

Recent *Allophaiomys*-like species in the Palaearctic: Pleistocene relicts or a return to an initial type

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Abstract. Recent *Allophaiomys*-like voles from the Palaearctic belong to *Blanfordimys*, *Phaiomys* and *Neodon* and form a group of about 6-8 species. They are characterized by a number of primitive features, e. g., simple molar morphology and high diploid chromosome numbers. Their ranges are small and located in the southern parts of the distribution of Arvicolini. All these features are characteristic of Pleistocene relicts. Mechanisms in the evolution of *Allophaiomys* – *Microtus* are discussed.

Key words: *Microtus*, *Allophaiomys*, *Blanfordimys*, *Phaiomys*, *Neodon*, Pleistocene, relicts, evolution.

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I. INTRODUCTION

Allophaiomys KORMOS, 1933 is a key taxon among fossil arvicolid rodents with regard to problems of the early history of *Microtus* SCHRANK, 1798. It is commonly treated as a transitional form between Pliocene voles belonging to the genus *Mimomys* F. MAJOR, 1902 and Recent representatives of *Microtus*. Some authors consider *Allophaiomys* a separate genus of Arvicolini (e. g., GROMOV & POLYAKOV 1977; REPENNING 1992), while others include it within the genus *Microtus* as a subgenus (e. g., CHALINE 1972; FEJFAR & HORÁČEK 1983; RABEDER 1981; VAN DER MEULEN 1973).

Crucial to understanding the evolution and taxonomy of the fossil *Allophaiomys* group are studies of Recent *Allophaiomys*-like taxa. The aim of this study is to discuss morphological, karyological and biogeographical data on these forms.

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II. WHAT IS THE ALLOPHAIIOMYS

In recent decades *Allophaiomys* has been discovered in numerous localities of Early Pleistocene age in Europe, Asia and North America. At first recognized as one widespread species, *Allophaiomys pliocaenicus* KORMOS, 1933, it is now regarded by most authors as a group of sibling species (AGUSTÍ 1991). *Allophaiomys* is ancestral to most recent Arvicolini (ca. 50 species of *Microtus* s.l.).

However, the lack of a precise definition of this taxon has led to different applications of the nomen *Allophaiomys* and in consequence to misunderstandings (cf. e. g., REPENNING 1992). CHALINE (1966) and most of European authors subsequent to him have treated *Allophaiomys* as a variable form including both primitive and morphologically advanced taxa (CHALINE 1972; AGUSTI 1991). Most Russian (e. g., GROMOV & POLYAKOV 1977; MARKOVA 1982) and Ukrainian (e. g., REKOVETS 1994; TOPACHEVSKY 1965) authors as well as REPENNING (1992) consider *Allophaiomys* a genus separate from *Microtus* and refer to it only forms with a simple dental pattern.

The best evidence for *Allophaiomys* being different from *Microtus* (s.l.) would be the coexistence of both groups at the same place and time. The fossil evidence is as yet not precise, but there exist "intermediate" forms between "typical" *Allophaiomys* and "typical" *Microtus* in the fossil record.

The general characters of *Allophaiomys* as defined in the present paper can be summarised as follows: (1) molars without roots, (2) the anteroconid of M₁ variable, with a distinct predominance for simple patterns (only 3 closed triangles are present), (3) enamel differentiation of *Microtus*-type in most species (with the exception of *A. deucalion*), (4) "Microtus" type of postpalatine, (5) simple pattern of M³.

III. RECENT ALLOPHAOMYS-LIKE SPECIES

Among extant *Microtus* (s.l.) in the Palaearctic some 6-8 species share the *Allophaiomys* features as far as dental traits are concerned. It is significant that these taxa represent independent vole lineages. In the Palaearctic, the following species or groups (sensu ZAGORODNYUK 1990a) can be tentatively considered as *Allophaiomys*-like forms: *Blanfordimys* (*bucharensis* – *afghanus* group), *Phaiomys* (*leucurus* group), *Neodon* (*juldaschi* – *irene* – *sikimensis* group). All these taxa are characterized by a very simple M³. The M₁ pattern vary from primitive to more complicated. In some other European or Asiatic forms [e. g., *Lasiopodomys* and *Terricola* (*thomasi* group)] there occur species characterized by a simple M³ of *Allophaiomys*-type; however, their M₁ structure is much more advanced and characteristic of *Microtus* (s.s.). Such species are not considered here as belonging to the *Allophaiomys*-like forms. In North America, *Allophaiomys*-like forms are also present, especially in Mexico and Guatemala [*Herpetomys guatemalensis* (MERRIAM, 1898), *Orthriomys umbrosus* MERRIAM, 1898] (MARTIN 1987).

Tooth morphology

The simplest dental patterns of the first lower and third upper molar are to be found in the "Microtus" *afghanus* group, traditionally proposed as a subgenus of *Microtus*. Currently, they are sometimes considered a separate genus, *Blanfordimys* ARGYROPULO, 1933 (MUSSEY & CARLETON 1993; ZAGORODNYUK 1990a), which includes the species *B. afghanus* (THOMAS, 1912) and *B. bucharensis* (VINOGRADOV, 1930). Especially the latter species shows a tooth morphology that is almost identical to that of *Allophaiomys* (GOLENISHCHEV & SABLINA 1991; this paper Fig. 1).

Similar morphological features are shown by *Phaiomys leucurus* BLYTH, 1863 (REPENNING 1992) which is so close to *Allophaiomys* that MARTIN (1987) synonymised the two. The dental pattern of M₁ is very stable while M³ is more variable (Fig. 2).

The third group of *Allophaiomys*-like taxa belongs to the genus *Neodon* HODGSON, 1849 and consists of at least three species. All these forms are characterised by much greater variation in M₁ (Figs 2 and 3) than can be found in representatives of *Blanfordimys* and *Phaiomys*. In the case of *N. irene* (THOMAS, 1911) distinct differences occur even at the subspecific level. In the latter species, as well as in *N. sikimensis* HODGSON, 1849, dental variation is so great (Figs 2 and 3) that we may in these cases be dealing with a group of sibling species. In general, the dental pattern of *Neodon* resembles that of observed in advanced forms of European *Allophaiomys*, e. g., *A. burgondiae* and *A. nutiensis* from Les Valerots (CHALINE 1972).

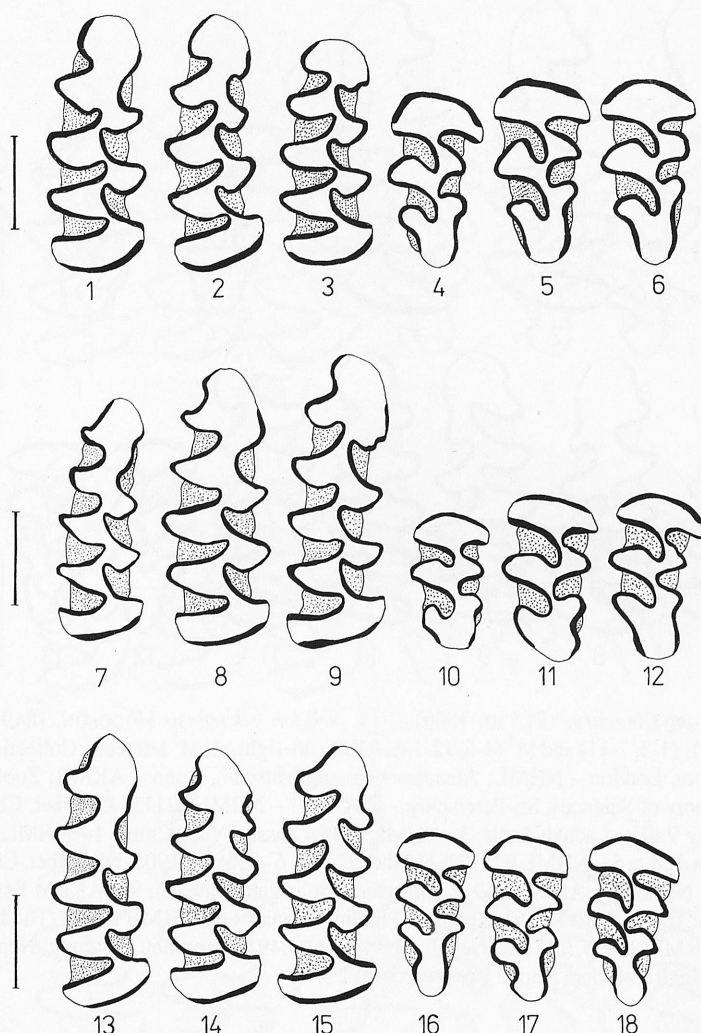


Fig. 1. 1-6: *Blanfordimys bucharensis* (VINOGRADOV, 1930); 7-12: *B. afghanus* (THOMAS, 1912); 13-18: *Neodon juldaschi* (SEVERTSOV, 1879). Morphological variability of M_1 (1-3, 7-9, 13-15) and M^3 (4-6, 10-12, 16-18). All M_1 are right, all M^3 left teeth. Collections: Zoological Institute, Russian Academy of Sciences, St.-Petersburg – ZIANP; Senckenberg Museum, Frankfurt am Main – SMF; Naturhistorisches Museum, Wien – NHMW; Zoological Museum, Moscow State University, Moscow – ZMMU. 1 – ZIANP 77429, Pendzhikent, Tadzhikistan; 2 – ZIANP 20557 Denay, Buchara, Uzbekistan (paralectotype); 3 – ZIANP 20556 Denay, Buchara, Uzbekistan (paralectotype); 4 – ZIANP 20556 Denay, Buchara, Uzbekistan (paralectotype); 5 – ZIANP 73155, Pendzhikent, Tadzhikistan; 6 – ZIANP 77429, Pendzhikent, Tadzhikistan; 7 – SMF 47939, Kushka, Badkhis, Turkmenia; 8 – SMF 47939, Kushka, Badkhis, Turkmenia; 9 – NHMW 32139, Badchiskiy Zap., S Turkmenia; 10 – SMF 47941, Kushka, Badkhis, Turkmenia; 11 – NHMW 32140, Badchiskiy Zap., S Turkmenia; 12 – NHMW 32139, Badchiskiy Zap., S Turkmenia; 13 – ZMMU 132206 Oshskaya Oblast, Kirghizstan; 14 – SMF 54433, Gissarskiy Range, Tadzhikistan; 15 – SMF 47944, Chechekti, Murghab Dis., Tadzhikistan; 16 – SMF 47944, Chechekti, Murghab Dis., Tadzhikistan; 17 – SMF 54433, Gissarskiy Range, Tadzhikistan; 18 – ZMMU 132196 Oshskaya Oblast, Kirghizstan. Bars represent 1 mm.

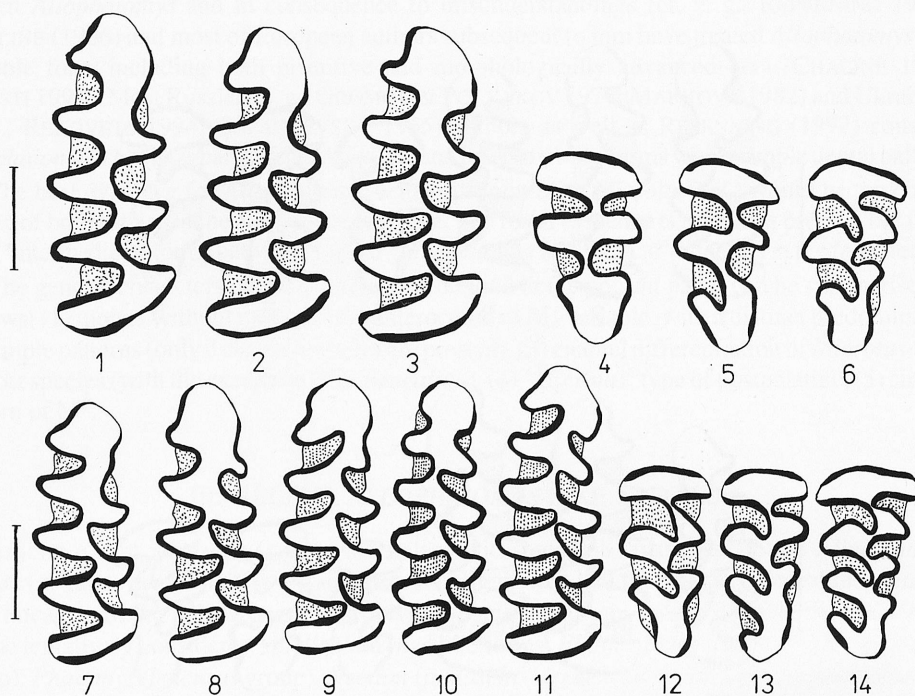


Fig. 2. 1-6: *Phaiomys leucurus* (BLYTH, 1863); 7-14: *Neodon sikimensis* HODGSON, 1849. Morphological variability of M_1 (1-3, 7-11) and M^3 (4-6, 12-14). All M_1 are right, all M^3 left teeth. Collections: The Natural History Museum, London – NHML; Alexander Koenig Museum, Bonn – AKMB; Zoological Institute, Russian Academy of Sciences, St.-Petersburg – ZIANP. 1 – NHML 921121, N Tibet, China; 2 – NHML 610311, Karong Valley, Ladakh, India; 3 – NHML 5465, Lhassa, Tybet, China; 4 – NHML 610311, Karong Valley, Ladakh, India; 5 – NHML 921121, N Tibet, China; 6 – ZIANP 1908, NW Tibet, China; 7 – AKMB 8437, Tukche, Nepal; 8 – AKMB 84918, Dorpatan, Uttar-ganga, Nepal; 9 – AKBM 84905, Thakkhola, Tukche, Nepal; 10 – AKMB 84910, Khumbu, Phulung, Nepal; 11 – AKMB 84915, Thodung, Ramechep, Nepal; 12 – AKMB 84835, Tukche, Nepal; 13 – AKMB 84910, Khumbu, Phulung, Nepal; 14 – AKMB 84915, Thodung, Ramechep, Nepal. Bars represent 1 mm.

Karyological data

The chromosome number varies in *Microtus* (*s.l.*) from 18 to 62 (ZAGORODNYUK 1990b). According to CHALINE & MATTHEY (1971), the hypothetical karyotype of *Allophaiomys pliocaenicus* was $2n=56$, which can also be regarded as ancestral for the whole group. This point of view was accepted by AGADZHANIAN & YATSENKO (1984). It must be noted that such a chromosomal set is also characteristic of other Recent voles outside the Arvicolini. Reconstructions based on more current data gave slightly different results: $2n=54$ with $NF=58$ (ZAGORODNYUK 1992). Approximately one third of the recent Arvicolini (19 of 63 species studied) show $2n=54$, and only a few species have higher chromosome numbers (Fig. 4). Investigation of karyotype variability showed that $2n=58$ is a "frozen" karyotype which was most probably formed from the evolutionarily unbalanced karyotype $2n=62$ as a result of two fusions (ZAGORODNYUK 1990b). This process can be considered one of the first steps in the karyotype differentiation of Arvicolini. The karyotype of *B. afghanus*, ($2n=58$) with one large autosome, is probably the oldest within *Microtus* (*s.l.*)

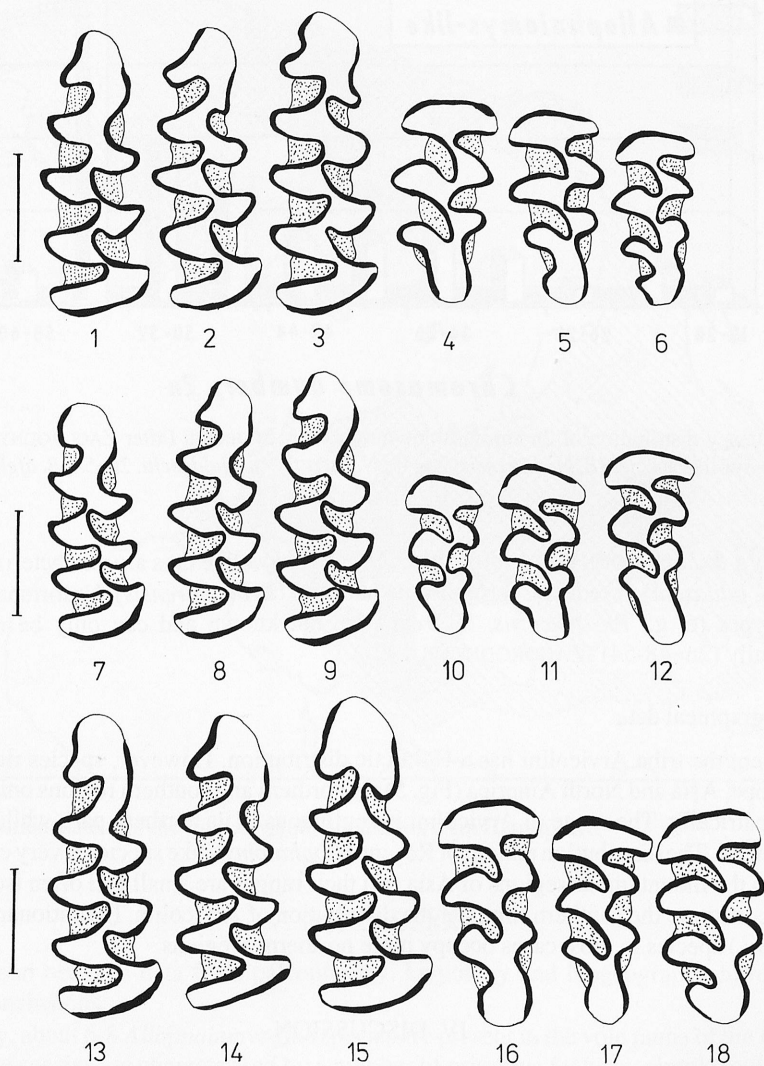


Fig. 3. 1-6: *Neodon irene irene* THOMAS, 1911; 7-12: *N. irene oniscus* THOMAS, 1911; 13-18: *N. irene forresti* HINTON, 1923. Morphological variability of M_1 (1-3, 7-9, 13-15) and M_3 (4-6, 10-12, 16-18). All M_1 are right, all M_3 left teeth. Collections: The Natural History Museum, London – NHML. 1 – NHML 2242910, Mu Li, SW Sichuan, China; 2 – NHML 1121195, holotype, Ta-tsien, W. Sichuan, China; 3 – NHML 541076, W Nepal; 4 – NHML 541076, W Nepal; 5 – NHML 1121195, holotype, Ta-tsien, W. Sichuan, China; 6 – NHML 662583, Damyon, Nepal; 7 – NHML 128544, Tao-Chou, Gansu, China; 8 – NHML 128542, Tao-Chou, Gansu, China; 9 – NHML 128545, Tao-Chou, Gansu, China; 10 – NHML 128544, Tao-Chou, Gansu, China; 11 – NHML 128541, Tao-Chou, Gansu, China; 12 – NHML 128545, Tao-Chou, Gansu, China; 13 – NHML 662001, Mekong-Yangtse Divide, Yunnan, China; 14 – NHML 653852, Mekong Valley, China; 15 – NHML 662001, Mekong-Yangtse Divide, Yunnan, China; 16 – NHML 662001, Mekong-Yangtse Divide, Yunnan, China; 17 – NHML 653852, Mekong Valley, China; 18 – NHML 653851, Mekong Valley, China. Bars represent 1 mm.

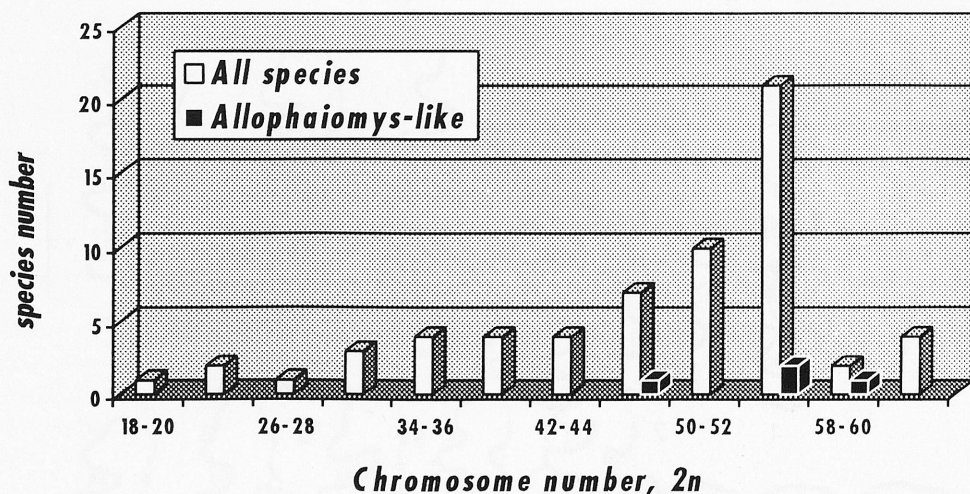


Fig. 4. Frequency distribution of 2n chromosome numbers in Arvicolini (after ZAGORODNYUK 1992) and *Allophaiomys*-like species (*B. bucharensis*, 2n=48; *N. carruthersi-juldaschi*, 2n=54; *B. afghanus*, 2n=58).

(LYAPUNOVA & ZAGORODNYUK 1990). Other *Allophaiomys*-like taxa are characterized by modal (2n=54) (*N. juldaschi*) or reduced chromosome numbers (*B. bucharensis*). Unfortunately, most of the karyotypes (e. g., *Ph. leucurus*, *N. irene*) are not known and can only be reconstructed hypothetically (2n=48-54) (ZAGORODNYUK 1991).

Biogeographical data

At present the tribe Arvicolini has a Holarctic distribution. However, species richness varies across Europe, Asia and North America (Fig. 5). In northern and southern regions only 1-3 species occur sympatrically. The range of Arvicolini is continuous in its northern part, while in the south it is fragmented. The distribution pattern of Recent *Allophaiomys*-like species is very characteristic. All occur in the mountainous regions of Asia and their ranges are small and often isolated. These territories constitute the southern limits of the distribution of Arvicolini. Evolutionarily advanced *Microtus* (*s.l.*) species in most cases occupy more northerly regions.

IV. DISCUSSION

A model of gradualistic evolution of the *Allophaiomys-Microtus* group in the Palaearctic during the Early Pleistocene is generally accepted. The transformation of *Allophaiomys* to *Microtus* took place during a relatively long period in several regions of the Northern Hemisphere, peripheral to the glaciated regions of the Pleistocene. It is probable that allopatric sibling species of *Allophaiomys* existed in the Early Pleistocene.

All Recent *Allophaiomys*-like forms are characterized by some distinct features. All these taxa are steppe or mountain ecotypes with small, isolated ranges and are mutually allopatric. Their distributions lie south of the Pleistocene ice-sheets or are montane. Such distributions are characteristic of Pleistocene relicts. More advanced *Microtus* (*s.l.*) species occur in more northerly parts of the Arvicolini range. Karyologically, all recent *Allophaiomys*-like species differ from other Arvicolini. They show either ancestral (2n=58, e. g., *B. afghanus*), "frozen" (2n=54, e. g. *N. juldaschi*) or relatively advanced (2N=48, e. g., *B. bucharensis*) karyotypes.

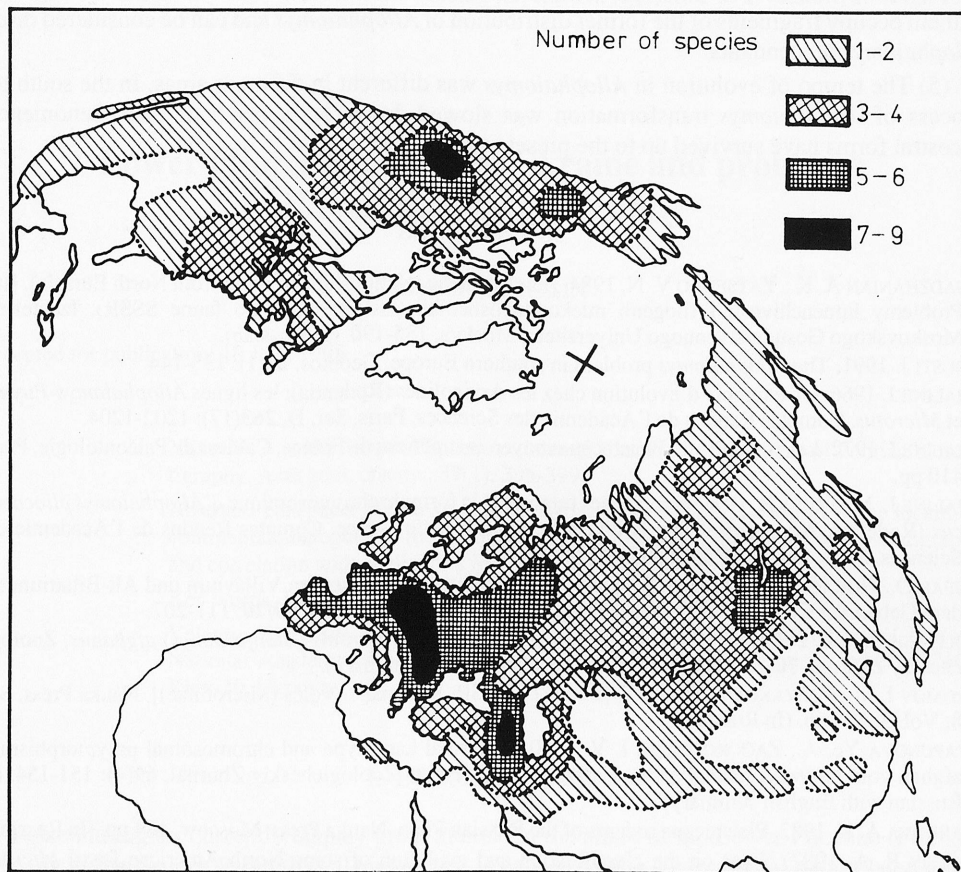


Fig. 5. Distribution pattern of the tribe Arvicolini in the Northern Hemisphere.

V. CONCLUSIONS

Comparison between data from paleontology, karyology and biogeography have led to the following conclusions:

(1) Today, about 6-8 *Allophaiomys*-like species are present in the vole fauna of the Palearctic. Most of these species are characterised by a number of primitive features: simple molar morphology, higher diploid chromosome number, small range and a southern distribution pattern.

(2) A group of fossil species belonging to *Allophaiomys* (including advanced forms) occurred in the Northern Hemisphere during a relatively long period of time (Early Pleistocene). The transformation from *Allophaiomys* to *Microtus* took place according to the model of phyletic gradualism in a similar way as in the *Mimomys-Arvicola* lineage. This transformation took place simultaneously in several regions peripheral to the Pleistocene glacial zones.

(3) The genus *Allophaiomys* presumably consisted of a few allopatric sibling species which are probable ancestors of the *Microtus* (*s.l.*) group. The hypothetical mechanism of the rapid taxonomic differentiation of *Microtus* is its wide karyotypic variability and "chromosomal" speciation, which resulted in the appearance of numerous sibling species pairs.

(4) The extant *Allophaiomys*-like forms occur in the southern part of the Arvicolini range. All of them occupy fragments of the former distribution of *Allophaiomys* and can be considered direct *Allophaiomys* descendants.

(5) The tempo of evolution in *Allophaiomys* was different in different areas. In the south the process of *Allophaiomys* transformation was slowed down. As a result of this phenomenon, ancestral forms have survived up to the present time.

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