### 2. CHARACTERISTICS OF THE SPECIES

# 2.1. Taxonomic Position, Geographical Range, and the Ecology of Distribution

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#### 21.1. Taxonomic Position of the Bank Vole

The bank vole, *Clethrionomys glareolus* (Schreber, 1780), represents the most abundant group of recent rodents — voles. The voles are most frequently classified as the subfamily *Microtinae* of the family *Cricetidae* (Simpson, 1945; Gromov & Polyakov, 1977; Corbet, 1978, and others). Simpson (1945) characterizes the taxonomic position of the bank vole as follows:

Cohort
Order
Suborder
Superfamily
Family
Subfamily
Tribe
Genus

Glires Rodentia Myomorpha Muroidea Cricetidae Microtinae Microtini Clethrionomys

Linnaeus, 1758 Bowdich, 1821 Brandt, 1855 Miller et Gidley, 1918

Miller et Gidley, 19 Rochebrune, 1883 Miller, 1896 Simpson, 1945 Tilesius, 1850

According to Gromov (Gromov & Polyakov, 1977) the genus Clethrionomys belongs to the tribus Clethrionomyini Hooper et Hart, 1962, which is subdivided to three subtribes: Pliomyi, Alticoli, and Clethrionomyi (all names nov., Gromov, 1977). Thus, red-backed voles (after Corbet, 1978) are phylogenetically related to the genera Pliomys (forms abundant in the late Pliocene and extinct in the Pleistocene) and Dinaromys, now represented by Dinaromys bogdanovi in high reaches of the Balkan Mountains, Europe (both Pliomyi groups), and also to sister species of the genus Alticola, represented by the recent mountain voles of central Asia, with scarce species of the genera Hyperacrius (high-mountain Himalayan forms) and Anteliomys which are mountain forms living in south-east Asia (Group Alticoli).

The group Clethrionomyi is geographically much more widely distri-

buted than other groups due to the species diversity of the main genus Clethrionomys. The genus Eothenomys, which belongs to the same group, consists of few high-mountain species inhabiting south-eastern Asia. Thus, except for a few genera spread over mountain habitats of the Old World, only the genus Clethrionomys is characterized by a large geographical expansion and high ecological adaptability. This genus is abundantly represented in the Pleistocene fauna of Eurasia and North America, and it constitutes an important component of the known faunas of the glacial epoch. The present distribution of the subspecies of the bank vole in Europe is ascribed to the effects of the last glaciation.

Within this family only the genus *Microtus* is more abundant and diversified than the genus *Clethrionomys*.

# 2.1.2. Geographical Distribution of the Genus Clethrionomys

At present, the genus *Clethrionomys* consists of 7—9 species ranging over vast areas of the northern Holarctic.

The New World is inhabited by:

Clethrionomys gapperi (Vigors, 1830) — the species representing a distinct line of American red backed voles. It is the Nearctic counterpart of Clethrionomys glareolus. It inhabits North America within a large belt from the east to the west coasts of Canada and northern United States, and along the Appalachian and Rocky Mountains southwards to  $34^{\circ}$  northern latitude.

Clethrionomys occidentalis (Merriam, 1890) — the range of this species is limited to a narrow strip western coastal Canada and the United States (British Columbia and northern California) (Hall and Kelson, 1959).

The species inhabiting both Palaearctic and Nearctic are represented only by:

Clethrionomys rutilus (Pallas, 1779) — a Holarctic species living in northern parts of Eurasia and North America, i.e., from northern Scandinavia through Siberia and Japan to Alaska and northern Canada. In Europe, the southern range extends to Karelia, in Asia to southern reaches of the Urals, southern Kazakhstan and Mongolia, and southeastern China. It inhabits tundra and taiga to the north and forest-steppe to the south. This species exemplifies the invasion of Siberian fauna to North America.

The group of Palaearctic species consists of:

Clethrionomys rufocanus (Sundevall, 1846) — the species living in northern part of Scandinavia, northern part of the European USSR.

Siberia and Far East (Kamchatka, Sakhalin), and to the south extending to southern part of the Ural and Altai Mts., northern Mongolia, and southeastern China. The form typical of taiga extends northwards to tundra nad forest-tundra. In Europe it occupies the boreal part of the Clethrionomys glareolus range, occurring there sympatrically with Clethrionomys rutilus.

Clethrionomys glareolus (Schreber, 1780) — the species typical of Europe, except of its southernmost nad northernmost parts. Its southern range crosses Asia Minor. Eastwards it covers European part of the Soviet Union, southern Urals, western Siberia, and mountains of central Asia (Altai, Sayan) to Lake Baikal. The southern part of its range in eastern Europe and in Asia is poorly documented. In addition to these widely distributed species, two species have been distinguished in Japan (Corbet, 1978):

Clethrionomys rex Imaizumi, 1971 — on Hokkaido, and Clethrionomys andersoni (Thomas 1905) — on Honshu.

Two more species inhabits Asia (Gromov and Polyakov, 1977):

Clethrionomys sikotanensis Tokuda, 1935 — the species described from southern Sakhalin and Shikotan.

Clethrionomys frater Thomas, 1908 — the species occurring in the Thian Shan Mts.

### 2.1.3. Geographical Distribution of Clethronomys glareolus

The European range of the bank vole (Fig. 2.1) is presented on the basis of the available original data, especially in border areas, thus it contains more detail than the popular book by van den Brink (1972) and the monograph by Bashenina (1981). This range is shown in a generalized form. Obviously, within this range there are areas not occupied by the bank vole. This situation is an effect of both man-induced environmental changes and local habitat heterogeneity, along with geographically conditioned patterns of physiocoenoses not suitable for this species (tundra, steppe, or high mountains). Geographical reasons for discontinuous distribution are of particular importance at the edges of the continuous distribution and in the regions with a strongly diversified relief. In some geographical regions the mammal fauna is poorly studied and the distribution of the bank vole remains unclear.

In the northernmost part of their range bank voles extend beyond the Arctic Circle, where they live in deciduous forests (Siivonen, 1967). In northern Scandinavia, however they do not inhabit the zone of subalpine birch scrub, a typical habitat of *Clethrionomys rufocanus* (Kalela et al., 1971). At the northern border of forests, bank voles occur sympatrically with *C. rufocanus* and *C. rutilus*. They do not occur in Iceland,

although their distribution is continuous over mainland Europe, being restricted southward in the Mediterranean climatic zone. On the British Isles they occupy all of England and Scotland, except northern islands of the archipelago, while in Ireland they occupy only an isolated area in the southwestern part of the island. This suggests that the island is being colonized by this species as a result of introduction. The dura-

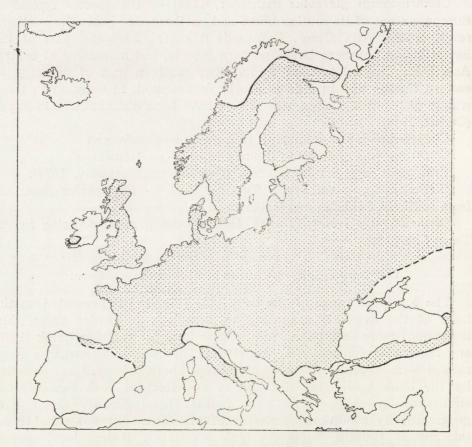


Fig. 2.1. A schematic map of the distribution of *Clethrionomys glareolus* (Schreber, 1780) in Europe (Original data). Uncertain boundaries of the range are denoted by a dashed line.

tion of this process and the ways of invasion are not known, however (Fairley and O'Donnel, 1970). Well known populations of the bank vole occupy such British islands as Jersey, Rassay, Skomer, and Mull. They are taxonomically well defined and exhibit a high morphological diversity. According to recent views, the bank vole is a secondary faunal element there, due to a casual introduction by man (Corbet, 1964).

In the Mediterranean zone the range of the bank vole is not continuous for ecological reasons. On the Iberian Peninsula, which has been little studied so far, bank voles were recorded behind the Pyrenees and in the Cantabrian Mountains (Malec and Storch, 1964; Niethammer, 1956).

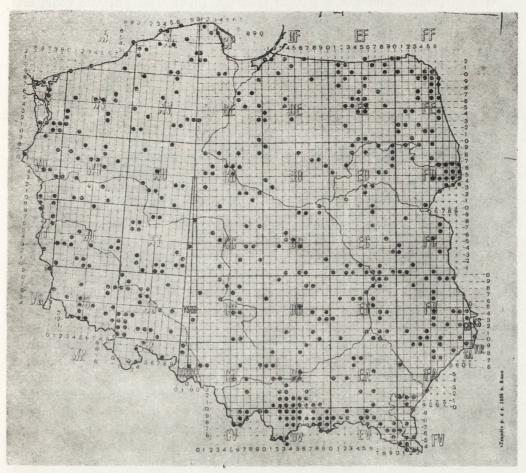


Fig. 2.2. A point map of the distribution of Clethrionomys glareolus (Schreber, 1780) in Poland.

The sites are cumulated in squares of 10×10 km in the UTM grid (after Raczyński, 1983).

On the Apennine Peninsula, the range of the bank vole is not contiguous. Its distribution in mountain and forested areas depends on the local bioclimate resembling that of the temperate zone. This species does not occur on small and large islands of the Mediterranean Sea (Amori et al., 1983). Bank vole population of the Monte Gargano shows, like other faunal elements of this region, some similarity to the Dalma-

tian populations of the Balkan Peninsula (Hagen, 1958). Major parts of the Balkan region (Dulić and Tortić, 1960; Atanassov and Peschev, 1963) and western coast of the Black Sea are occupied by this species. The southern limit of distribution passes through Macedonia in northern Greece (Felten and Storch, 1965; Ondrias, 1966). The Adriatic coast on the Balkan Peninsula, extending from Istria (Dulić, 1962) southwards along the Dinaric Alps is inhabited by mountain populations of the bank vole (Dulić, 1961, 1971). In some parts of its Balkanian range, this species does not occur. This is the case of north-eastern part of Yugoslavia (Petrov, 1968). Pontic populations, occupying a narrow belt of the most humid southern and partly eastern coast of the Black Sea are of similar origin as the Balkanian populations. In Asia Minor, the occurrence of the bank vole is limited to the already mentioned Pontic region (Neuhäuser, 1936; Spitzenberger and Steiner, 1962), reaching Batumi on the north. This species was not recorded in the Caucasus region (Ognev. 1950). Further investigations are needed of the distribution of the bank vole on the southern coast of the Black Sea, in Crimea, in the Sea of Azov region, between the Don and the Caucasus, in Transcaucasia, and also in the northern part of the range, along the European coast east of the White Sea as no records of the bank vole are available about these areas (see Bobrinskij et al., 1965).

The distribution of the bank vole in Poland is presented on the map with a UTM (Universal Transverse Mercator) grid with 10 km squares (Fig. 2.2). About 720 sites of bank vole occurrence (literature data and collections) are distributed over the whole country. The degree of the coverage of the map reflects only the state of the investigation of particular regions of Poland where the range of this species is continuous. Detailed distribution depends only on environmental conditions. In the mountains, bank voles reach the upper boundary of the contiguous range of the dwarf mountain pine (in the Tatra Mountains).

## 2.1.4. Ecological and Biological Determinants of Distribution

Ecological success in terms of increasing number of occupied habitats, depends mostly on adaptability, a high ecological flexibility which enabling survival and often also expansion of the species. Dynamic expansion processes usually occur under variable habitat conditions in both time and space. The present distribution of *C. glareolus* was influenced by the ice age with its successive periods of glaciation alternating with interglacial periods, coupled with respective changes in the plant cover. In historical times, even more violent changes in physiocoenoses occurred

as a result of human activity. In this way, the biological capacity of the species, on the one hand, and changes in the biotic environment, on the other, determine geographical distribution of the species. The considerations below deal with some general problems of the bank vole distribution. A detailed analysis of habitat preference will be presented in section 3.1.

The bank vole belongs to the rodents that colonized the zone of primaeval forests of Europe, and forest habitats determined its geographical range. They now inhabit both boreal coniferous forests of taiga and high mountains and broad-leaved oak and beech forests on the south. Deforestation related to the development of human settlements and agriculture accounts for the contraction of bank vole habitat, and at the same time it releases the ability to occupy secondary habitats. On the British Isles, bank voles inhabit shrubby escarpments, embankments, and hedegerows, and they do not avoid places covered only with forbs and grass (Southern, 1964; Corbet and Southern, 1977). Also in western Europe they occupy hedgerows and shrubberies, and rarely croplands. Some cases are known, however, where they occupied croplands as well, in the absence of competition with other voles. This was noted on Belle-Ile in France (Saint Girons & Beaucournu, 1970), However, a typical habitat of the bank vole is forest with dense undergrowth providing shelter and secret runways. These features of the habitat are stressed by many workers as particularly preferred. Wrangel (1940) lists the following habitat requirements of this species: forests with dense undergrowth, forest edges, shrubberries, park gardens, and parks. Dense forests without undergrowth (e.g. old pine forests) are not a suitable habitat; bank voles are more abundant in mixed or deciduous forests on humus soils and in beech forests, being most abundant at the edges of these forests.

Undoubtedly, the areas covered with ferns on the Skomer Island in Great Britain, represent secondary habitats of the bank vole (Fullgar et al., 1963). This is also the case of uncultivated meadows far northwards in Scandinavia (Hansson et al., 1978). In southern parts of their range, bank voles distribution is closely related to forest habitats, and in the Mediterranean region, also to climatic conditions. In the Balkan area and in Asia Minor, these rodents live in dense forests covering mountain ranges, thus under cooler climatic conditions. In the Balkan and Appenine Peninsulas, bank voles prefer habitats with low temperature amplitudes. These are interiors of dense forests in ravines, where the forest bottom is cooler than in warm coniferous forests on exposed slopes (Hagen, 1958; Dulić, 1971). They also occupy such microhabitats as crevices in rocks

and stones, where thermal conditions are more uniform. According to Dulić (1971), the presence of suitable shelters determines the distribution of the bank vole in this extreme part of the range of this species.

Among environmental factors influencing the occurrence of the bank vole, most important are those determining the possibility of burrowing, providing shelters, and securing food. The burrowing ability of the bank vole is relatively poor, so they prefer soft, humus soils in deciduous and mixed forests, easily accessible corridors within root systems of trees growing in clumps in alder forests, or suitable shelters among stones in mountain forests. Their preference for a good shelter in the form of plant cover or stony ground might be related to their relative poor agility and prolonged activity period, which includes some daylight hours. Wrangel (1940) analysed a number of morphological adaptations related to the activity pattern in the bank vole.

The diversity of habitats is closely related to the diversity of food available for bank voles. Broad possibilities of using natural resources are discussed in detail in section 3.1 on the diet. A typical example of adaptative changes in the diet is given by Koshkina (1957) from the Kola Peninsula. In northern areas sparsely covered with herbaceous plants, bank voles commonly use lichens growing on trees, fungi, and roots of trees, with an addition of animal food. The bulk of the diet of this species consists of green plant parts, seeds, and fruits of herbaceous plants (Gębczyńska, 1976).

A large variability in the diet of the bank vole over the annual cycle and from one geographical zone to another suggests that food is not a factor limiting geographical distribution of this species. It is probable that an entire set of ecological factors in forests has an effect on the occurrence of this species. The geographical range of this species at least in Europe, seems to be filled with respect to the geographical distribution of the habitats occupied. Possibilities of a further expansion of this species seem very limited, particularly in view of increasing urbanization and other kinds of human impact. Forests will remain the principal refuge of this species, including pine monocultures especially of lower age classes, which provide suitable habitat conditions. Agrocoenoses, independent of the crop structure, do not seem to ensure much chance for a future expansion of the living space for the bank vole.