dusheti district, Kobi.

Diagnosis: Faint heterochromatin is present in most chromosomes of this species. Few centromeric blocks are present in medium-sized or small autosomes. In 4 pairs weak telomeric heterochromatin is revealed, except for a single chromosome with a large telomeric block which has no corresponding chromosome. This heteromorphic pair, approximately no. 12, serves as marker of this karyotype in populations from the Caucasus and the reserve Askania Nova studied by us. The X-chromosome lacks centromeric heterochromatin and carries distal interstitial blocks. Different from all karyotypes mentioned above, NORs are exclusively centromeric. In some meta-

phases, silver staining is sometimes successful in the distal third of the X-chromosome (Kozlovsky et al. 1990).

The first diagnostic biochemical characters were fixed unique alleles at the loci SDH and Sod-2 (Mezhzherin 1990). Recent authors suggest that slow Hb and fast Np alleles allow a simple discrimination of sympatric taxa (Lavrenchenko & Likhnova 1995).

Nomenclatural remarks: Reasons for the use of the specific name *fulvipectus* were given by Vorontsov et al. (1992). The conspecificity of *A. falzfeini* (Mezhzherin & Zagorodnyuk 1989) from Askania Nova and Caucasian "*fulvipectus*" was demonstrated electrophoretically by Mezhzherin et al. (1992) and has since been confirmed by us (unpubl. data) also karyologically. The confirmation of the validity of the species name *fulvipectus*, however, requires further analyses of this form from the type locality.

Distribution: Karyologically tested specimens are known from NE Azerbaijan (Khachmas district), a neighbouring district of Daghestan (Khunsah) (Figs 1-3) and E Ukraine. Sympatric occurrence with *A. ponticus* and *A. ciscaucasicus* was reported from the first site (Kozlovsky et al. 1990; Bulatova et al. 1991). According to electrophoretically tested specimens this species is widely distributed in steppe regions of E Caucasus and Transcaucasia; in the Ukraine it is known from the Kherson region (Askania Nova Reserve) only (Vorontsov et al. 1992). In the region between the extreme NE Caucasus (Daghestan) and SW Transcaucasia (Black Sea coast near Batumi) the species was electrophoretically identified in samples which also included *A. ponticus* and *A. ciscaucasicus* (Vorontsov et al. 1989, 1992; Lavrenchenko & Likhnova 1995).

Superspecies *Apodemus uralensis*

This superspecies is widely distributed in Eurasia from C Europe to the Altai. Two European species of this group are characterized by a similar electrophoretic protein variability, and this fact, together with a certain morphological congruence, led Vorontsov et al. (1992) to unite them under the name *uralensis*. We consider the unification of *A. microps* and the C Russian form *mosquensis* only on the basis of allozyme data (Vorontsov et al. 1992) premature due to revealed chromosomal differentiations in this group.

6. *Apodemus (S.) mosquensis* (Ognev, 1913) — East European wood mouse.

Type locality: Moscow.

Diagnosis: Centromeric heterochromatin is expressed in most but not all autosomes (like in *A. sylvaticus*). In 5 medium-sized pairs both centromeric and telomeric heterochromatic blocks are revealed. The X-chromosome has centromeric heterochromatin and interstitial bands in the proximal half of its length. NORs are in centromeric position in one medium-sized pair (approximately no. 10) and in telomeric position in 4 other pairs (approx. nos. 9, 14, 15, 19) (Figs 1-4). The centromeric NOR is attached to a block of centromeric heterochromatin in chromosomes without telomeric heterochromatin. Telomeric NORs are located in pairs both with and without telomeric heterochromatin but with centromeric blocks always present.

Up to 10 loci were used for the identification of the species of which three, Hb, Idh-1 and Xdh, were found only in the eastern part of range (Mezhzherin et al. 1992).

In its small size, the dark back and the relatively short tail the species is similar to W European *A. sylvaticus* s. str. From representatives of *A. ciscaucasicus* from Caucasus and the Carpathian Mts it differs in size.

Nomenclatural remarks: We use the senior synonym *uralensis* as the name for the superspecies because wood mice of the Ural, interfluvium Volga-Ural and N Kazakhstan differ karyologically from *A. mosquensis* (Kozlovsky, unpubl. data) and therefore may represent a different species.

Distribution: We studied this species karyologically in some regions of Russia (Novgorod, Voronezh) and in Crimea. An identical karyotype was found in a specimen from S Slovakia kindly presented by S. Mezhzherin. According to electrophoretically studied specimens the species is widely distributed in Ukraine, in the European part of Russia and in Crimea (Mezhzherin 1990; Mezhzherin & Zykov 1991). Its allozyme markers are shared with *A. ciscaucasicus* (Mezhzherin et al. 1992). The western limits of the species remain uncertain, however. In principle the distribution may range from C Europe to the Volga River basin, and from the northern limit of wood mice in E Europe to Crimea. The southern limits of this species are still unsettled, as is its relation to *A. ciscaucasicus* (sympatry? hybrid zone?). In the right-river bank Ukraine, the Gomel and Brjansk regions this species is likely sympatric with *A. vohlynensis*. There is no doubt that it occurs widely in sympatry with *A. flavicollis*.

7. *Apodemus (S.) ciscaucasicus* (Ognev, 1924) — Lesser wood mouse

Synonym: *A. microps* Kratochvil & Rosicky, 1952.

Type locality: North Ossetian Republic, Vladikavkaz.

Diagnosis: Centromeric heterochromatin is restricted to a small number (up to 8 pairs) of the largest autosomes. Some pairs lacking centromeric blocks carry telomeric heterochromatin (Figs 1-5). The X-chromosome has a centromeric block and 1-2 interstitial C-bands in its proximal half. NORs are localized near centromeres in one middle-sized pair and at the telomeric ends of 3—4 smaller pairs.

Nomenclatural remarks: We suggest to unite little wood mice of the Carpathian Mts and the Balkans (*A. microps*) and the Caucasian *A. ciscaucasicus* (a senior synonym) and separate both from the karyotypically distinct E European *A. mosquensis*. In that case *microps* and *ciscaucasicus* could be used as subspecies names.

Distribution: The area of this species covers the Carpathian Mts, Balkans and Caucasus.

Discussion

Morphological characters and genetic markers

Systematists rarely consider the genetical basis of the characters they work with. Morphological characters are often preferred because they are convenient and more easily accessible. However, the genetic basis of characters determines their value in species and infraspecies systematics.

Taxonomically useful characters with a monogenic drive are rare in mammals. Practically all morphological characters, be it colour, skull or tooth characters,

appear to be polygenic, and their variability and heritability therefore is rather complicated.

Modern zoologists seem to underestimate the importance of principals formulated by the Russian geneticist A. S. Serebrovsky, the founder of genegeography. In his work "Problems and methods of genegeography" (Serebrovsky 1930) he wrote, "...the geography of characters, on the one hand, and the geography of genes, on the other hand, are two absolutely different problems the confusion of which, generally saying, is totally inadmissible, and if sometimes they may coincide, they are only a casual exception"

By applying chromosomal, allozymic, immunological and molecular methods, an entire group of monogenic or condominant characters can be obtained: chromosomal rearrangements, allozymes, variable DNA sequences, etc. This class of taxonomic characters may be called genetic markers. Also peculiarities of colour, tooth structure and other morphological features may be taken as markers when their monogeny has been rendered by the analysis of hybrids. Only genetic markers allow the study of microevolutionary processes in contact zones and to prove reproductive isolation between sympatric or parapatric forms.

In the present study diagnoses of allopatric and sympatric species of wood mice of the subgenus *Sylvaemus* are based on genetic markers only. The variability of morphological characters often obscures the true picture of specific and intraspecific differentiation. For example, Argyropulo (1940) noted the similarity of all northern populations of *A. sylvaticus* from Sweden to the Ural Mountains and stated that their size increased to the south and that their colour changed from mainly grey to chestnut in the same direction. However, this pattern of geographic variability does not coincide with the pattern of genetic variation.

According to present data three species occur sympatrically in W Europe: *A. flavicollis*, *A. alpicola* and *A. sylvaticus*. In C Europe further two species, *A. ciscaucasicus* (syn. *A. microps*) and *A. vohlynensis*, occur and possibly also a third one, *A. mosquensis*. In E Europe the sympatry of four species, *A. flavicollis*, *A. mosquensis*, *A. vohlynensis* and *A. fulvipectus*, is established. Species diversity of wood mice increases eastward. The knowledge of the distribution of the superspecies and included allopatric semispecies is still incomplete. The eastern border of superspecies *A. sylvaticus* and the western border of superspecies *A. uralensis* remain obscure.

We have no doubt that the species mentioned above represent morphologically similar but reproductively isolated biological species. Their morphological variability should be studied in genetically identified specimens. The microevolutionary processes in contact zones of allopatric semispecies such as *A. sylvaticus/A. vohlynensis* and *A. mosquensis/A. ciscaucasicus* are not known. They may be parapatric but the existence of hybrid zones cannot be excluded.

Evolutionary classification and trinomial nomenclature

The traditional classification of the genus *Apodemus* was based on the polytypic species concept, which simplifies the classification but also conceals the real biological diversity. Based on the present study we propose to recognize eight European species of *Sylvaemus* instead of four. Is this interpretation of karyological and electrophoretic data justified?

Table 1: Categories of evolutionary classification and trinomial nomenclature in the subgenus *Sylvaemus* of genus *Apodemus*.

| Taxon | | | | Evolutionary classification | Trinomial nomenclature |
|---|--|-----------------------|--|---|------------------------|
| <i>Sylvaemus</i> | | | | species group | subgenus |
| <i>A. flavicollis</i> s. l. | <i>A. sylvaticus</i> s. l. | <i>A. fulvipectus</i> | <i>A. uralensis</i> s. l. | superspecies, sympatric species, biological species | superspecies |
| <i>A. flavicollis</i> s. str. | <i>A. sylvaticus</i> s. str. | <i>A. fulvipectus</i> | <i>A. mosquensis</i> | allopatric species, semispecies | species |
| <i>A. alpicola</i> | | | | | |
| <i>A. ponticus</i> morphological forms of <i>A. flavicollis</i> | <i>A. vohlynenis</i> morphological forms of <i>A. sylvaticus</i> | not studied | <i>A. ciscaucasicus</i> | megasubspecies subspecies | subspecies |
| | | | <i>A. c. ciscaucasicus</i> <i>A. c. microps</i> | | |

The biological species concept, which requires reproductive isolation of species, is widely accepted among systematists. However, it strictly applies only to sympatric species. Besides the biological species concept other concepts exist, such as “phylogenetic”, “evolutionary” and “zoogeographical” ones (e.g. Haffer 1986). We will not go into details but only note that in none of these reproductive isolation plays such an important role as in the biological concept and that they mostly combine features of the biological and morphological species definitions. Species limits are relative and a sharp line between intraspecific and interspecific differentiation cannot always be drawn. A number of transitions between the systematic categories of “subspecies” and “species” exists due to the continuity of evolution and speciation processes.

We have singled out no less than four intermediate categories between subspecies and biological (sympatric) species (Table 1). Only some of the lower categories are correlated with the European taxa of the genus *Apodemus* (subgenus *Sylvaemus*). It is very possible that hybrid zones between some allospecies will be detected, similar to the better known cases in *Mus*. In this genus the major allopatric forms are divided into morphological and genetic forms of lower rank. *Mus musculus* s. str. includes several morphologically differentiated forms (i.e. the desert form referred to as *wagneri*), while *M. domesticus* contains a number of chromosomally diverse and even reproductively isolated forms. A similarly graded classification may be used only in technical works on evolution. For the routine taxonomic work the evolutionary classification must be squeezed into the Procrustean bed of trinomial nomenclature.

If *M. musculus* s. str. and *M. domesticus* are defined as subspecies in the trinomial nomenclature system (Boursot et al. 1993), then all forms included in these megasubspecies will have no scientific name. Forms without a name are easily lost in the biological record. It may even be impossible to argue for the protection of an endangered taxon which has no name. The classification applied here preserves the genetical diversity of wood mice of the subgenus *Sylvaemus*, although the degree of reproductive isolation between these clades is not always known.

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Zusammenfassung

Es wird eine Übersicht und neue Klassifikation der europäischen Formen der Untergattung *Sylvaemus* (Gattung *Apodemus*) gegeben. Anhand von biochemischen Markern (Proteinelektrophorese) und vor allem anhand von Merkmalen bandengefärbter Chromosomen können in Europa mit Einschluß des Kaukasus bis zu acht Taxa unterschieden werden, die vermutlich Spezies- oder Semispeziesrang haben. Diese werden zu vier Superspezies zusammengefaßt. Von diesen kommen in Westeuropa *A. flavicollis* (Semispezies *flavicollis*, *alpicola*, *ponticus*) und *A. sylvaticus* (Semispezies *sylvaticus*, *vohlynensis*) sympatrisch vor, in Zentraleuropa tritt eine dritte, *A. uralensis* (Semispezies *ciscaucasicus*, *mosquensis*), und in Osteuropa mit *A. fulvipectus* eine vierte Superspezies auf. Die Artenvielfalt nimmt somit in östlicher Richtung zu.

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