

Taxonomy and zoogeography of *Lemmus* spp. (Rodentia: Arvicolinae), with notes on laboratory-reared lemmings

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Introduction

Lemmings of the genus *Lemmus* Link, 1795, have long attracted interest because of the high numerical densities attained at intervals by their populations. In earlier times, in northern Europe, such events seemed so remarkable as to be explained by some as a consequence of the animals' having fallen from the sky (HÖGSTRÖM 1749). During the last 25 years, lemmings have been the object of intensive ecological investigation in Eurasia and North America, although there has been no consensus concerning their taxonomic relationships.

In 1959, a colony of brown lemmings from arctic Alaska was established in our laboratory, primarily to provide experimental animals for the study of zoonoses indigenous to arctic and subarctic North America. A colony of lemmings from Fennoscandia was similarly established in 1964. The lemmings proved to have advantages as laboratory animals, and at the same time the existence of the colonies permitted observations to be made on their biological characteristics and comparisons of chromosomes to be undertaken for the two forms and their hybrids. The results of these observations and comparisons, with a review of the zoogeography of *Lemmus*, are reported in the present paper.

Materials and methods

For convenience of reference, the nomenclature for North American lemmings is according to HALL and KELSON (1959).

A colony of *Lemmus trimucronatus alascensis* Merriam from Point Barrow (arctic coast of Alaska) was first established in 1954 but was lost in 1958. After re-establishment in October 1959, with 8 individuals from the same locality, it has been maintained to the present time. A subcolony of individuals of *L. t. subarcticus* Bee and Hall, from north-eastern Alaska (Beaufort Lagoon), and *L. t. alascensis* has been maintained since 1970. The colony of *L. lemmus* (Linnaeus) was established in 1964 with 11 animals from Norway, and cross-breeding between *L. lemmus* and *L. trimucronatus* was carried on during 2 years. Three males of *L. nigripes* (True) from St. George Island (Pribilof Islands) were crossed with females of *L. trimucronatus* and *L. lemmus*. Additional subcolonies of *L. trimucronatus* consisted of melanistic animals and hairless mutants. Complete data for the 30—35 generations of *L. trimucronatus* produced during the 14.5 years of the colony's existence (2 generations per year were most common, but 3 were occasional) are not summarized here; the information given is intended to provide a basic definition of characteristics of laboratory-reared animals. Biological data were recorded for many individuals from birth to death.

Tissues for microscopic examination were fixed in 10 % formalin, embedded by the paraffin method, sectioned at 0.005—0.010 mm, and stained routinely in hematoxylin-eosin. Special stains were applied as necessary.

For cytogenetic studies, animals trapped or taken from the colonies were: *L. trimucronatus alascensis*, 10 ♂♂, 5 ♀♀; *L. t. alascensis* x *L. t. subarcticus*, 2 ♂♂, 3 ♀♀; *L. t. subarcticus*, 1 ♀; *L. t. yukonensis* Merriam, 1 ♂; *L. nigripes*, 2 ♂♂; and *L. lemmus*, 5 ♂♂, 3 ♀♀. The series of *L. t. alascensis* included individuals with normal (brown) pelage and melanistic

pelage, as well as hairless mutants. Preparations were made also from crosses: *L. trimucronatus* x *L. lemmus*; *L. t. alascensis* x *L. nigripes*; and from progeny obtained by crossing F₁ hybrids back to parental forms.

The animals were given 0.4 ml of 0.05 % colcemid intraperitoneally, after which tissues were collected and treated with 1 % sodium citrate, stained in 2 % acetic orcein, frozen on solid CO₂, and mounted permanently on slides (CONGER and FAIRCHILD 1953; NADLER and BLOCK 1962). From *L. nigripes*, only testicular preparations in lactic-acetic-orcein were studied (WELSHONS et al. 1962). Preparations to demonstrate G-bands were made following the method of SEABRIGHT (1972), but with the use of marrow and flame-dried as recommended by Dr. C. F. NADLER (personal communication). Chromosomes were counted in 10 to 50 cells from each animal. Experimental karyotypes were assembled from photographs of 36 cells in mitotic metaphase, and total lengths of acrocentric chromosomes and arm-ratios of metacentric-subtelocentric chromosomes were recorded for 5 ♂♂, 5 ♀♀, Point Barrow-Beaufort Lagoon origins; 1 ♂, Seward Peninsula; and 1 ♂, St. George Island. Such ratios were obtained for subtelocentric chromosomes in specimens of hybrids and back-crosses. Measurements of sex-chromosomes in meiotic preparations were recorded for 5 ♂♂ (*L. t. alascensis*). For comparison, karyotypes were assembled for 2 ♂♂ and 2 ♀♀ of *L. lemmus*. The karyotypes, each from a single cell from marrow, spleen, or testis were arranged by pairing chromosomes by length and conformation. Examination of meiotic preparations was helpful in selecting the sex-chromosomes. The identity of pairs was also established by correlation of G-bands in 5 *L. t. alascensis*, 2 *L. t. alascensis* x *L. t. subarcticus*, and 3 *L. lemmus*.

Characteristics of laboratory-reared lemmings

When the colony was well established, with reproduction occurring regularly, the breeding stock of *L. trimucronatus* was selected for large, relatively docile animals, eliminating the smaller, hyperactive individuals that were usually more aggressive. Inbreeding was avoided to the extent possible within the constraints of a colony numbering usually 100–120 animals, of which about 20 pairs were breeding. However, brother-sister matings were made occasionally, and this practice was routine in attempts to perpetuate a mutation (see below). Numbers of *L. lemmus* were kept at the minimum required to maintain the colony, i. e., not more than 50 individuals, of which 4–6 pairs were reproducing.

Housing

The rodents were kept in stainless-steel cages, 46 × 33 × 16.5 cm in size, with slip-over lids covered by 5 mm stainless-steel mesh. Shavings of wood were used as litter, with cotton for nesting; nest-boxes were not provided. After losses due to disease had occurred on several occasions, a regime was established under which cages were cleaned twice weekly, thoroughly washed as required, and autoclaved whenever signs of disease were noted. Eventually, too, all animals were kept under constant illumination at temperatures from 13 to 18° C. Until the colony was moved from Anchorage to Fairbanks in 1967, relative humidity could not be controlled; since 1967, it has ranged from 30 to 40 % in the animal room.

Diet

Two similar diets proved to be suitable for *L. trimucronatus* as well as for most arvicoline rodents of other species that were maintained. These consisted of: 1) lettuce and carrot *ad libitum*, supplemented with alfalfa pellets and commercial mouse-diet (crude protein, 24 %; crude fat, 4 %); and 2) mouse-diet, alfalfa pellets, carrot, and water *ad libitum*. Water-intake by brown lemmings averaged 30 ml per animal over a 24-hour period. Approximately equal numbers of *L. trimucronatus* were maintained on each diet. The colony of *L. lemmus* received only the second

diet, supplemented with small quantities of lettuce. The use of mosses as food for *L. lemmus* was economically not feasible, although such vegetation has been considered important for the maintenance of this species in captivity (FRANK 1962; DE KOCK 1966; MARCSTRÖM 1966).

Growth and development

For *L. trimucronatus*, weights were recorded for individuals in litters born throughout the year to pairs maintained on the first diet, beginning on the day of birth and continuing until death. The mean birth-weight of 46 animals (24 ♂♂, 22 ♀♀) was 3.97 gm, with a range of 3.0–5.2 gm. At the time the young were removed from the breeding-cages, individual weights ranged from 13.5 to 30.1 gm (avg. of 41: 20.6 gm). After the animals were a month old, mean bi-weekly gains in weight (not including pregnant females) ranged from 1.2 to 4.0 gm until an age of about 5 months (140 days), after which the rate of growth decreased or stabilized. Mean weight at an age of 140 days was 59.5 gm. The maximum weights recorded were: males, 131.4 gm; nonpregnant females, 95.4 gm; and pregnant females, 114.2 gm.

A light dorsal pelage was apparent 2–3 days after birth; the pinnae became well defined in 3–6 days; a dorsal stripe was evident in 4–6 days; and the pelage was becoming brownish at 6 days. The eyes opened 6–8 days after birth; the lower incisors were visible after 3 days; the upper incisors were visible after 6 days, as were the nails and the ventral pelage. The young were active in the cage 8–9 days after birth, and began to eat solid food at an age of 12–14 days. The sex of young animals could be determined macroscopically within 7–10 days after birth.

Total lengths of brown lemmings less than 14–18 days old were not recorded routinely; at an age of 2 days, the animals ranged in length from 44.5 to 50 mm. At 26–34 days of age, mean total lengths were 104.8 mm for 35 males and 110.1 mm for 35 females, combining animals on both diets. When fully grown, at an age of 5 months or more, total lengths ranged from about 140 to 160 mm. The maximum life-span of the laboratory-reared animals was about 2 years, although few were kept so long.

Reproduction

Lemmings of both species were usually paired for breeding at an age of about 2 months. The pairs remained permanently together for up to a year, after which, to sustain productivity in the colony, they were replaced with young animals. Litters were produced regularly throughout the year, and the sex-ratio of the progeny was approximately 1:1. The young animals were removed from the breeding-cages when 14–18 days old.

Copulation usually took place immediately after pairing, and postpartum copulation was characteristic thereafter. The gestation period (minimum interval between litters) of *L. trimucronatus*, not calculated to the hour, was 20–21 days. One pair established when the female was 48 days old had 5 litters at intervals of 20, 21, 20, 21, and 21 days, beginning with the first copulation. The length of intervals between litters tended to increase after about the sixth. One pair produced 8 litters 21, 20, 23, 19, 23, 21, and 40 days apart, after which the male died; another male was introduced, and the next litter was born 21 days after pairing, followed by others at intervals of 42, 23, 58, and 22 days, when the pair was replaced with young stock. For a series of 101 litters, the intervals ranged from 17 to 197 days, with a mode of 21. Recorded intervals of less than 20 days were: 17 days, 1; 18 days, 2; and 19 days, 8.

The mean size of litters of *L. trimucronatus* was between 4 and 5. In 56 litters produced by animals on the first diet, numbers ranged from 1 to 10 (avg. 4.4; mode 4), for a total of 248 progeny. In 88 litters produced by animals on the second diet, the range was the same, with a mean of 4.2 and a mode of 3, for a total of 371 progeny. A mean litter-size of near 7 has been reported for wild *L. trimucronatus* based on embryo-counts (KREBS 1964; MULLEN 1968).

The females attained sexual maturity at an early age; the vagina was perforate in many animals at an age of 14 days. During 1962–63, an unusual number of young females was found to have been inseminated by the male parent before the young had been removed from the breeding-cages. For some, pregnancy was confirmed when the animals were killed for examination at an age of 20 to 31 days, and maximum ages at which insemination could have occurred (i. e., ages at time of removal from the breeding-cages) were 14 days, 1; 15 days, 2; 16 days, 1; 17 days, 4; 18 days, 2; and 19 days, 2. In addition, 4 young females produced litters at ages of 35, 36 (2), and 39 days. The earliest age at which spermatozoa were found in the epididymis of a male was 22 days; the testes of this animal measured 7×6 mm. Wild females have been estimated to attain sexual maturity at an age of 3 to 4 weeks (KREBS 1964; MULLEN 1968); KREBS considered that males become sexually mature at an age of 4 to 5 weeks.

During 1962–63, the early attainment of sexual maturity in young females was correlated with increased productivity in the colony. For the period January–April 1961, as a comparison, 17 pairs produced 169 progeny, for an average of 9.9 per pair, whereas during the same period in 1963, 33 pairs produced 409 progeny, for an average of 12.4 per pair. That extrinsic factors were responsible for this variation was not apparent.

The gestation period of *L. lemmus* was also 20–21 days, as reported by KALELA (1961) and FRANK (1962). For 26 litters produced by 4 pairs, the range in number was 1 to 7 (avg. 4.8; mode 4), for a total of 125 progeny. For wild lemmings, based on small numbers of embryo-counts, WILDHAGEN (1953) reported a mean of 5.9; for captive animals, means were 4.1 (FRANK 1962), 5.1 (KALELA 1961), and 5.3 (MARCSTRÖM 1966). The intervals between litters were usually less uniform than in *L. trimucronatus*, in our colonies, although the upper extremes were not so great. Nine litters produced by one pair were separated by intervals of 27, 17, 30, 23, 39, 23, 29, and 20 Days. Insemination of young females by the male parent in the breeding-cages occurred occasionally. FRANK (1962) observed that the vagina may be perforate in 12-day-old females, and the production of litters by females 35 and 39 days old was reported by KALELA (1961) and FRANK, respectively.

Diseases and abnormalities

During two years after the colony of *L. trimucronatus* was re-established in 1959, a significant mortality was associated with fatty metamorphosis of the liver, the cause of which was not specifically determined. In early stages of the disorder, the liver was pale yellow and somewhat enlarged. It was found in sections that hepatic cells around the central veins were usually first affected, and the changes progressed to extensive cirrhosis. After it became possible to maintain uniform low temperatures in the animal room, this condition was no longer a problem. In laboratory rats, it has been found that lower temperatures have a lipotropic effect, preventing fatty metamorphosis in the liver of animals receiving a diet low in choline (cf. MASORO 1966), and we presume that a similar mechanism was involved in the case of the lemmings. Macroscopic signs of this condition were not observed in other arvicoline

rodents receiving the same diets, although evidence of slight hepatic lipidosis was sometimes found microscopically in varying lemmings, *Dicrostonyx* spp., and red-backed voles, *Clethrionomys rutilus* (Pallas).

Dental disorders, a serious problem, usually involved excessive growth of the incisors. Overgrowth of the molars ventrad or dorsad within the alveoli, often associated with periodontal disease, abscess-formation, and pressure-effects (e. g., on the optic nerve), has rarely been observed in *Lemmus*, although it was not unusual in certain other species (e. g., *Dicrostonyx* spp.; *Microtus abbreviatus* Miller) in the laboratory. This condition we attributed to insufficient abrasion of the molar surfaces.

Bacterial infections, both acute and chronic, occurred occasionally in lemmings as well as in rodents of other species. In *Lemmus*, enteritis and pneumonitis were the disorders most frequently observed. The pathogen commonly associated with pulmonary disease and occasionally with infections of the middle ear was identified as *Klebsiella pneumoniae*. Other organisms isolated from diseased lemmings were *Proteus* sp., *Alcaligenes metalcaligenes*, *Escherichia coli*, *Pseudomonas fluorescens*, *Aerobacter cloacae*, *Streptococcus pyogenes*, and *S. uberis*. Losses from such infections were much reduced under conditions of controlled low temperatures and increased humidity.

Neoplasia were found rarely in *Lemmus*, as compared with some of the other arvicoline rodents in the colonies. Gastric papillomatosis, occurring frequently in *M. abbreviatus* (cf. RAUSCH and RAUSCH 1968), was recorded once in *L. trimucronatus*. Single cases were observed also of the following: adenocarcinoma of the pancreas, with possible metastasis to the ovary; adenocarcinoma of mammary origin; subcutaneous lipoma; and mesothelioma, extensively involving the serosal surfaces of the abdominal cavity. A subcutaneous mass identified macroscopically as a tumor in one animal was found to be a mycotic abscess, probably mucormycosis. This condition has been reported in other species of rodents in our colonies (OHBAYASHI 1971).

A mite, *Laelaps lemmi* Grube, has been perpetuated since the colony of *L. trimucronatus* was established, and sometimes caused local irritation around the eyes of the animals. No helminths were perpetuated under laboratory conditions.

A mutation, congenital hypotrichosis, occurred in the colony of *L. trimucronatus* (Fig. 1); all mutants were descendants of a pair trapped at Point Barrow in 1959. In contrast to the mutation "hairless" (hypotrichosis cystica) in the laboratory mouse, *Mus musculus* Linnaeus, and described in *Microtus arvalis* (Pallas) by FRANK (1962a), early growth of hair did not occur in the mutant brown lemmings. However, an apparently similar mutation has been described in the golden hamster, *Mesocricetus auratus* Waterhouse, by FESTING and WRIGHT (1972). The first mutant brown lemming was born on 24 June 1961, after which additional specimens were obtained by inbreeding. The subcolony numbers about 40 animals at the present time.

The affected animals varied in degree of hypotrichosis, and completely hairless individuals were rare. In most, the body was hairless, normal-appearing pelage extended anteriorly from the eyes, vibrissae were well developed, and the feet were hair-covered. Sometimes sparse hair was present dorsally over the anterior portion of the body, or the entire dorsum was covered by a thin pelage. Excessive growth of nails seemed to be an associated condition, but no abnormalities were observed in the teeth. Hairless pairs did not produce uniformly hairless progeny, but the size of litters was small, suggesting the possibility that homozygosity is genetically lethal. The findings suggest that the pattern of inheritance of this mutation is consistent with that of an autosomal dominant gene expressing incomplete penetrance, as in hidrotic ectodermal dysplasia in man (J. W. LINDSAY, personal communication).



Fig. 1. A hairless mutant lemming with normal littermates. The animals are F₂ progeny, 20 days old, from a normal x hairless cross, *Lemmus trimucronatus alascensis*

Hairless animals were recognizable at birth by their uniform pink color, contrasting with the darker dorsum of normal or partially hairless individuals. The hairless skin did not change macroscopically with age, and cyst-formation characteristic of the mutation "hairless" was not observed. Under low magnification, numerous short, colorless hairs were visible in ostensibly hairless areas, and isolated guard-hairs were occasionally present. The surface of the skin was usually covered by sebum, with discrete accumulations extending from each hair-canal. When formalin-fixed skin was dehydrated and cleared in xylene, dissolving the sebum, hair-canals were found to be abundant, but few contained hairs. The openings of the canals at the surface were much distended, ranging in diameter from about 0.015 to 0.080 mm. There was no indication that the characteristics of the skin of hairless animals were affected by different ambient temperatures. The mutants tolerated higher temperatures than did normal animals.

Microscopically, the skin of hairless areas was characterized by scarcity and hypoplasia of hair-follicles, defective structure of hairs, usually hyperplasia of sebaceous glands, and distended hair-canals (Fig. 2). The stratum corneum was usually not thickened. The dermis consisted mainly of a loose stroma in which a few hypoplastic follicles of guard-hairs were scattered. Such hairs as developed usually lacked a medulla. The more superficial follicles associated with the under-fur were relatively numerous and contained defective, unpigmented hairs that rarely extended above the stratum corneum. The sebaceous glands were characteristically hyperplastic, with some variation in degree from area to area. Sebum accumulated in the hair-canals distal to the openings of the sebaceous ducts, causing marked distension. In the hairless females, the epidermis of all 8 teats was frequently hyperplastic, with deep fissures and hyperkeratosis. Since this condition prevented sucking, litters from such females usually died soon after birth. The mammary glands were usually normal histologically. FRANK (1962a) observed high mortality among litters of voles showing the mutation "hairless", because of dysfunction of the mammary glands.

The juxtaauricular glands (SCHAFER 1940, p. 235; MACPHERSON and GIBSON 1965) and the glandular area in the dorsal skin at the base of the tail (WALLIN 1967) were readily visible in the hairless animals. Microscopically, these glands appeared to be identical in structure. They may produce identical pheromones.

In 1953, when lemmings were abundant at Point Barrow, the population included

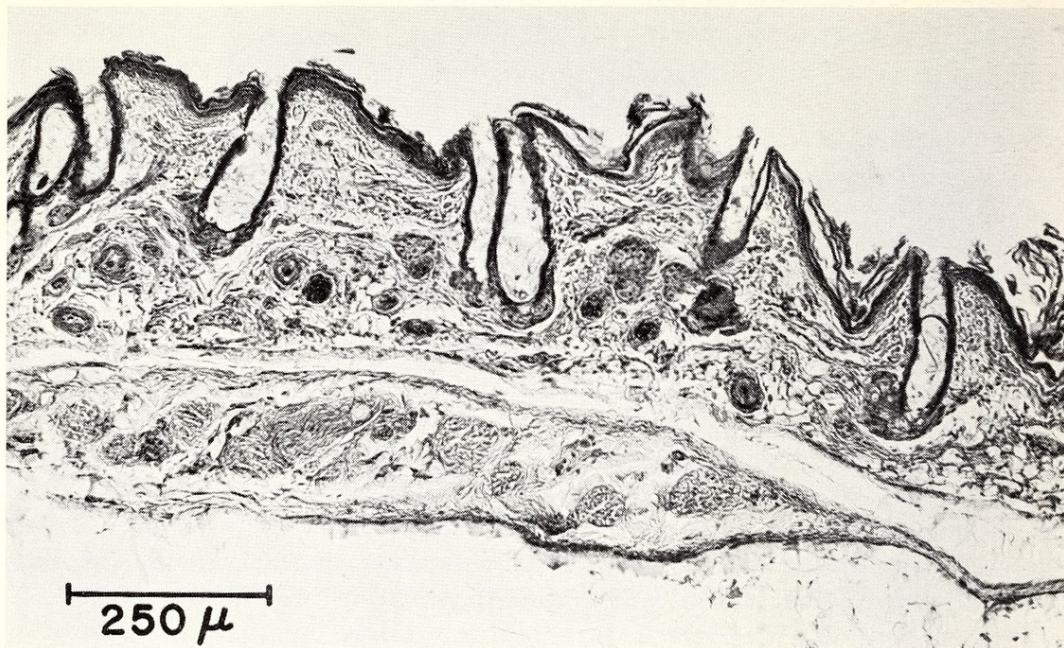


Fig. 2. Section of dorsal skin from a hairless mutant lemming. Hematoxylin-eosin

a small proportion of melanistic animals, some of which were sent to Anchorage and maintained in the laboratory. This character was inherited as a simple recessive. An iapparent mutation was observed in *L. lemmus* in 1966. The affected animals had a pure white juvenile pelage that was replaced by adult pelage of normal color and pattern.

Hybridization

For cross-breeding, mixed pairs of *L. trimucronatus* and *L. lemmus* were established in the laboratory under conditions described above. Of 15 pairs established, 11 produced 69 F_1 progeny in 16 litters ranging in size from 3 to 7 (avg. 4.3). The number was not recorded for an additional litter that was born dead. In pelage, the F_1 hybrids exhibited color-patterns like those of the parental types and intermediate (Fig. 3). Four litters (6, 6, 3, and 3) with the following combinations were typical: 1. 3 like *trimucronatus* and 3 intermediate, tending more toward *lemmus*; 2. 3 like *trimucronatus* and 3 like *lemmus*; 3. 3 like *trimucronatus*; 4. 3 intermediate, tending more toward *lemmus*. The pelage of the *lemmus*-like hybrids often showed a preponderance of black. The sex-ratio of the hybrids was approximately 1:1, and no correlation of sex with phenotype was discerned.

Eleven pairs of F_1 hybrids were maintained for 4 to 6 months, a period sufficient to permit breeding. The animals copulated readily, but none produced young, and it was determined microscopically from sections of testes that the males were typically sterile. The testes macroscopically were normal in size and development, but findings in sections indicated that early-stage failure of gametogenesis was characteristic. The epithelium of the testicular tubules was usually poorly developed, often with only a single layer of mixed Sertoli cells and spermatogonia; in some, a few primary spermatocytes were present (Fig. 4). Similar findings have been reported by SPANNHOF (1959) and ZIMMERMANN (1965) in male hybrids of red-backed voles, *Clethrionomys* spp. Five additional F_1 males produced no progeny when mated with females of the parental forms.

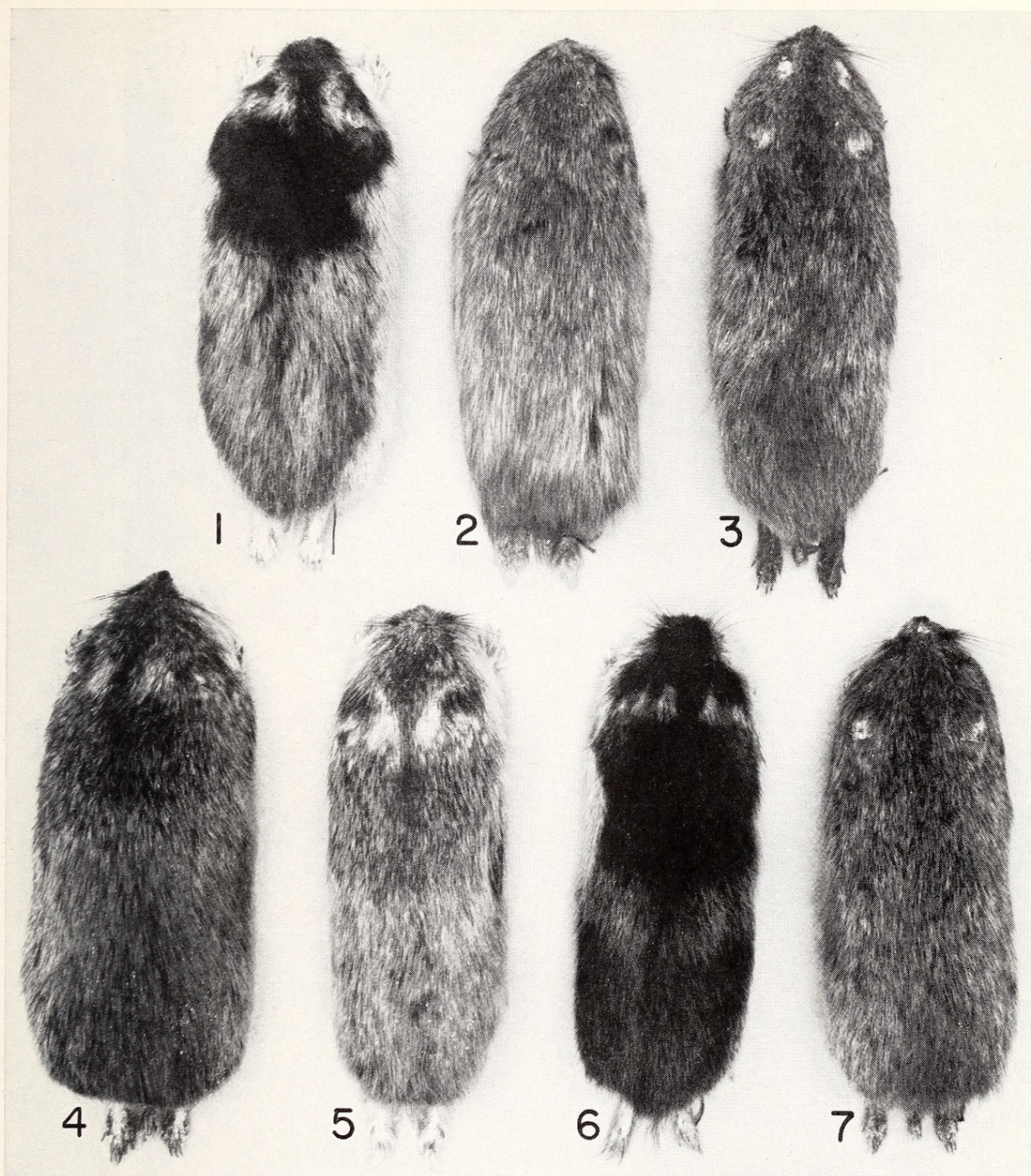


Fig. 3. Patterns of pelage of *Lemmus* spp. and their hybrids. 1 = *Lemmus lemmus*; 2 = *Lemmus trimucronatus*; 3 = *Lemmus nigripes*; 4—6 = Hybrids of *Lemmus trimucronatus* x *Lemmus lemmus*; 7 = Offspring of *Lemmus trimucronatus* x *Lemmus nigripes*

The F_1 females were usually, if not always, fertile. Eight crossed back to *L. trimucronatus* or *L. lemmus* produced 27 litters, totaling 94 young; numbers in 2 additional litters were not recorded. The average size of litters obtained from backcrosses was slightly smaller than that from crosses of parental forms. The sexes of the progeny were approximately equal, and no still-born young were recorded. In pelage, the progeny resembled the F_1 hybrids. Of 16 young (4 litters) produced by an F_1 female with *L. lemmus*, 14 were similar to *lemmus* and 2 were like *trimucronatus*. In other cases, intermediate patterns were observed.

In males produced by F_1 females crossed back to either parental form, the expected

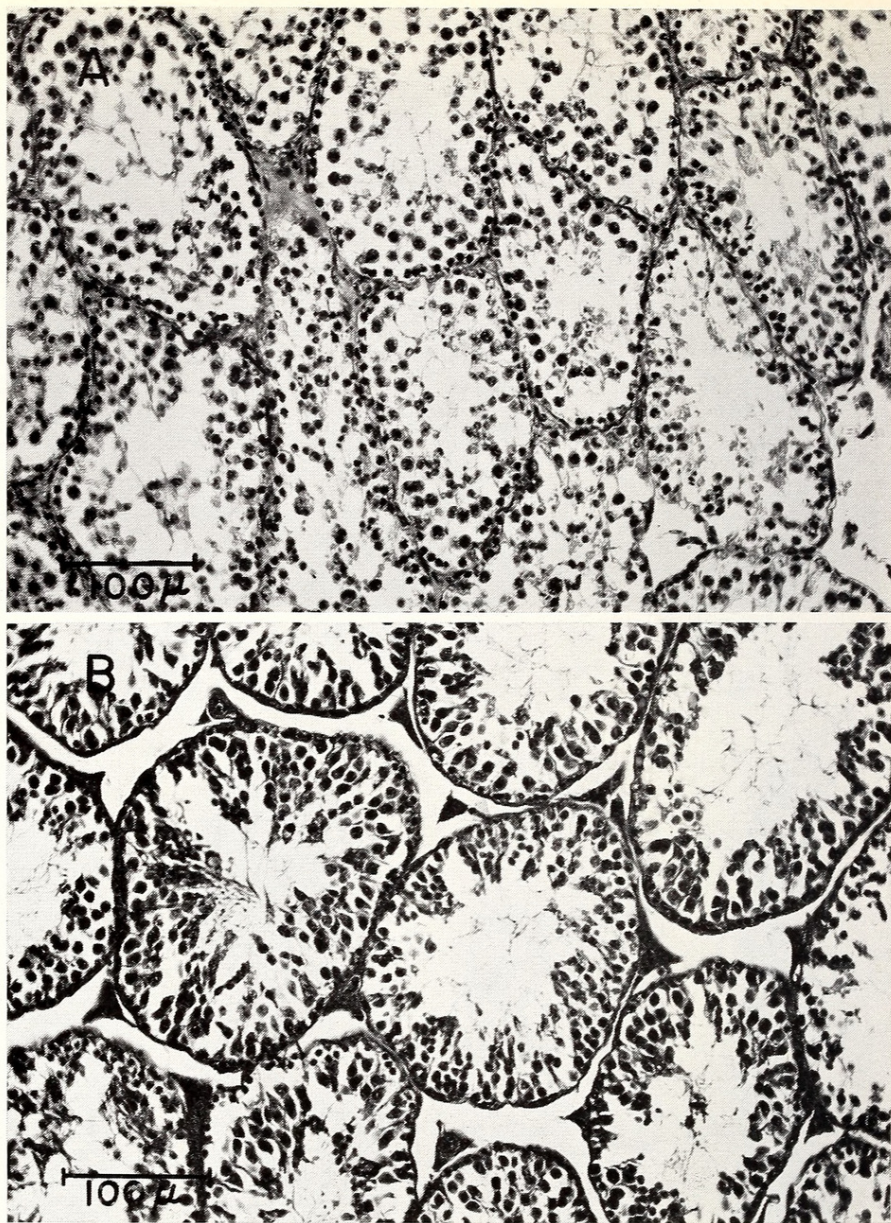


Fig. 4. Sections of testes of F₁ males from *Lemmus trimucronatus* ♂ x *Lemmus lemmus* ♀, showing gametogenic failure. A = Age 6.5 months. B = Age 11 months. Hematoxylin-eosin

ratio of fertile to infertile individuals would be 1:1, if it is assumed that normal gametogenesis would take place in half the males, i. e., those possessing compatible sex-chromosomes (see below). In sections of testes, the conditions observed ranged from near germinal-cell aplasia, with the tubular epithelium consisting of but a single layer of cells, to complete spermatogenesis (Fig. 5). In sterile males, developmental arrest occurred at various stages of gametogenesis; in those ostensibly fertile, in which gametogenesis had been complete, the spermatozoa sometimes had degenerated in situ, suggesting that fertility was at least reduced. In the few epididymides sectioned, the tubules were filled with eosinophilic debris, and no spermatozoa were identifiable. Male fertility was demonstrated by the mating of a male obtained from a back-cross with a similar female [*(L. trimucronatus* x *L. lemmus*) x *L. lemmus*]; however, only a single offspring was produced.

Only 2 males of *L. nigripes* were used for breeding. Each was mated successively with 2 female *L. trimucronatus*, resulting in a total of 10 F₁ progeny. In pelage-color, these were somewhat intermediate between the parental types (cf. Fig. 3). Both

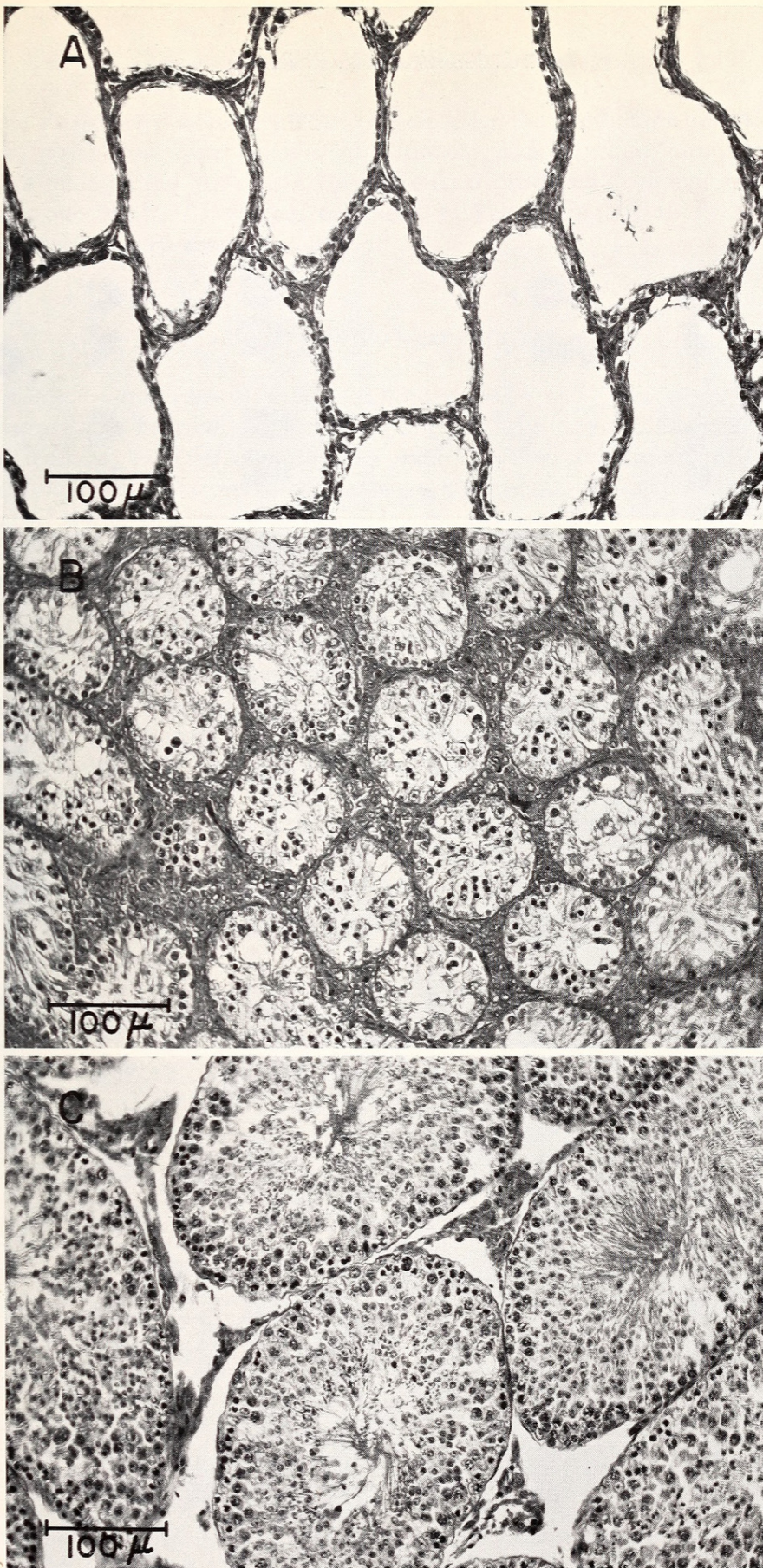


Fig. 5. Sections of testes from back-crosses of *Lemmus lemmus* ♂ x (*Lemmus trimucronatus* x *Lemmus lemmus*) F₁ ♀, showing variation in gametogenesis. A = Age 5 months. Aplasia of testicular epithelium. B = Age 5 months, littermate of A. Early gametogenic failure. Karyotype shown in Fig. 11, II. C = Age 5 months. Complete gametogenesis with degeneration of spermatozoa in the lumina of the tubules. Hematoxylin-eosin

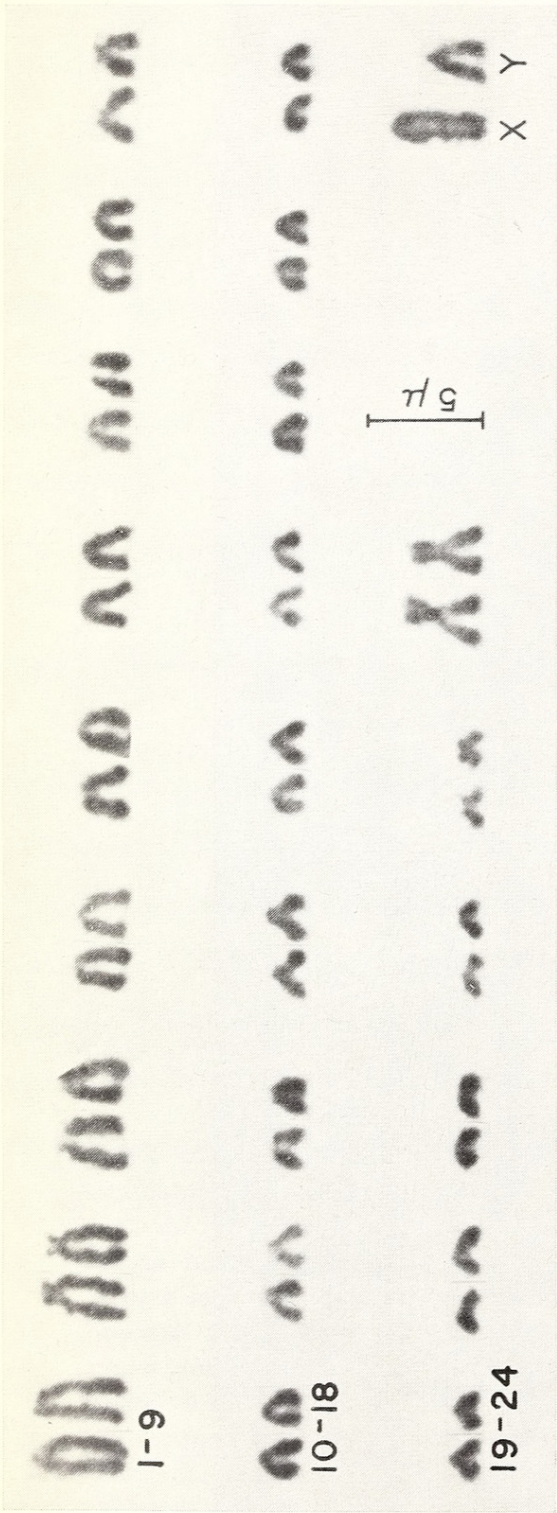


Fig. 6. Karyotype of *Lemmus trimucronatus*, male, $2n=50$. From marrow, orcein stain

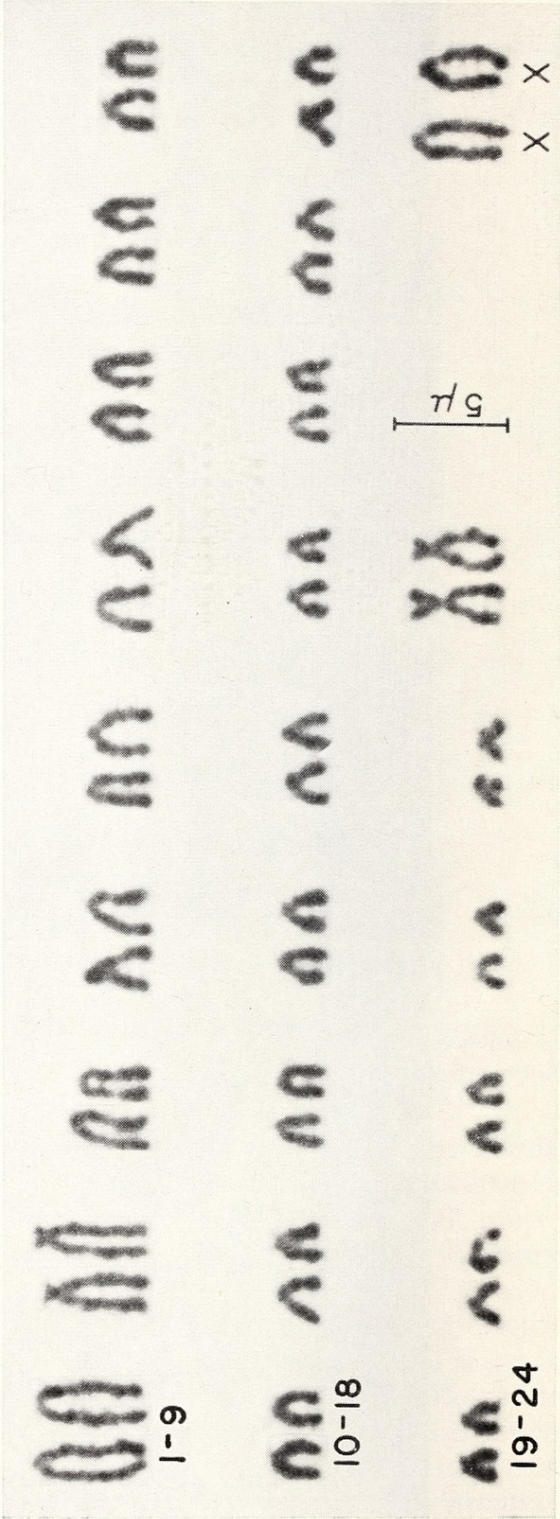


Fig. 7. Karyotype of *Lemmus trimucronatus*, female, $2n=50$. From marrow, orcein stain

sexes of the F_1 progeny were fertile, as indicated by the production of 24 young by the two F_1 pairs that were established. Crossing back of these animals also was successful; a male paired with an *L. trimucronatus* produced 8 young, and a female paired with one of the *L. nigripes* produced 4. The mating of an F_1 female with *L. lemmus* resulted in 10 progeny.

Description of karyotypes

Lemmus trimucronatus ($2n=50$). The diploid number was 50 and the NF 52 for animals from Point Barrow, Beaufort Lagoon, and the Seward Peninsula. In both males and females, 23 pairs of autosomes were classified as acrocentric (arm-ratios ≥ 6.05), although accurate measurements were not always obtainable because of the minute size of the small arms. Two of the largest autosomes in this group (pair No. 2 in the karyotypes) were near subtelocentric, and the small arms were well defined; the arm-ratio in this pair averaged 6.87, but the range was 6.05 to 8.20; classification of this pair as subtelocentric would bring the NF to 54. One autosomal pair was metacentric to subtelocentric (arm-ratio 1.58–3.95). The X-chromosome was identified as a large acrocentric element. The Y-chromosome, selected partly on the basis of measurements of the sex-bivalent in haploid figures, was acrocentric, and was near $3/5$ of the total length of the X. The chromosomes of one male cell and one female cell, with 23 acrocentric pairs of autosomes graded by size, and one metacentric-subtelocentric pair (No. 24) placed last among the autosomes, are arranged in karyotypes (Figs. 6 and 7). A meiotic preparation from a male is shown in Fig. 8.

Variation was noted in the arm-ratios of the individuals of pair No. 24. The centromeres in these chromosomes either were median, with arm-ratios as a result to a minimum of 1.58, or were subterminal in position. Such variation was observed

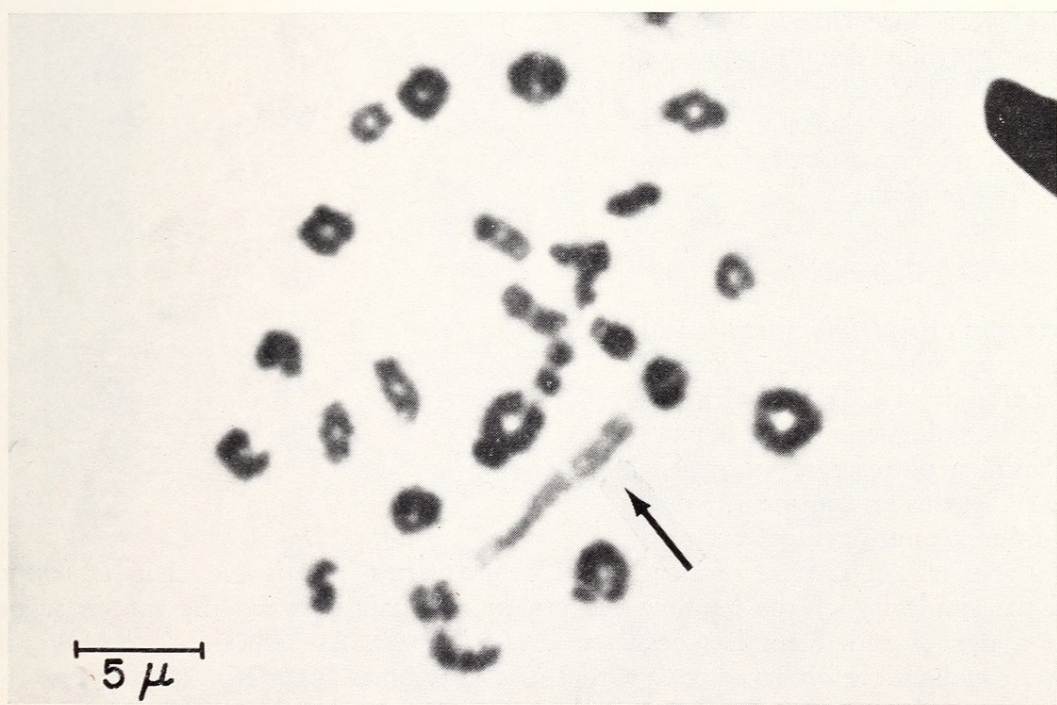


Fig. 8. Meiotic preparation from testis, *Lemmus trimucronatus*. Arrow indicates sex-chromosome bivalent

among different animals of common origin (e. g., stock from Point Barrow) and was seen in animals of all pelage-types. In some cells, the 2 individuals of this polymorphic pair also differed slightly in total length. In the male *L. t. yukonensis* (Seward Peninsula), the arm-ratio ranged from 3.10 to 3.95 for this pair.

Lemmus nigripes ($2n=50$). Twenty-three pairs of autosomes were acrocentric (arm-ratios ≥ 6.85), and one pair (No. 24 in the karyotype; Fig. 9) was subtelocentric, with lower arm-ratios (3.00–3.23). Pair No. 2 ranged in arm-ratio from 6.85 to 8.75. The X- and Y-chromosomes selected were relatively large, and both were acrocentric. The NF was 52. The karyotype of this taxon appears to be indistinguishable from that of *L. trimucronatus*.

Lemmus lemmus ($2n=50$). Our findings for this species were in agreement with those reported by MATTHEY (1957), i. e., 24 pairs of autosomes and the sex-chromosomes were acrocentric, and the karyotypes thus demonstrated an NF of 50. The X-chromosome was one of the larger elements. The Y-chromosome was approximately half the size of the X.

G-Bands

Karyotypes of *L. trimucronatus* and *L. lemmus* with autosomes graded by size (pairs 1–23) and with apparent homologues matched in pairs by banding patterns are shown in Fig. 10. In this arrangement, 3 major differences are evident between the 2 species. An absence of small, well defined arms in pair No. 2 in *L. lemmus* and the similarity of the banding pattern in this pair between the species suggest that a loss of such arms has occurred in *L. lemmus*. As well, in *L. lemmus*, the pattern of banding observed in 2 acrocentric autosomes (pair No. 24) suggests that they are equivalent to the polymorphic pair in *L. trimucronatus*, but that a loss of the small arms has occurred in *L. lemmus*. The polymorphism noted in this pair in *L. trimucronatus* appears to be a result of a pericentric inversion in one element

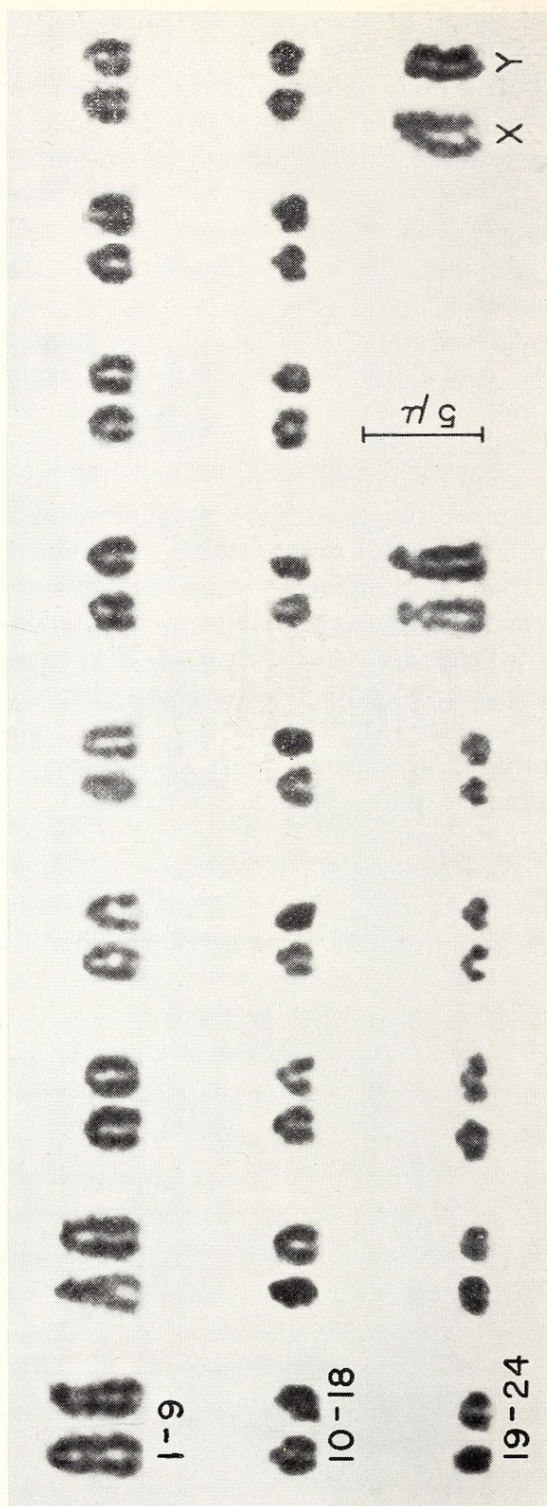


Fig. 9. Karyotype of *Lemmus nigripes*, male, $2n=50$. From testis, lactic-acetic-orcein

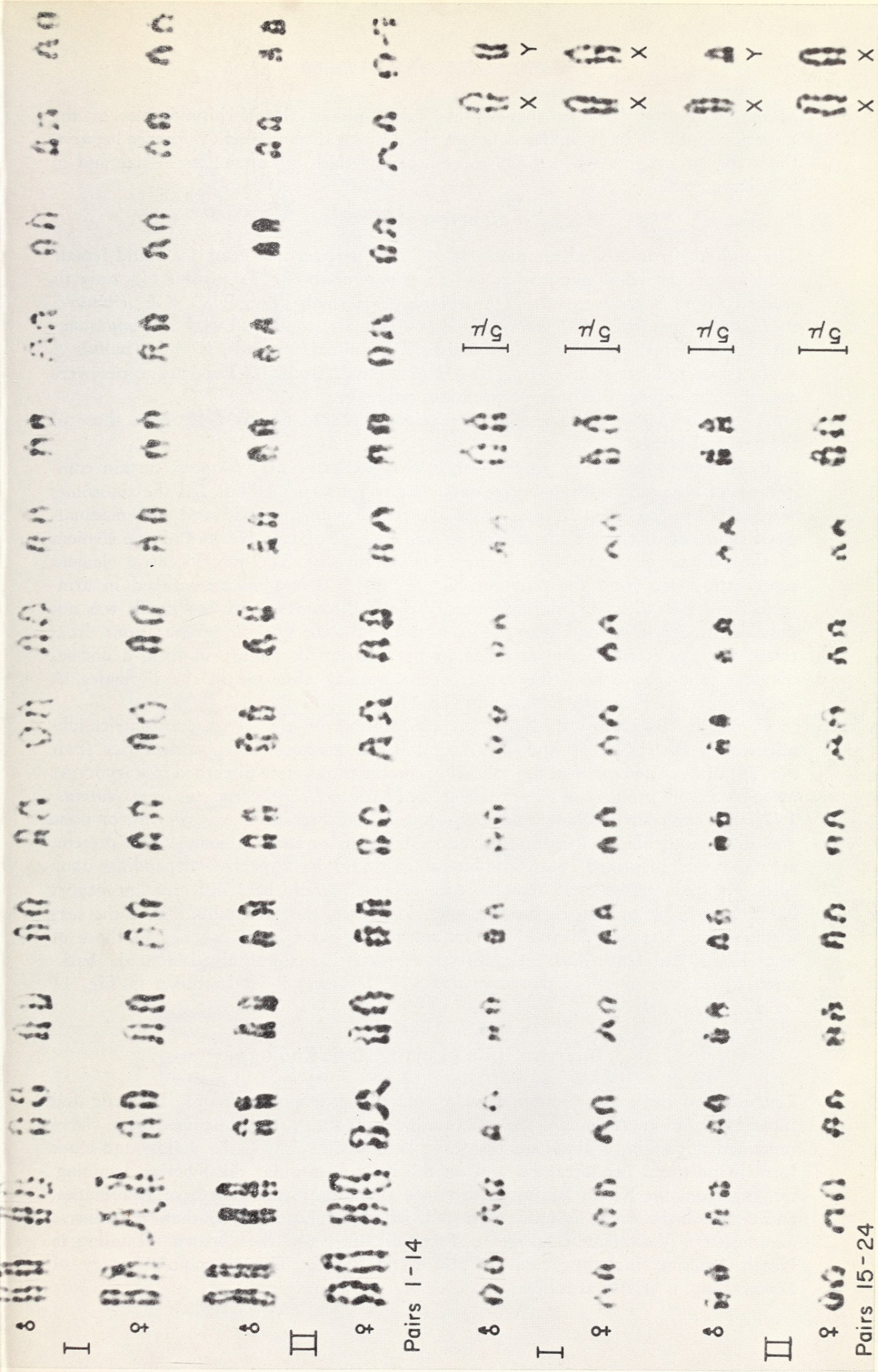


Fig. 10. Karyotypes of lemmings, showing banding patterns with Giemsa stain. I = *Lemmus trimucronatus*, male and female. II = *Lemmus lemnius*, male and female

as the pattern of banding suggests has taken place. The X-chromosomes of the 2 species appear to have similar bands. A third major chromosomal difference between the 2 species is apparent in the Y-chromosomes, which are dissimilar in size and in banding pattern.

Karyotypes of hybrids

The diploid chromosomal number was 50 in all preparations from male and female progeny of the combinations: A = *L. trimucronatus* x *L. nigripes* (3 animals studied); B = *L. trimucronatus* x *L. lemmus* (11 animals studied); C = *L. lemmus* ♂ x (*L. trimucronatus* x *L. lemmus*) F₁ ♀ (14 animals studied); D = *L. trimucronatus* ♂ x (*L. trimucronatus* x *L. lemmus*) F₁ ♀ (2 animals studied); E = *L. lemmus* ♂ x (*L. trimucronatus* x *L. nigripes*) F₁ ♀ (2 animals studied). The karyotypes were assembled from orcein-stained preparations only.

A. Karyotypes of *trimucronatus* x *nigripes* appeared not to differ from those of the parental forms.

B. In karyotypes of F₁ progeny of *L. trimucronatus* x *L. lemmus*, certain components of both parental types were immediately apparent. All but 2 of the autosomes were acrocentric. These 2, one large acrocentric-subtelocentric and one medium-sized subtelocentric, were identifiable as one element of pair No. 2 and one element of the polymorphic pair No. 24 in *L. trimucronatus*. The subtelocentric element representing one from the polymorphic pair of *L. trimucronatus* ranged in arm-ratio from 3.10 to 3.70. Discrimination of the Y-chromosome in F₁ animals was not possible in orcein-stained material (mitoses). In some meiotic preparations from testes, a dissociation of the sex-chromosomes was noted. Failure to form a normal bivalent might have been the cause of the sterility observed in the F₁ males. A karyotype of an F₁ female is shown in Fig. 11.

C, D, E (Back-crosses). Based on observation of the large acrocentrics-subtelocentrics (pair No. 2) and the medium-sized metacentrics-subtelocentrics (pair No. 24) of *L. trimucronatus*, the following combinations were discerned in karyotypes assembled from progeny of F₁ females crossed back to *L. trimucronatus* or *L. lemmus*: 1. 2 large acrocentric-subtelocentric autosomes were present, 1 was present, or none was distinguishable; 2. 2 medium-sized subtelocentrics were present, 1 was present, or none was identified. Such combinations would be expected, depending upon species of male mated to F₁ females. Also expected would be 3 different karyotypes based on pairing of the sex-chromosomes. However, the discrimination of the sex-chromosomes was not possible without morphological criteria other than those of total length and arm-ratios. A karyotype of a sterile male obtained from the back-cross *L. lemmus* ♂ x (*L. trimucronatus* x *L. lemmus*) F₁ ♀ is shown in Fig. 11 (cf. Fig. 5).

Interpretation of cytogenetic findings

Lemmings of the genus *Lemmus* have a holarctic distribution, mainly in arctic and subarctic tundra. Although the relationships of the various named forms have remained uncertain, 3 types usually have been distinguished: the yellow-and-black form in northern Fennoscandia and on the Kola Peninsula; the Siberian lemming, ranging from the Kanin Peninsula eastward to Bering Strait, northern Kamchatka, and some of the arctic islands, with a disjunct population in southeastern Siberia (southeastern Verkhoyansk Range to Transbaikalia); and the "brown" lemming in North America, including some of the arctic islands. The taxonomic history of *Lemmus* spp. is briefly as follows.

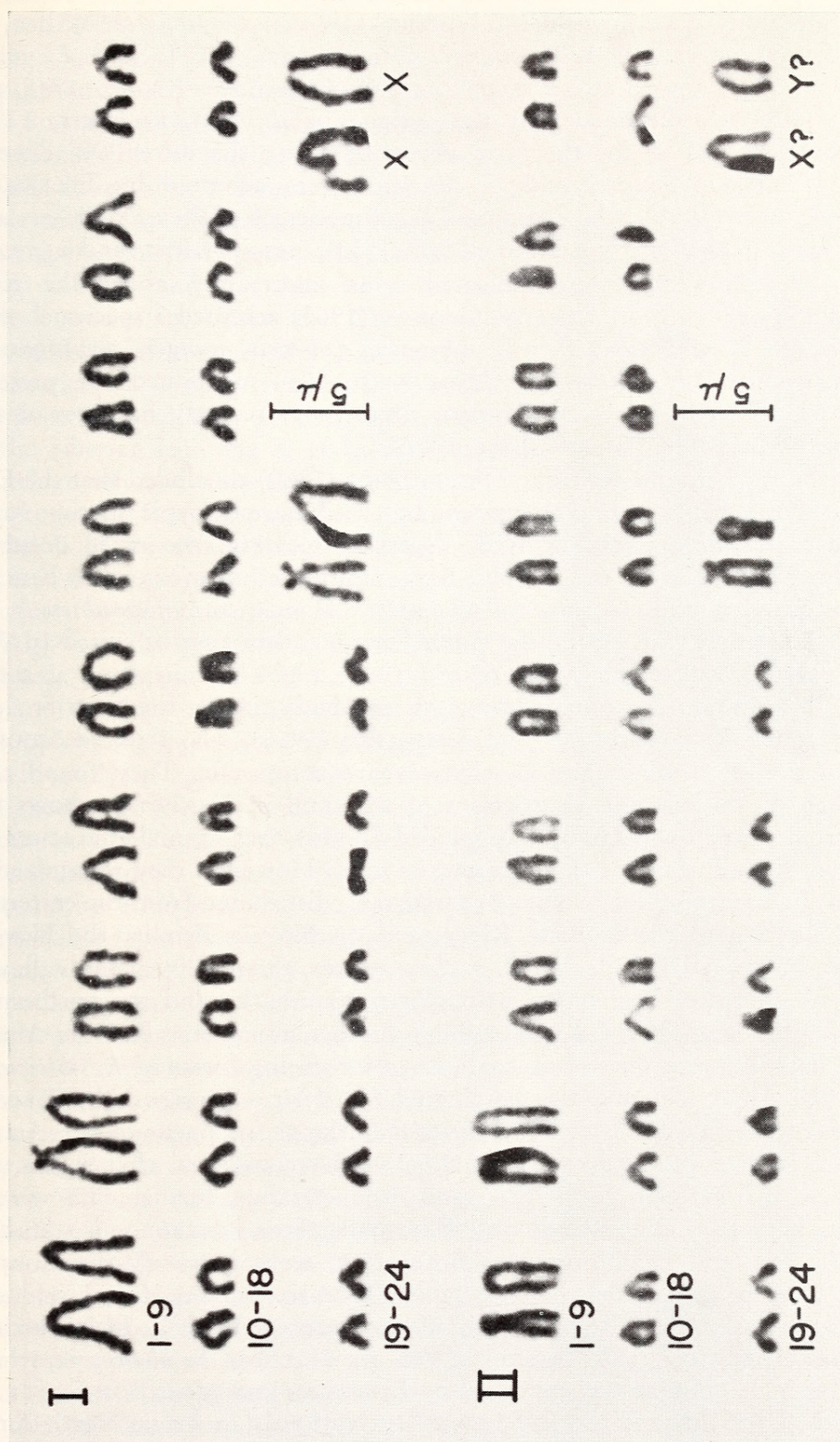


Fig. 11. Karyotypes of hybrid lemmings. I = F₁ female from *Lemmus trimucronatus* ♂ x *Lemmus lemmus* ♀, 2n=50. From marrow, orcein stain. II = Male from back-cross of *Lemmus lemmus* ♂ x (*Lemmus trimucronatus* x *Lemmus lemmus*) F₁ ♀, 2n=50. From marrow, orcein stain

OGNEV (1948) recognized 3 species in Eurasia: *L. lemmus* (Linnaeus, 1758); *L. obensis* (Brants, 1827), with 4 subspecies [*obensis*; *chrysogaster* (Allen, 1902); *novosibiricus* Vinogradov, 1924; *bungei* Vinogradov, 1925]; and *L. amurensis* Vinogradov, 1924, known at the time from only 4 specimens (OGNEV 1948, p. 473). ELLERMAN (1949) determined that the designation *L. sibiricus* (Kerr, 1792) has priority over *L. obensis* for the form occurring along the lower Ob' River. Two Eurasian species, *L. lemmus* and *L. sibiricus*, were accepted by ELLERMAN and MORRISON-SCOTT (1951), who recognized 6 subspecies of *sibiricus*: *sibiricus*; *amurensis*; *chrysogaster*; *kittlitzii* (von Middendorff, 1853); *novosibiricus*; and *ognevi* Vinogradov, 1933. However, they indicated some uncertainty about the status of *amurensis* and *ognevi*. More recently, GROMOV (1963) accepted 3 species: *L. lemmus*; *L. obensis* (= *L. sibiricus*), with 4 subspecies (*obensis*, *bungei*, *chrysogaster*, and *novosibiricus*); and *L. amurensis*. GROMOV (p. 571) mentioned the presence on Vrangeli Island of an undescribed form, which more recently has been designated *L. sibiricus portenkoi* by CHERNIAVSKII (1967).

On the basis of craniometric data, SIDOROWICZ (1960) concluded that the Eurasian lemmings of the genus *Lemmus* represent but a single, polytypic species, for which the name *L. lemmus* (Linnaeus, 1758) is applicable. He recognized 3 subspecies: *lemmus*, in Fennoscandia and on the Kola Peninsula; *sibiricus*, elsewhere on the Eurasian continent and on some of the arctic islands; and *novosibiricus*, on the Novosibirsk Islands. Concerning the Amur lemming, SIDOROWICZ stated (p. 73) that "It may only be assumed that as a relict form it might be considered as a separate subspecies." Variation in cranial characters and body-size in the Siberian lemming was investigated by KRIVOSHEEV and ROSSOLIMO (1966), who rejected SIDOROWICZ' conclusion that *L. lemmus* and *L. sibiricus* are conspecific. They found that the variation in dimensions and proportions of the skull in *L. sibiricus* shows a clinal pattern from north to south, and concluded (p. 15) that cranial characters do not suffice to distinguish taxa at the infraspecific level. However, they recognized 2 subspecies on the basis of pelage-color: *L. s. sibiricus*, distributed from the eastern shores of the White Sea to the Kolyma River, and on Novaia Zemlia, the Novosibirsk Islands, and Vrangeli Island; and *L. s. chrysogaster*, ranging from the valley of the Anadyr and shores of Bering Sea to northern Kamchatka and the northern shores of the Okhotsk Sea. They did not establish the taxonomic status of the Amur lemming but noted its resemblance to small, taiga-inhabiting forms of *L. sibiricus*. More recently, the Amur lemming was designated *L. sibiricus amurensis* by KRIVOSHEEV (in TAVROVSKII et al. 1971, p. 287). Seven additional specimens of the Amur lemming were studied by RUBINA et al. (1973), who considered that in view of its morphologic and biologic peculiarities and disjunct range, further data were necessary before any categorical assertion could be made about its taxonomic status.

In reference to the North American *L. trimucronatus* (Richardson, 1825), HINTON (1926, p. 209) stated that it exhibits "Essential cranial, dental, and external characters as in *L. obensis*." Comparison of specimens of *Lemmus* from northeastern Siberia and Alaska convinced OGNEV (1948, p. 470) that *L. obensis* is a holarctic species. A similar opinion was expressed by ELLERMAN and MORRISON-SCOTT (1951), who stated (p. 655) that *L. sibiricus* occurs "... variously in Arctic North America". North American forms, including *L. nigripes* (True, 1894), were accordingly considered as subspecies of *L. sibiricus* by RAUSCH (1953). HALL and KELSON (1959) recognized 2 North American species: *L. nigripes*, on St. George Island, and *L. trimucronatus*, with 7 subspecies [*trimucronatus*; *helvolus* (Richardson, 1828); *alascensis* Merriam, 1900; *yukonensis* Merriam, 1900; *minusculus* Osgood, 1904; *harroldi* Swarth, 1931; and *subarcticus* Bee and Hall, 1956] on the continent and

various adjacent islands. An eighth subspecies, *L. t. phaioccephalus* Manning and Macpherson, 1958, occurring on Banks and Victoria Islands in the Canadian Arctic Archipelago, was not included by HALL and KELSON (1959).

Large series of skulls of lemmings from Eurasia and northern Alaska were compared by SIDOROWICZ (1964), who discerned no significant morphological differences. In accordance with his earlier (1960) revision of the palaearctic lemmings, SIDOROWICZ concluded that *Lemmus* is a monotypic genus, with *L. lemmus* being the applicable name for the holarctic species. He considered that most of the North American subspecies had been distinguished on the basis of characters of doubtful taxonomic validity, and that there were insufficient grounds for their discrimination when the lemmings in Alaska and Siberia did not differ significantly. SIDOROWICZ (1964) would therefore recognize 3 subspecies of *L. lemmus* in Eurasia, and 2 in North America: *L. l. trimucronatus* and, conditionally until adequate comparative material becomes available, *L. l. nigripes*. KRIVOSHEEV and ROSSOLIMO (1966) considered the Siberian lemming to be holarctic and grouped the Alaskan forms on the basis of pelage-color with the northeast-Siberian *L. sibiricus chrysogaster*.

The cytogenetic findings presented above provide some additional criteria for the interpretation of the relationships of taxa in the genus *Lemmus*. The morphologic differences in karyotypes, different fundamental numbers, and sterility of male hybrids indicate that the Fennoscandian and North American lemmings represent different species. Although the cytogenetic characteristics of *L. sibiricus* in Eurasia have not been defined, the apparent absence of other characters that would distinguish the Siberian and Alaskan populations in combination with zoogeographic evidence (see below) supports the conclusion at present that they are conspecific. We are therefore provisionally in agreement with KRIVOSHEEV and ROSSOLIMO (1966) in recognizing 2 species, *L. lemmus* and *L. sibiricus*. However, as noted by RUBINA et al. (1973), the taxonomic status of the Amur lemming is uncertain.

The lemming on St. George Island, in the Bering Sea, usually has been accorded specific rank by American mammalogists. However, its karyotype appears to be indistinguishable from that of lemmings from northern Alaska, and the crossing of the 2 forms in the laboratory produced progeny that were indefinitely fertile. These findings indicate that the 2 are conspecific. The relatively small auditory bullae (DAVIS 1944) and the distinctive color-pattern of the lemming on St. George Island would seem to justify its recognition as *L. sibiricus nigripes* (True, 1894).

Of the nominal subspecies of *L. sibiricus* in North America, *trimucronatus* has the most extensive geographic range, including northern Canada from western Yukon Territory east to the shores of Hudson Bay and Southampton Island, and to the north, King William, Prince of Wales, Somerset, and Baffin Islands in the Canadian Arctic Archipelago (MANNING and MACPHERSON 1958; HALL and KELSON 1959; MACPHERSON and MANNING 1959; MANNING and MACPHERSON 1961). The subspecies *phaioccephalus* occurs on Banks and Victoria Islands, to the southwest (MANNING and MACPHERSON 1958). The subspecies *harroldi* is restricted to Nunivak Island, near the southwestern coast of Alaska at lat. 60° N. In addition to *trimucronatus*, 5 subspecies have been distinguished on the continent: *alascensis*, along the central arctic coast of Alaska, south to about lat. 70° N; *subarcticus*, on the remainder of the arctic slope of Alaska and south into the Brooks Range; *yukonensis*, in suitable habitat from the Brooks Range south to the Yukon-Kuskokwim deltas, including the Seward Peninsula and extending into northern Yukon Territory to the east; *minusculus*, in the region along the northern shores of Bristol Bay and on the Alaska Peninsula south at least to Port Heiden (F. H. FAY and R. L. RAUSCH, unpublished); and *helvolus*, in the mountains of western Canada from southern Yukon Territory

to lower British Columbia (ca. lat. 52° N) (COWAN and GUIGUET 1960). Karyotypes of lemmings representing 3 of the nominal subspecies in Alaska (*alascensis*, *subarcticus*, and *yukonensis*) appeared to be identical and indistinguishable from that of *nigripes*, although this conclusion concerning *yukonensis* is based on the examination of a single male.

The nominal subspecies of *L. sibiricus* in North America are slightly differentiated, and some are of questionable validity. DAVIS (1944) did not recognize *yukonensis* and considered *minusculus* to be only weakly differentiated from *alascensis*. As in Siberia (KRIVOSHEEV and ROSSOLIMO 1966), lemmings in Alaska seem to show a clinal decrease in size from north to south, *minusculus* being the smallest form on the mainland. However, *harroldi* on Nunivak Island is similar in size to *alascensis*, occurring in northern Alaska (R. L. RAUSCH, unpublished).

Zoogeography of *Lemmus*

Distributional history

Lemmings indistinguishable from Recent forms in dental and cranial characteristics apparently had an extensive distribution in northern Eurasia by Günz time. Remains identified as *L. lemmus* were found by HELLER (1930) in deposits of Günz II age (KURTÉN 1968, p. 220) in Sackdilling Cave, in the Oberpfalz. The stratigraphic correlation was confirmed by further excavations at the same site (HELLER and BRUNNACKER 1966). GUTHRIE and MATTHEWS (1971) identified remains of *Lemmus* cf. *sibiricus* in deposits of probable pre-Mindel age in western Alaska (Cape Deceit), and SHER (1971, p. 59) reported *Lemmus* cf. *obensis* (= *sibiricus*) from the early-Pleistocene (not younger than Mindel) Olërsk deposits in the lower Kolyma River region.

The range of the precursor of the Recent species of *Lemmus* was probably divided by a major glacial advance of early Pleistocene time (cf. CHARLESWORTH 1957, fig. 192), which left disjunct populations in western and eastern Eurasia. During subsequent glacial periods, lemmings apparently had a restricted distribution in periglacial tundra in what is now western Europe, as has been pointed out by JÁNOSSY (1961, p. 47): „Es mag hervorgehoben werden, daß die Reste der Berglemminge (*Lemmus*) sowohl im Alt- als auch im Jungpleistozän sich auf die westlichen und nördlichen Teile Mitteleuropas beschränkten und das heutige Gebiet Ungarns nie erreichten.“ Contraction of range northward during periods of deglaciation would result in the ultimate isolation in northern Fennoscandia of lemmings and other arctic-adapted animals, as is suggested by the pattern of the present distribution of *L. lemmus*. Newer concepts of the patterns of glaciation in northern Europe indicate that survival of lemmings in unglaciated refugia in Fennoscandia was unlikely (LINDROTH 1969).

During glacial periods, lemmings in the east would seem to have been restricted mainly to arctic lowlands from the region of the Lena delta eastward, including suitable habitat in Beringia, since even during Würm time the continental glacier extended to the east over the Taimyr Peninsula and Severnaia Zemlia (CHARLESWORTH 1957, fig. 192). In addition to the glacial barrier, the depth of the sea east of Severnaia Zemlia would prevent the westward dispersal of terrestrial mammals during intervals of maximal lowering of sea-level. The present geographic range of *L. sibiricus* does not include the islands of Severnaia Zemlia. Its occurrence on Novaya Zemlia, to the west, may be attributable to comparatively recent colonization.

Lowering of sea-level by about 100 m below the present would have exposed the broad continental shelf that extends northeastward from the Taimyr Peninsula, with a consequent position of shoreline well to the north of the Novosibirsk Islands and Vrangeli Island (cf. Atlas SSSR 1969, p. 67). Remains of *L. obensis* (= *L. sibiricus*) have been found in late-Pleistocene deposits on Bol'shoi Liakhovsk Island, in the Novosibirsk group (VANGENGIM 1961). *L. sibiricus* could have colonized islands in the East Siberian and Chukchi Seas as recently as ca. 20,000—15,000 years ago, during the glacial maximum of Würm time (cf. HOPKINS 1972), but its occurrence there probably has been continuous from a much earlier period. Southward dispersal of lemmings in northeastern Siberia occurred relatively early, as indicated by remains in deposits of Riss age in the basin of the Aldan River, south of the Verkhoiansk Range (VANGENGIM 1961).

Until recently, the known occurrence of *Lemmus* in eastern Beringia (i. e., east of the present Bering Strait) dated only from late-Pleistocene (Würm) deposits in central Alaska (REPENNING et al. 1964; REPENNING 1967; GUTHRIE 1968), and the pattern of the Recent distribution of lemmings in North America was taken by RAUSCH (1963) to indicate post-glacial dispersal from Beringia. A similar interpretation was made by MACPHERSON (1965), who also considered the possibility that the montane *L. s. helvulus*, in northwestern Canada, is a post-glacial derivative of a southern (periglacial) population. The recent determination by GUTHRIE and MATTHEWS (1971) that *Lemmus* cf. *sibiricus* was a component of a cold-adapted Beringian fauna of pre-Mindel age is consistent with evidence for the occurrence of lemmings in northeastern Siberia by at least Mindel time (SHER 1971, p. 61). Considering then that *Lemmus* was present in Beringia since the early Pleistocene, its dispersal from the refugium into North America seems to have been curiously inhibited, as indicated by the lack of relict populations or evidence of its occurrence in periglacial tundra. Since *L. sibiricus* characteristically occupies lowland tundra where grasses and sedges predominate (SUTTON and HAMILTON 1932; OGNEV 1948; WATSON 1956; PITEKA 1957), its apparently limited dispersal might have been partly attributable to a lack of suitable habitat as a result of northward shifting of vegetational zones during periods of interglacial warming (cf. DORF 1959; HOPKINS 1972). However, its dispersal also might have been inhibited by the competitive superiority of other arvicoline rodents that occupied the same biotope.

The present distribution of *L. sibiricus* in North America and on adjacent islands beyond the limits of former Beringia appears to have been the consequence of post-Würm dispersal. As pointed out by MACPHERSON (1965), lemmings on Banks and Victoria Islands might have been derived from a population that survived the last glaciation in a refugium near the western limits of the Canadian Arctic Archipelago (cf. CRAIG and FYLES 1960). Although the range of *L. s. helvulus* extends farther to the south than does that of other species considered to be post-glacial emigrants from Beringia [e. g., *Ochotona collaris* (Nelson); *Citellus parryi* (Richardson); *Ovis dalli* Nelson], it seems clearly to be the result of post-glacial extension from the north. Within the bounds of the former Beringia, insular populations of *L. sibiricus* are few, possibly again because of the competitive superiority of arvicoline rodents of other species.

Interspecific competition and ecological segregation

In the Canadian Arctic Archipelago, *L. sibiricus* is present on all of the islands that lie south of lat. 75° N, not having succeeded in crossing the relatively wide straits to the north. These islands are occupied also by one other arvicoline rodent, a

varying lemming (*Dicrostonyx*), but the two are usually segregated ecologically (cf. MANNING and MACPHERSON 1961, p. 206). Within the limits of former Beringia, coexisting insular populations of *L. sibiricus* and *Dicrostonyx* are found only on Wrangel' Island (cf. OGNEV 1948, 1950), where also they are ecologically segregated (CHERNIAVSKII 1969).

On St. Lawrence Island, situated farther south, in the Bering Sea, a more diversified mammalian fauna is present. This island remained connected with the North American continent until only about 10,000 years ago (HOPKINS 1972). Three species of arvicoline rodents, not including *L. sibiricus*, occur there, and their ecological segregation is well defined. A varying lemming, *Dicrostonyx exsul* Allen, and a red-backed vole, *Clethrionomys rutilus albiiventer* Hall and Gilmore, are restricted respectively to relatively dry alpine tundra and rocky areas on the higher slopes, although their habitats overlap to some extent. A large form of the northern vole, *Microtus oeconomus innuitus* Merriam, occupies the extensive lowland tundra. In the course of observations on this island over a period of more than 20 years, it has been found that neither varying lemmings nor red-backed voles have been numerous, nor has either been found in wet tundra where the northern voles occur. When the northern voles are abundant, they occupy areas at higher elevations. The extensive lowland tundra, supporting predominantly grasses and sedges, is typical of habitat of *L. sibiricus* elsewhere. The vegetation of St. Lawrence Island has been described by YOUNG (1971), and the distribution there of the northern vole has been discussed by FAY (1973).

The only arvicoline rodent present on Nunivak Island, near the western coast of Alaska at lat. 60° N, is *L. sibiricus harroldi* [this island was included within the geographic range of *M. oeconomus* by HALL and KELSON (1959)]. When abundant, lemmings on Nunivak Island occur on uplands in vegetation consisting mainly of mosses and ericaceous plants, as well as in wet lowlands (R. L. RAUSCH, unpublished).

No terrestrial mammals other than *L. sibiricus nigripes* and the arctic fox, *Alopex lagopus* (Linnaeus), are indigenous to St. George Island. When numerous, the lemmings are present everywhere with the exception of areas of volcanic rock grown to lichens (F. H. FAY, personal communication). Situated near the western edge of the continental shelf, the Pribilof Islands were included within Beringia during intervals when sea-level was about 100 m below the present (HOPKINS 1972). St. George Island was partly ice-covered during the penultimate glacial period, and was probably unglaciated during Würm time (HOPKINS and EINARSSON 1966). Bathymetric and other data suggest that during the last 100,000 years, St. George Island was once briefly connected with the mainland between about 20,000 and 16,000 years ago (D. M. HOPKINS, personal communication).

The depauperate faunas of the remaining Beringian islands do not include *Lemmus*, but ecological segregation is well defined wherever 2 arvicoline species coexist. *Microtus abbreviatus*, a divergent form of the Beringian *M. miurus* Osgood, is the only arvicoline rodent on the St. Matthew Islands, which lie to the north of the Pribilof group. On the largest of these islands, the voles occupied diverse habitats at a time of high numerical density (RAUSCH and RAUSCH 1968). The presence of a nearctic species of flea, *Megabothris groenlandicus* (Wahlgren), characteristically found on *Dicrostonyx* and *Lemmus* (G. P. HOLLAND 1963, and personal communication), suggests that one or both of these rodents once might have occurred on the St. Matthew Islands.

In the eastern Aleutian Islands, near the southwestern reaches of Beringia, there is a progressive decrease in numbers of mammalian species from east to west and, with the possible exception of the red fox, *Vulpes vulpes* (Linnaeus), no indigenous

species occurs on islands that lie west of Umnak. The easternmost island, Unimak, separated from the Alaska Peninsula by the 1.6 km width of Isanotski Strait, has a continental fauna; the faunas of the next two, Akun and Akutan, are incompletely known. Two arvicoline species occur on the fourth island, Unalaska; there, *M. oeconomus unalascensis* Merriam, occupies the extensive lowlands, becoming abundant at intervals, while a varying lemming, *Dicrostonyx unalascensis* Merriam, is presumably restricted to the uplands. This lemming, known from only 2 specimens, seems always to be rare. Another varying lemming, *D. stevensoni* Nelson, is the only small mammal present on Umnak Island, where, at times of high numerical density, it occupies a range of habitats including the lowlands (F. H. FAY, personal communication).

L. sibiricus thus does not coexist with *Microtus* on any of the Beringian islands, and wherever they occur on these islands, voles occupy the characteristic habitat of *Lemmus*. Where 2 or more arvicoline species are present, they are segregated ecologically. Voles of the genus *Microtus* appear to be competitively superior to rodents of the genera *Clethrionomys*, *Dicrostonyx*, and *Lemmus* under insular conditions.

On the mainland, ecological segregation of arvicoline rodents is not so readily discernible, and interactions among species are more obscure. Two or more species may ostensibly coexist, but major fluctuations in their numbers seem rarely to be synchronous (PITELKA 1957). In Alaska, highest densities of *L. sibiricus* have been recorded in a region of the arctic coastal plain, where a varying lemming, *D. rubricatus* (Richardson), is the one other arvicoline species present. The numbers of varying lemmings seem clearly to vary inversely with numbers of brown lemmings in this region (PITELKA 1973), a pattern consistent in principle with the vertical segregation of the 2 species on the arctic islands.

In the interior of Alaska, *L. sibiricus* is usually found in areas covered by tussock-forming sedges or in moss-heath associations, while *M. oeconomus* typically occupies moist areas around lakes, ponds, and drainages, expanding into other habitat at times of high numerical density. Only once during the past 25 years have we known of synchronous high densities of *L. sibiricus* and *M. oeconomus* in the same area. During the autumn of 1963, when arvicoline rodents were generally abundant in southwestern Alaska, voles and lemmings were present in similar numbers at Ugashik Lake, on the upper Alaska Peninsula, in the dense mat of mosses and ericaceous plants covering low slopes. On the assumption that individuals of the dominant species would exhibit fewer wounds resulting from possible interspecific strife, the perforations visible on the inside of the skin were counted of all animals trapped at one locality (117 voles; 78 lemmings). The ratio of wounded to non-wounded lemmings (4:1) was higher than that in voles (1:3); moreover, the average number of wounds per lemming was approximately twice that in the voles (F. H. FAY and R. L. RAUSCH, unpublished). These findings indicate that *M. oeconomus* was dominant in the association with *L. sibiricus*.

Discussion

The geographic distribution of *Lemmus* would seem to have been continuous in the arctic lowlands of northeastern Siberia and Beringia during glacial periods. Conversely, that of some arctic-montane species of mammals was discontinuous, permitting chromosomal evolution to occur, with consequent formation of species-pairs whose ranges are now separated by Bering Strait [e. g., *Microtus gregalis* (Pallas) and *M. miurus*; *Ovis nivicola* Eschscholtz and *O. dalli*]. As noted by GUTHRIE and

MATTHEWS (1971), the dentition of *Lemmus* cf. *sibiricus* attained a high degree of complexity early in Pleistocene time, and no subsequent change is discernible. They remarked (p. 506) that the lack of change in dentition "... probably means that the specialized habitat which *Lemmus* occupies was constantly available even while the regional character of treeless northern environments was changing." The hypothesis that the distribution of *L. sibiricus* was continuous and that the species is holarctic, is supported also by the presence of a host-specific cestode, *Paranoplocephala lemmi* Rausch, 1952, in lemmings on both sides of Bering Strait (cf. GUBANOV and FEDOROV 1970).

From the information available, we consider that the genus *Lemmus* includes 2 species, *L. lemmus* and *L. sibiricus*, that appear to be indistinguishable by cranial and dental characters. The high degree of such phenotypic uniformity in these lemmings seems to have been maintained by homeostatic mechanisms since the early Pleistocene, when their precursor already had become adapted to a distinctive habitat.

Assuming that the biotope occupied by *L. sibiricus* has remained essentially constant since early Pleistocene time, as has been postulated, selective pressures would seem to have been minimal. The probability of chromosomal evolution might have been greater in the western (European) population, in response to adaptive pressures associated with the successive latitudinal shifts in range that have occurred as a result of glacial advances and recessions since at least Günz time. If the karyotype of *L. sibiricus* more closely resembles that of the precursor of *Lemmus* spp., chromosomal change leading to the karyotype of *L. lemmus* would have involved the deletion and loss of 2 arms of the metacentric-subtelocentric pair, loss of the minute arms of the acrocentric-subtelocentric pair, and possible deletion and loss of material in the Y-chromosome. In *L. sibiricus*, the polymorphism exhibited by one pair may be the result of a relatively recent modification.

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Summary

Chromosomal characteristics were defined for lemmings of the genus *Lemmus* Link, 1795: *L. lemmus* (Linnaeus, 1758) (Norway); *L. trimucronatus* (Richardson, 1825) (Alaska); *L. nigripes* (True, 1894) (Pribilof Islands); and progeny from crosses and back-crosses. *L. lemmus* ($2n = 50$; $NF = 50$) has 24 pairs of acrocentric autosomes; the North American lemmings ($2n = 50$; $NF = 52$) have 23 pairs of acrocentric and one pair of metacentric-subtelocentric autosomes. The Y-chromosomes differed morphologically and in pattern of G-bands. The crossing of *L. lemmus* with North American lemmings resulted in many F_1 progeny, of which the males were sterile. These findings confirm that *L. lemmus* and *L. trimucronatus* (including *L. nigripes*) are distinct species. Palaeontologic and zoogeographic evidence indicates that the geographic range of *Lemmus* was divided by a glacial advance of early Pleistocene time, with isolation of a population in central Europe and another in Siberia. Since the eastern population had an apparently continuous distribution in arctic lowlands of Siberia and Beringia during glacial periods, it is provisionally (until Siberian specimens can be investigated cytogenetically) agreed with KRIVOSHEEV and ROSSOLIMO (1966) that *L. trimucronatus* is conspecific with the Eurasian *L. sibiricus* (KERR, 1972). The probability of chromosomal evolution would seem to have been greater in the western (European) population of *Lemmus*, in response to adaptive pressures associated with latitudinal shifts in range caused by successive glacial advances and recessions. The characteristics of lemmings reared under laboratory conditions are briefly described.

Zusammenfassung

*Taxonomie und Zoogeographie von Lemmus spp. (Rodentia: Arvicolinae),
mit Beobachtungen an Lemmingsen als Zuchttiere*

Die Chromosomen-Merkmale von Lemmingsen der Gattung *Lemmus* Link, 1795 wurden beschrieben: *L. lemmus* (Linnaeus, 1758) (Norwegen); *L. trimucronatus* (Richardson, 1825), einschließlich 3 Unterarten (Alaska); *L. nigripes* (True, 1894) (Pribilof Inseln); und Nachkommen aus verschiedenen Kreuzungen und Rückkreuzungen. Der Karyotypus von *L. lemmus* ($2n = 50$; $NF = 50$) besteht aus akrocentrischen Chromosomen, während der Chromosomensatz der nordamerikanischen Formen ($2n = 50$; $NF = 52$) ein Paar meta-subtelocentrische Autosomen enthält. Die Y-Chromosomen unterscheiden sich morphologisch und durch verschiedene G-Bandmuster voneinander. Die aus Kreuzungen resultierenden Nachkommen hatten eine Chromosomenzahl, die mit der der beiden Ausgangsformen identisch ist. Die weiblichen Bastarde waren fertil bei Rückkreuzungen mit Männchen beider Ausgangsarten; die Männchen der F_1 -Generation hingegen waren steril. Auf Grund der vorliegenden Ergebnisse gelten *L. lemmus* und *L. trimucronatus* (einschließlich *L. nigripes*) als verschiedene Arten. Paläontologische und zoogeographische Angaben sprechen dafür, daß *Lemmus* schon während des Altpleistozäns seine Anpassung an die arktischen Lebensbedingungen vollzogen hatte, und daß das ursprüngliche Verbreitungsgebiet durch eine altpleistozäne Vereisung getrennt wurde, wodurch Populationen im Westen (Mitteleuropa) und im Osten (Sibirien) isoliert wurden. Die im Osten vorkommende Form von *Lemmus* hatte während der Glazial-Phasen anscheinend eine ununterbrochene Verbreitung in den ebenen Tundragebieten Ostsibiriens einschließlich Beringia. Bis auf weiteres wird mit KRIVOSHEEV und ROSSOLIMO (1966) angenommen, daß *L. trimucronatus* mit dem paläarktischen *L. sibiricus* (Kerr, 1792) identisch ist. Da *L. lemmus* an den arktischen Klimabereich gebunden war, und dessen räumliche Schwankungen im Laufe des Pleistozäns mitgemacht haben dürfte, wurde bei dieser Art Karyotypenevolution wahrscheinlich durch erheblich größere Anpassungsbedürfnisse gefördert als bei *L. sibiricus* im Osten. Die biologischen Merkmale der Lemmingsen im Laboratorium wurden kurz besprochen.

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Extreme Varianten des M₁ der Feldmaus (*Microtus arvalis* Pallas) in Ungarn

II.

Von D. JÁNOSSY und E. SCHMIDT

Eingang des Ms. 24. 6. 1974

In einer früheren Arbeit berichteten wir bereits über einige besondere Varianten der ersten unteren Molaren (M₁) an aus ungarischen Gewölle stammenden Feldmausmandibeln (JÁNOSSY und SCHMIDT 1960). Hier sollen weitere Extremmuster dargestellt werden, die wir unter 2256 ersten Unterkiefermolaren aus Ungarn gefunden haben. Das Material stammt von verschiedenen, das Land annähernd gleichmäßig bedeckenden Orten (Tabelle).

Die für *Microtus gregalis* typische Ausprägung (Abb. 4) fanden wir je einmal in Szászberek und Karcag, zweimal in Kamond. Bereits 1960 hatten wir 3 solche Zähne unter 1180 festgestellt.

Vereinzelt erinnern die Paraconid-Kappen an die Verhältnisse bei *Pitymys* wie bei dem in Abb. 6 gezeigten Stück von Bácsalmás. Natürlich fehlt der *Pitymys*-Rhombus.

In dem Material von Tornyosnémeti entdeckten wir ein zweites Exemplar mit dem für *Phaiomys* charakteristischen M₁-Muster (Abb. 1).

Je ein Stück, das an *Microtus nivalis* oder *M. oeconomus* erinnert, fanden wir in Hódmezővásárhely, Perbál und Kamond (Abb. 5).

An *Lagurus lagurus* gemahnt ein M₁ von Csömör (Abb. 2). Natürlich hat der zu-



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