

Table 1 summarizes some of the diagnostic characteristics as well as the geographic distribution of the 10 lemming species; for further details, see Chapter 3. Table 2 summarizes the habitat use, during summer and during winter, of the various lemming species.

Lemmings have from ancient time (i.e. at least back to the 16th century) been known to shift habitats seasonally (see Chapters 8, 10 and 11); the Norwegian lemmings have also been known (for at least the past 700–800 years to move occasionally in great numbers over long distances (see also Chapters 8 and 9). In Chapter 8, Henttonen & Kaikusalo provide an explanation for how the seasonal migrations can occasionally give rise to mass movements.

Table 1 Diagnostic characteristics of living lemming species and their geographic distribution

Species*	Pelage	Geographic distribution†	Sources
<i>Lemmus lemmus</i>	Black, yellow, brownish (see front page); extensive individual variation in coloration; colour changes with age	Fennoscandian alpine and subarctic areas	Our own observations and Tast (1982)
<i>L. sibiricus</i>	Summer pelage: brownish.	Siberian tundra	Ognev (1948) and Corbet (1978)
<i>L. amurensis</i>	Winter pelage: grey Smaller than <i>L. sibiricus</i> ; otherwise similar	Mountains, south of Siberia	Ognev (1948) and Corbet (1978), Ognev described this species on the basis of three specimens
<i>L. trimucronatus</i>	Very similar to <i>L. sibiricus</i>	Northern part of North America	Banfield (1974) and Hall (1981)
<i>Dicrostonyx groenlandicus</i>	Summer pelage: greyish to brownish with distinct black stripes. Winter pelage: white. In winter, claws on forefeet become extended and bifurcated	North American tundra; northern Greenland	Banfield (1974) and Hall (1981)
<i>D. torquatus</i>	Very similar to <i>D. groenlandicus</i>	Siberian tundra	Ognev (1948) and Corbet (1978)
<i>D. hudsonicus</i>	Very similar to <i>D. groenlandicus</i>	Tundra zone of the Quebec-Labrador peninsula	Banfield (1974) and Hall (1981)
<i>Myopus schisticolor</i>	Ash-grey with reddish spot on back	Euro-Asian taiga	Our own observations and Niethammer & Henttonen (1982)
<i>Synaptomys cooperi</i>	Brownish all year round	East and central North America	Banfield (1974) and Hall (1981)
<i>Mictomys borealis</i>	Similar to <i>S. cooperi</i>	North America from Labrador to Alaska	Banfield (1974) and Hall (1981)

* According to Jarrell & Fredga (Chapter 3).

† See maps in Chapter 3.

Table 2 Habitat use of living lemming species; based upon Ognev (1948), Banfield (1974), Corbet (1978), Hall (1981), Niethammer & Krapp (1982) as well as other chapters in this volume

Species*	Main habitat type		Movements
	Summer	Winter	
<i>Lemmus lemmus</i>	Wet, often paludified, areas on bogs or close to open water	Snow bed vegetation; drier areas on mineral soil	Extensive dispersal during peak years from alpine to subalpine areas sometimes extending down to sea level or deep into the taiga
<i>L. sibiricus</i>	Areas with many sedges	Mossy areas with dwarf birch (with permanent snow cover)	Much movements across the tundra in peak years
<i>L. amurensis</i>	Taiga regions	?	?
<i>L. trimucronatus</i>	Wet tundra rich in grasses and sedges	Moves to wet meadows in winter	Moves down into the valleys in peak years
<i>Dicrostonyx groenlandicus</i>	Elevated drier areas	Lower areas with sedges	?
<i>D. torquatus</i>	Dry upland tundra	?	Young individuals are known to move to higher areas in peak years
<i>D. hudsonicus</i>	Similar to <i>D. groenlandicus</i>	Similar to <i>D. groenlandicus</i>	Similar to <i>D. groenlandicus</i>
<i>Myopus schisticolor</i>	Climax coniferous forest with a dense moss carpet. In peak years also on peat bogs and on paludified ground in forest	Drier areas in winter than in summer	Dispersing individuals may reach agricultural and urban areas during peak years
<i>Synaptomys cooperi</i>	Boggy areas with <i>Sphagnum</i> mosses	Move to drier areas	?
<i>Mictomys borealis</i>	Similar to <i>S. cooperi</i>	Similar to <i>S. cooperi</i>	?

* According to Jarrell & Fredga (Chapter 3).

WHERE DO THE LEMMINGS COME FROM?

What is the evolutionary history of the various lemming species? Lemmini are represented by fossils being distinct from Microtini and Ellobiini from at least 4.5–5 Myr ago (see Chaline, 1974, 1987; Gromov & Poliakov (1977; cited from Catzefflis *et al.* 1987)). Fossil records of *Dicrostonyx* and *Lemmus* in Europe and North America date back to the early and middle Pleistocene (cf. Guthrie & Matthews, 1971; Kowalski, 1977; Meldgaard & Bennike, 1989; Harrison, Bates & Clayden, 1989). Outside Alaska, fossil remains of *Lemmus* have not been found in North America. Fossils of *Myopus* are found only in the Old World (Kowalski, 1977).

Based on available paleontological evidence, the Lemmini is found to be an artificial polyphyletic group (Kowalski, 1977; Koenigswald & Martin, 1984). The only

How many kinds of lemmings? A taxonomic overview

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Keywords: *Synaptomys* – *Mictomys* – *Lemmus* – *Myopus* – *Dicrostonyx* – chromosomal evolution – lemming – holarctic – Beringia.

Abstract

Current literature is reviewed on the taxonomic status and zoogeography of the rodent tribes Lemmini and Dicrostonychini. Bog lemmings (*Synaptomys* and *Mictomys*) are two monotypic genera restricted to North America. Norway and brown lemmings (*Lemmus*) share similar, though apparently primitive, karyotypes but there is intersterility or reduced fertility between four potential species; the most significant barrier may be associated with past isolation in the Beringian glacial refugium. The monotypic wood lemming (*Myopus*) has a derived and somewhat variable karyotype. Collared lemmings (*Dicrostonyx*), aside from *D. hudsonius* of Ungava, appear to be a centric fusion/fission complex (Robertsonian fan) of chromosome races. Thus, much of their chromosome variability in North America may cause clinal gradients of intersterility rather than discrete races. Nevertheless, the many chromosome differences between populations in Siberia and populations of probable Beringian origin preclude interfertility. We suggest three names for collared lemmings but the number of species in both *Dicrostonyx* and *Lemmus* is indefinite.

INTRODUCTION

In any specific locality, there is little difficulty in distinguishing lemming species. But, from a geographic perspective, populations may be difficult to fit into discrete categories. Also, because rodents are a diverse rapidly evolving group, even their higher taxonomic categories are fluid. Consequently, the nomenclature of lemming taxonomy is unstable and confusing. Our objective is to brave this chaos and attempt a useful overview of the taxonomy and zoogeography of recent lemmings. Within the Norway and brown lemmings (*Lemmus* Link) and within the collared lemmings (*Dicrostonyx* Gloger), breeding experiments and chromosome studies have shown that representatives of several named subspecies are intersterile to various degrees. Because much work is still needed, we hesitate to answer the question in our title with a simple integer and our effort is not a taxonomic revision. Nevertheless, we do amalgamate the recent work of others and offer a classification which we hope is useful and reflects recent understanding.

Like many common names, the world 'lemming' corresponds only approximately with a formal taxon. All rodents called lemmings are members of the larger family or subfamily variously referred to as Microtinae (Simpson, 1945), Arvicolidae (Chaline, Mein & Petter, 1977), or Arvicolinae (Carleton & Musser, 1984). Included in this group with lemmings are voles and muskrats.

Simpson (1945) divided Microtinae into three tribes: Lemmini, Microtini, and Ellobiini. Simpson's Lemmini includes four recent genera: *Dicrostonyx*, *Synaptomys* Baird, *Myopus* Miller, and *Lemmus*. Within Microtini, *Lagurus* Gloger are often called grey lemmings or steppe lemmings and, within Ellobiini, *Ellobius* Fischer are sometimes called mole lemmings. For our purposes, the general term 'lemming' is equivalent to Simpson's Lemmini. Chaline (1972) relegated the collared lemmings (*Dicrostonyx*) to a separate subfamily of Arvicolidae, *Dicrostonychinae*. And Rausch (1980) argued that collared lemmings should be regarded as a separate tribe (*Dicrostonychini* Kretzoi) within Simpson's subfamily Microtinae. Thus, within the arvicolines, lemmings may not be monophyletic. A diphyletic origin implies independent origin of the X-linked mutation giving rise to XY females common to wood lemmings (Fredga *et al.*, 1976) and collared lemmings (Gileva & Chebotar, 1979). This phenomenon appears to be ubiquitous within both genera (Kozlovsky, 1985; Malcolm, Brooks & Bogart, 1986; Jarrell, unpubl.).

Though collared lemmings have unique features, the position of the lower incisor in the mandible is a diagnostic feature shared with other lemmings. In lemmings, the root of the incisor is completely medial to the molars, whereas, in voles, the root of the incisor is much longer and passes distally under the molars and often onto the condylar process of the mandible.

Lemmings are often recognized easily by their front feet. The thumb is small but the nail is large and flattened (ligulate) in all but the collared lemmings. In these, the front feet develop distinctive winter claws. On digits III and IV, both the unguis and subunguis extend together but separate to form two tips on each claw; hence the generic name (Gr. *dikeros* + *stonyx* = forked, or cloven point) and the Russian common name, hoofed lemmings.

But most obviously, lemmings epitomize arvicoline rodents: short-legged, short-tailed, short-eared, northern mice with continuously growing prismatically cusped molars. Table 1 is a classification of lemmings using the higher categories of Carleton

Table 1 A classification of recent lemmings. All names of indefinite status are included for *Lemmus* and *Dicrostonyx*. The extent of synonymy by various recent authorities is indicated as follows: (1) cytotypes suggested by Pokrovski *et al.* (1984) and by Gileva *et al.* (1984); (2) synonymy according to Honacki *et al.* (1982); (3) synonymy according to Corbet (1978) and Musser & Carleton (1993); (4) synonymy according to Hall (1981); (5) this chapter

Order RODENTIA	
Family MURIDAE	
Subfamily ARVICOLINAE	
Tribe LEMMINI Simpson, 1945	
Genus <i>Synaptomys</i> Baird, 1858	
<i>S. cooperi</i> Baird, 1858 (southern bog lemming)	
Genus <i>Mictomys</i> True, 1894	
<i>M. borealis</i> (Richardson, 1828) (northern bog lemming)	
Genus <i>Lemmus</i> Link, 1795 (Norwegian and brown lemmings)	
<i>L. lemmus</i> (Linnaeus, 1758)	1
<i>L. amurensis</i> Vinogradov, 1924	2
<i>L. sibiricus</i> (Kerr, 1792)	3
[= <i>L. obensis</i> Brants, 1827]	
<i>L. chrysogaster</i> Allen, 1903	1
<i>L. trimucronatus</i> (Richardson, 1825)	
[includes <i>L. nigripes</i> (True, 1894)]	
<i>L. novosibiricus</i> Vinogradov, 1924	
Genus <i>Myopus</i> Miller, 1910	
<i>M. schisticolor</i> Lilljeborg, 1844 (wood lemming)	
Tribe DICROSTONYCHINI Kretzoi, 1955	
Genus <i>Dicrostonyx</i> Gloger, 1841 (collared, hoofed, or varying lemmings)	
<i>D. hudsonius</i> (Pallas, 1778)	3
<i>D. torquatus</i> (Pallas, 1778)	
<i>D. vinogradovi</i> Ognev, 1948	5
<i>D. exsul</i> G.M. Allen, 1919	
<i>D. groenlandicus</i> (Traill, 1823)	4
<i>D. kilangmiutak</i> Anderson and Rand, 1945	
<i>D. nelsoni</i> Merriam, 1900	
<i>D. richardsoni</i> Merriam, 1900	
<i>D. rubricatus</i> (Richardson, 1889)	
<i>D. unalascensis</i> Merriam, 1900	

& Musser (1984). Division of lemmings into two tribes follows the view of Chaline (1972) and Rausch (1980).

BOG LEMMINGS

Bog lemmings were formerly viewed as two species in the genus *Synaptomys*. In a recent revision (Koenigswald & Martin, 1984), northern bog lemmings were elevated to their own genus, *Mictomys* True, on the basis of molar structure. Other paleontologists (i.e. Reppening & Grady, 1988) accept this view but neontologists Musser & Carleton (1993) apparently dismiss it, continuing to list both species as *Synaptomys*. Koenigswald & Martin recognized the similarities between these two

genera by including both in the tribe Synaptomyini. This designation could be maintained as a subtribe under the Lemmini, if the classification we have inferred (Table 1) is accepted.

The southern bog lemming, *Synaptomys cooperi* Baird, and northern bog lemming, *Mictomys borealis* (Richardson), are two recent species restricted to North America (Fig. 1). Fossil *Synaptomys* from Russia are the earliest known lemmings (Koenigswald & Martin, 1984).

Synaptomys cooperi has 50 chromosomes; the autosomes are a graded series of single-armed (telocentric) chromosomes (Hoffman & Nadler, 1976; Modi, 1987). A similar karyotype is found in *M. borealis* except that there are four more telocentric autosomes (Matthey, 1973a). Both species have biarmed X chromosomes. Karyotypes such as those of the bog lemmings, that is, 46–56 telocentric autosomes, are thought to be near the ancestral arvicolid condition (Matthey, 1973b; Modi, 1987). Studies are few (Fig. 1), but, given these presumably conserved characteristics, intraspecific chromosome variation may be minimal in bog lemmings.

NORWEGIAN AND BROWN LEMMINGS

The Norway lemming, *Lemmus lemmus* (Linnaeus), and the brown lemmings, *L. sibiricus* Kerr (*sensu lato*), form a closely related circumpolar complex (Fig. 2). Their

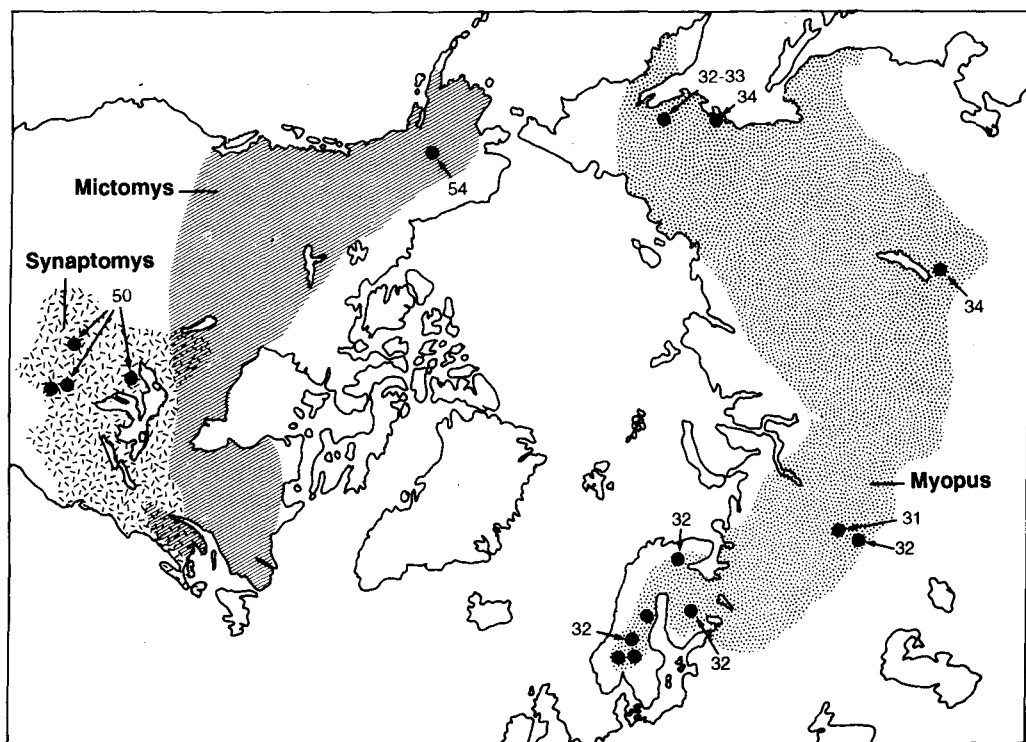


Figure 1 The distribution of *Synaptomys cooperi*, *Mictomys borealis* and *Myopus schisticolor*. Chromosomes have been studied in lemmings from the localities indicated. Diploid numbers are given. For references, see text.

lemmings are as unique as they seem to be in this respect: what is the molecular basis for the particular X*-mutant occurring in these two lemming genera? We may, in this work, take advantage of the recent advances in gene technology.

Work on the wood lemming has over the past 30 years focused on 'why the extensive female bias'. Much less attention has been given to possible ecological and dynamical consequences of the greatly biased primary sex ratio. For example, what are the population consequences of this trait? And, what are the consequences of the highly female biased primary sex ratio on the spacing and mating systems and sexual selection? Both modelling work and empirical work are needed in order to untangle these puzzles: in particular, we might in this connection benefit from comparative studies on the ecology of wood lemmings and collared lemmings.

WHAT ABOUT THE BOG LEMMINGS *SYNAPTOMYS* AND *MICTOMYS*?

In Chapter 3, Jerrell & Fredga referred to five lemming genera. In this book we have focused primarily on *Lemmus*, *Dicrostonyx* and *Myopus*, with a whole section almost completely devoted to the latter genus. What about the two remaining genera?

Very little is, in fact, known about these two genera. From a search in the recent literature (Biosis and Zoological Records), only 125 references out of a total of 1277 on lemmings dealt with *Synaptomys* and *Mictomys*. Except for a few studies on demography (Gaines, Rose & McLenaghan, 1977; Beasley & Getz, 1986), dispersal (Gaines & McLenaghan, 1977), and habitat selection and interspecific competition (Linzey, 1984; Danielson & Gaines, 1987) on *Synaptomys cooperi*, most of these studies were based on either anecdotal accounts or were on topics other than population biology. More long-term studies on this species as well as on *Mictomys borealis* are required in order to establish a basis comparable to the studies on *Lemmus*, *Myopus* and *Dicrostonyx*. Such studies on *Synaptomys* and *Mictomys* may indeed be of great importance in our efforts to untangle the puzzles of the lemming cycle since these species, to a large extent, live in other (more southerly distributed) biomes than do *Lemmus*, *Myopus* and *Dicrostonyx*.

THE ECOSYSTEM CONTEXT OF THE LEMMING CYCLE

From lemmings to ecosystem complexity and stability, and back to lemmings again

As pointed out in Chapter 1, Elton (1924, 1942) initiated the modern area of research on the ecology of lemmings. With his book *The Ecology of Invasions by Animals and Plants*, Elton (1958) focused on another ecological topic, the analysis of food webs. These two fields of study are indeed more closely connected than often seems to be appreciated: population cycles are more prevalent in the fairly simple arctic and alpine systems, even though they do occur elsewhere (e.g. Pimm 1991). Indeed, the lemmings still represent a major challenge to much of the work within the field of community ecology and stability (cf. Pimm, 1991). We will review briefly the field of food web analysis as it pertains to lemming studies.

At the time of the publication of Elton's book, Robert MacArthur (1955) published

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