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Chromosomal banding comparisons among American and European Red-backed mice, genus *Clethrionomys*

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Abstract

G-banded chromosomes are presented for five species of *Clethrionomys: C. glareolus, C. rufocanus, C. gapperi, C. californicus,* and *C. rutilus.* Similar data are available in the literature regarding *C. andersoni.* The presence of a shared derived autosomal reciprocal translocation allies *C. glareolus, C. gapperi, C. californicus* and *C. rutilus,* while the primitive condition is retained in *C. rufocanus* and *C. andersoni.* Intraspecific and interspecific variability in C-banding patterns is limited. Variation in Y chromosome size and/or morphology apparently occurs convergently in populations of three species. Interspecific chromosomal variation is much less in *Clethrionomys* than in other genera of arvicolid rodents, and *Clethrionomys* have speciated without concomitant structural chromosomal differences. Ribosomal DNA (rDNA) transcriptional activity was assayed among five different tissues from individuals belonging to three species using the silver staining procedure. Fibroblast cells had a significantly greater number of nucleolus organizer regions (Ag–NORs) than did femur bone marrow cells from the same specimen. Among similar tissues, intraspecific variability in the mean number of NORs per cell may be equal to or greater than interspecific differences. Sister chromatid exchange was measured in a lung fibroblast cell line of *C. rutilus* using 5-bromodeoxyuridine (BrdU) incorporation. The mean number of exchanges per cell (8.0) was found to be equal to or less than that reported in studies of other rodents. Meiotic chromosome analyses of *C. californicus* indicate that a sex vesicle is present during pachytene and that end-to-end association between the centromeric region of the acrocentric X and the small-sized, C-band negative Y occurs in diakinesis.

Introduction

The Holarctic rodent genus *Clethrionomys* (family Arvicolidae) is currently thought to contain seven (Honacki et al. 1982) or eight (Corbet 1978) species. These species are difficult to distinguish morphologically, and controversy has traditionally existed among classical taxonomists regarding the systematics of the group. Several of these species have fairly broad geographic distributions in either Eurasia (*C. glareolus* and *C. rufocanus*) or North America *(C. gapperi),* while one species *(C. rutilus)* exhibits a circumpolar distribution. The remaining forms are much more restricted in distribution either in the Palearctic *(C. andersoni, C. centralis, C. sikotanesis)* or in the Nearctic *(C. californicus).* Habitats occupied by these animals are principally mesic situations in coniferous, deciduous and mixed forests where an abundant litter is available, although the more specialized *C. rutilus* is found in a boreal, tundra habitat.

Previous comparative analyses have indicated that species in the family Arvicolidae exhibit some of the most extreme interspecific karyotypic variability yet observed among vertebrates (summarized by Modi 1987a). In this vein, the present study was undertaken because several earlier studies have suggested that species of *Clethrionomys* may be much more chromosomally conservative than are some closely related genera (Gamperl 1982a; Obara 1986). Results from the comparative analyses of G-banding and C-banding patterns from a total of six species (including information derived from the literature) are presented and compared with systematic arrangements of the genus that are based upon

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other types of data. Additionally, results from silver-staining for the nucleolus organizer region, sister chromatid exchange and investigations on meiotic chromosomes are presented for several of these species.

Materials and methods

Karyotypic analyses were carried out on 17 specimens belonging to five species. Cells for chromosome preparations from *C. glareolus* and *C. rufocanus* were obtained from fibroblast cultures initiated from ear biopsies, grown in TC Medium Eagle, Earle BSS and supplemented with 20 % fetal calf serum. Cells from *C. rutilus* and all specimens of *C. gapperi* were obtained from fibroblast cultures initiated either from lung or ear biopsies and grown in McCoy's 5 A modified medium supplemented with 10 % fetal calf serum. Metaphase cells from three of the five specimens of *C. gapperi* were also derived from femur bone marrow following the yeast pretreatment procedure (Lee and Elder 1980), while preparations from *C. californicus* were obtained from spleen tissue (Modi 1985), femur bone marrow, or vertebral column bone marrow. Metaphase cell harvest, incubation, fixation, and slide preparation followed standard procedures. Slides were aged at 37 °C for 2–20 days before being banded.

G-bands were obtained on preparations from *C. glareolus* and *C. rufocanus* using a slightly modified version of the ASG technique (Sumner et al. 1971). Slides were incubated in 2× SSC (pH 7.0) at 60 °C for 8–16 h before being stained in 2 % Giemsa in sodium phosphate buffer (pH 6.8). G-bands from *C. gapperi, C. californicus* and *C. rutilus* were obtained by digestion with 0.025 % tgrypsin in Hanks' balanced salt solution for 20–200 sec, followed by dehydration in ethanol prior to staining in Giemsa (Seabright 1971). In Fig. 1 G-banded chromosomes are numbered following the designations proposed as phylogenetically primitive for the family Arvicolidae as defined by Modi (1987a). The chromosomes of *C. rufocanus* are arranged according to length, and the homologous elements from the other species paired accordingly (Fig. 1c).

C-bands were obtained from specimens of all five species following a variant of the BSG procedure of Sumner (1972). Slides were treated in 0.2 N HCl for 1 hr, followed by treatment in saturated $Ba(OH)_2$ for 2–20 min at 37 °C or 50 °C. Slides were then covered with 2× SSC and incubated at 60 °C for 1 hr prior to dehydration in ethanol and staining in 4 % Giemsa. Ag-NORs were obtained on the chromosomes of *C. gapperi, C. californicus* and *C. rutilus* following the AG-1 procedure of Bloom and Goodpasture (1976). Slides were flooded with a 50 % solution of $AgNO_3$ containing 0.03 % formalin and incubated at 60 °C for 1–4 hr. At least 50 silver-stained cells were examined per specimen and the number of chromosomes staining positively in each cell was recorded.

The frequency of sister chromatin exchange in a lung fibroblast cell line from *C. rutilus* was analyzed following a slight modification of the procedure of Perry and Wolff (1974). Cells were grown in the dark for 30 hr with 5-bromodeoxyuridine (BrdU) at a concentration of 30 µg/ml. Following slide preparation chromosomes were stained with Hoechst 33 258 (1 µg/ml) for 15 min, rinsed, dried and then flooded with 2× SSC and illuminated with long-wave UV light for 1 hr. Slides were stained in 2 % Giemsa in phosphate buffer (pH 6.8) for 2–4 min.

Finally, meiotic chromosomes were obtained from one male *C. californicus*. Seminiferous tubules were minced with curved scissors in a watch-glass in 2 ml of 0.7 % sodium citrate. An additional 8 ml of sodium citrate solution was added, and the mixture incubated at 37 °C for 25 min. Subsequent fixation and slide preparation followed traditional procedures.

The following specimens were examined: *C. rufocanus,* Sweden: Gällivare, 1 male. *C. glareolus,* Austria: Graz, 1 male, 1 female. Salzburg, 1 male. France: Savoie, 1 male, 2 females. *C. gapperi,* USA: Vermont, Chittenden Co., 1 male, 1 female. West Virginia, Randolph Co., 1 male; Virginia, Highland Co., 2 females. *C. californicus,* USA: Oregon, Tillamook Co., 1 male. Linn Co., 1 male, 2 females. *C. rutilus,* USA: Alaska, Fairbanks, 1 male.

Results

G-banded karyotypes were analyzed for all five species, including populations of *C. gapperi* from Vermont and Virginia and specimens of *C. glareolus* from two localities in Austria and one in France. No intraspecific differences in G-banding patterns were observed in either of these two species. Representative G-banded preparations for *C. rutilus* and *C. gapperi* are presented in Figures 1a–b. Illustrated in Figure 1c is a composite karyotype comparing the haploid complement from each of the five species. All species have $2n = 56$, $NF_a = 56$ with 25 pairs of acrocentric and one pair of small metacentric autosomes. Among the autosomes, pairs 1 and 9 of *C. rufocanus* differ from homologous

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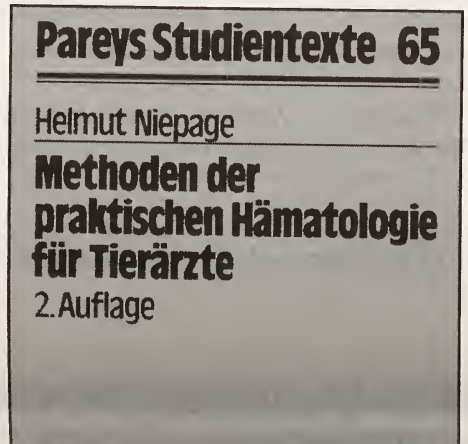

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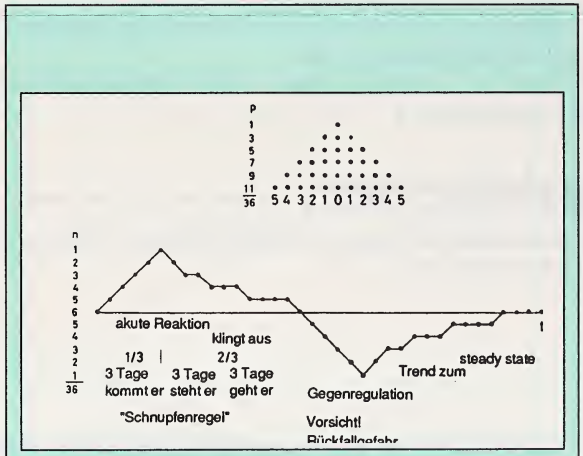

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elements in the karyotypes of the other four species by a reciprocal translocation. Complete homology appears to exist among the remaining autosomes and the X chromosome in all species, however, the variable quality of banding of several smaller-sized pairs from *C. rufocanus* (nos. 17, 22, and 25) makes these comparisons equivocal. Intraspecific and interspecific variability exists in the size and morphology of the Y chromosome. The Y in *C. rufocanus* and *C. gapperi* is a medium sized acrocentric. In *C. glareolus* from Austria and in *C. rutilus* it is metacentric, while in the *C. glareolus* specimen from France the element is submetacentric. The Y in *C. californicus* is an extremely small-sized acrocentric.

C-bands were examined from all five species, including specimens of *C. glareolus* from Austria and France, and *C. gapperi* from Vermont, Virginia and West Virginia. Presented in Figures 2a–b are C-banded karyotypes of *C. gapperi* and of *C. rutilus*, while C-banded karyotypes of *C. rufocanus, C. glareolus* and *C. californicus* are found elsewhere (Gamperl 1982a; Modi 1987b). Among all species, autosomal C-bands are found predominantly centromerically. The sizes of centromeric autosomal C-bands in *C. rufocanus* and *C. glareolus* (Austria) are larger than those in the other species or in the French specimen of *C. glareolus*. Further, both members of pair 27 in *C. rufocanus* are almost completely C-band positive. In the specimen of *C. gapperi* from West Virginia two different pairs of autosomes exhibit C-band heteromorphisms. In the first pair, one element has a large-sized centromeric C-band and C-band positive short arms, both of which are absent in the homologue. In the second pair, one element is completely heterochromatic (Fig. 2a). The other specimens of *C. gapperi* did not show this intraindividual C-band variation. The Y is completely C-band positive in all species except *C. californicus*, where it is C-band negative.

Metaphase cells from a total of five different tissues (femur bone marrow, vertebral column bone marrow, spleen, ear fibroblasts, and lung fibroblasts) from six specimens belonging to three species (*C. gapperi, C. californicus,* and *C. rutilus*) were examined using silver staining (s. Table). Representative cells from *C. gapperi* and *C. californicus* are shown in Figs. 2c–d. All Ag-NORs examined were found pericentromerically and never interstitially or telomerically. The mean number of Ag-NORs per cell ranged from 2.46 to 3.25 for femur bone marrow cells among the four specimens examined, and from 5.58 to 8.37 for fibroblast cells among the three specimens examined. The modal number of Ag-NORs per cell was lower for femur bone marrow cells than for cells from the other tissue types. The range between the minimum and maximum number of NORs staining per cell showed little variability among all specimens and tissues examined (s. Table).

Differences among the mean number of NORs staining per cell (s. Table) were tested for statistical significance using a one-way analysis of variance (ANOVA) in each of the following five comparisons: 1. *C. gapperi* 6 femur bone marrow versus ear fibroblast cells ($F = 106.9$, $p < 0.001$), 2. *C. gapperi* 7 femur bone marrow versus ear fibroblast cells ($F = 257.5$, $p < 0.001$), 3. *C. californicus* 3 femur bone marrow versus spleen cells ($F = 0.53$, $p > 0.10$), 4. femur bone marrow cells from *C. gapperi* 6, *C. gapperi* 7, *C. californicus* 2 and *C. californicus* 3 ($F = 3.34$, $0.02 < p < 0.05$) and 5. fibroblast cell lines from *C. gapperi* 6, *C. gapperi* 7 and *C. rutilus* 1 ($F = 78.79$, $p < 0.001$). These results indicate significant differences among group means in all analyses except the comparison of *C. californicus* 3 femur bone marrow versus spleen cells.

Next, two of the above analyses were repeated after deleting one sample from each. Three of the four femur samples (all except *C. californicus* 2) were compared and a lack of significance was found ($p > 0.10$). Similarly, two of the three fibroblast samples (except *C. gapperi* 6) were compared and the ANOVA was non-significant ($p > 0.10$). These last two analyses indicate that the two deleted samples differ significantly from the remaining samples in their respective groups which collectively represent rather homogeneous populations. The frequency distributions of the samples analyzed by the ANOVAs are plotted in Fig. 4.

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Fig. 1. G-banded karyotypes of *Clethrionomys*. a: Male *C. rutilus;* b: Haploid complements of a female *C. gapperi* from Vermont at three different stages of condensation; c: Composite karyotype comparing the haploid complement from each of five species. Elements, arranged from left to right in each set, are from *C. rufocanus, C. glareolus, C. gapperi, C. californicus,* and *C. rutilus*. Asterisks indicate chromosomes that have undergone rearrangement from the primitive condition as proposed by Modi (1987a)

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Table. **Results from the silver staining analyses for the nucleolus oganizer region**
Standard statistics regarding the number of Ag-NORS per cell among different tissues are given for three species of *Clethrionomys*

Specimen	Tissue	No. Cells	Mean	SD	Mode	Range
C. gapperi 6	f[1]	241	2.80	2.58	0	0–12
C. gapperi 6	e	169	5.58	2.78	6	0–11
C. gapperi 7	f	298	3.24	2.88	0	0–12
C. gapperi 7	e	117	8.37	3.05	10	0–13
C. californicus 2	f	141	2.46	2.07	2	0–9
C. californicus 3	f	115	3.25	3.07	0	0–11
C. californicus 3	s	105	3.54	2.80	3	0–12
C. californicus 4	v	123	5.16	3.22	3	0–13
C. rutilus 1	l	51	8.28	2.52	10	0–13

[1] Tissue sources from which metaphase chromosomes were derived: f = femur bone marrow, e = ear fibroblast cell line, s = spleen, v = vertebral column bone marrow, l = lung fibroblast cell line

Fig. 2. a: C-banded karyotype of a male *C. gapperi* from West Virginia with the arrowheads illustrating autosomal C-band heteromorphisms; b: C-banded karyotype of a male *C. rutilus*; c: Silver stained metaphase cell of female *C. gapperi* 7 from Vermont derived from an ear fibroblast cell line; d: Silver stained metaphase cell from female *C. californicus* 4 derived from vertebral bone marrow. In both (c–d) Ag-NORs are visible at the centromeres of eleven acrocentric chromosomes

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The frequency of sister chromatid exchange was recorded from 16 cells in a male specimen of *C. rutilus*. A representative metaphase cell is shown in Figure 3a. The mean number of exchanges per cell plus or minus one standard deviation was 8.0 ± 3.3 with a range of 5–14.

A total of 21 pachytene and 11 diakinesis cells was observed in meiotic preparations from a single male *C. californicus*. Twenty-seven autosomal bivalents and a conspicuous sex vesicle were observed in the pachytene cells (Fig. 3b). At diakinesis 27 autosomal bivalents were apparent, and an end-to-end association existed between the X and Y (Fig. 3c). It appears as though the centromeric end of the X synapses with the Y in the Giemsa stained cells.

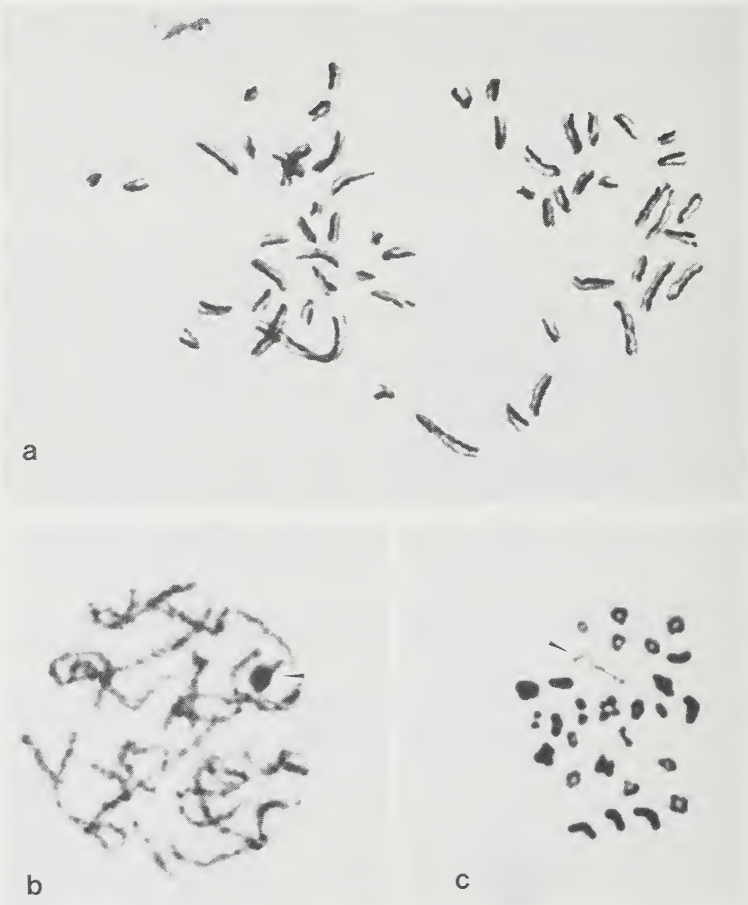

Fig. 3. a: Metaphase cell of *C. rutilus* after BrdU incorporation and modified FPG staining. An unusually large number of sister chromatid exchanges (eleven) may be noted. b: Giemsa stained pachytene cell from a male *C. californicus*, with the arrowhead pointing out the sex vesicle; c: Giemsa stained diakinesis cell from a male *C. californicus* with the arrowhead indicating the free end of the X

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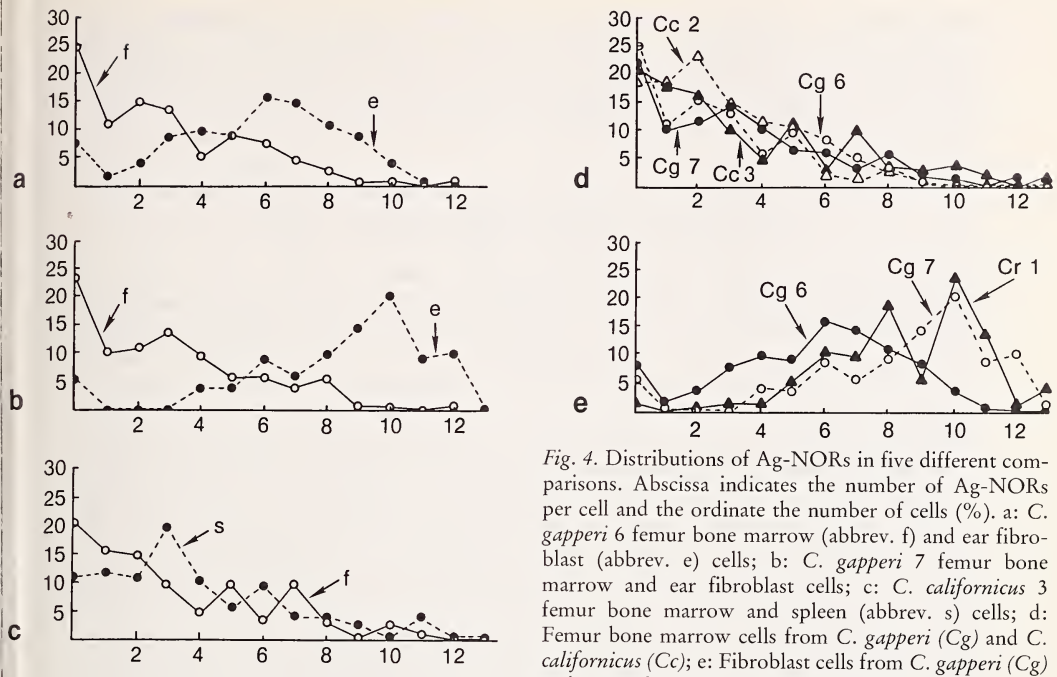

Fig. 4. Distributions of Ag-NORs in five different comparisons. Abscissa indicates the number of Ag-NORs per cell and the ordinate the number of cells (%). a: *C. gapperi* 6 femur bone marrow (abbrev. f) and ear fibroblast (abbrev. e) cells; b: *C. gapperi* 7 femur bone marrow and ear fibroblast cells; c: *C. californicus* 3 femur bone marrow and spleen (abbrev. s) cells; d: Femur bone marrow cells from *C. gapperi (Cg)* and *C. californicus (Cc)*; e: Fibroblast cells from *C. gapperi (Cg)* and *C. rutilus (Cr)*

Discussion

G-banding, C-banding and systematic relationships

The comparative cytogenetic data for the genus *Clethrionomys* derived both from the present study and from the literature may be summarized with respect to intraspecific and interspecific variability. Six species have been karyotypically examined, the five discussed here and *C. andersoni* (Obara 1986). All six species have 2n = 56 and NF_a = 56, with the exception of a specimen of *C. rutilus* from Alaska that was heterozygous for a centric fusion and thus had 2n = 55 (Rausch and Rausch 1975). Populations of *C. gapperi* from Vermont, Virginia and West Virginia (Modi 1987a, b; present study), Wisconsin, and Wyoming (Nadler et al. 1976) have now been examined using chromosomal banding procedures. With the exception of the two autosomal C-band heteromorphisms reported here in the male specimen from West Virginia, no intraspecific variability has been noted, although it is difficult to accurately compare our preparations with those of Nadler et al. (1976). Differences in the amount of pericentromeric autosomal C-bands were observed among individuals of *C. glareolus* from Austria and France (Gamperl 1982a). Nadler et al. (1976) suggested minor differences in G-banding patterns may exist among Soviet and Alaskan samples of *C. rutilus*. Finally, G-banding patterns between *C. rufocanus* from Japan (Mascarello et al. 1974) and Sweden (Gamperl 1982a) appear identical.

Three of these six species are known to exhibit intraspecific variability in Y chromosome size and/or morphology. Medium-sized acrocentric or metacentric elements are known in different populations of *C. rutilus* and *C. rufocanus* (Vorontsov et al. 1978), while acrocentric, metacentric (Král 1972; Vorontsov et al. 1978), and submetacentric (Gamperl 1982a) elements exist among *C. glareolus*. On the other hand, intraspecific Y chromosome variability has not yet been reported for the three remaining species. Among

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these, the Y in *C. californicus* is an extremely small-sized acrocentric (Modi 1985), while in *C. gapperi* and *C. andersoni* the element is a medium-sized acrocentric. Modi (1987b) has argued that a medium-sized acrocentric, C-band positive element is the primitive Y chromosome among species in the family Arvicolidae. If this is correct, then derived Y chromosomes are present among populations of four of the six species thus far karyotypically examined.

Interspecific comparisons of G-banded karyotypes indicate that *C. rufocanus* and *C. andersoni* have identical karyotypes, although minor differences in staining intensity exist among several pairs of autosomes (Obara 1986). These two species differ from the remaining four studied here due to the presence of the 1/9 reciprocal translocation. As suggested earlier (Gamperl 1982a) and supported elsewhere (Modi 1987a), based upon outgroup comparisons with G-banded chromosomes from other arvicolid and cricetid rodent species, the constitution of chromosomes 1 and 9 as found in *C. rufocanus* and *C. andersoni* is regarded as primitive, while the arrangement found in the other four species is derived.

The isolated systematic position of *C. rufocanus* and *C. andersoni* relative to the related *C. rutilus, C. glareolus, C. californicus* and *C. gapperi* as suggested by the 1/9 translocation is supported by several other studies. Traditional morphological comparisons assign *C. rufocanus* to a monotypic subgenus (Miller 1900). Additionally, Corbet (1978) and Obara (1986) feel that *C. rufocanus* and *C. andersoni* are more closely related to one another than to any other living forms. Viable F_1 hybrid offspring have been produced in laboratory breeding studies between *C. glareolus* and *C. gapperi* (Grant 1974), and between *C. glareolus* and *C. rutilus* (Spannhof 1960; Rauschert 1963; Zimmermann 1965); while attempted crosses between *C. rutilus* and *C. gapperi* have been unsuccessful (Matthey 1953; Zimmermann 1965). Nadler et al. (1976) have suggested that *C. rutilus* may be a derivative of *C. glareolus* and that an ancestral *glareolus-gapperi*-like form may have had a trans-Beringian mid-Pleistocene distribution. They also point out that *C. rufocanus* and *C. rutilus* are well differentiated morphologically from one another throughout most of their considerably overlapping geographic distributions. Based upon protein electrophoresis Graf (1982) found *C. rufocanus* and *C. glareolus* to be more closely related to species belonging to other genera of arvicolids than to one another. Using DNA-DNA solution hybridization, Catzeflis et al. (1987) studied eight species of arvicolids including three species of *Clethrionomys*. They found the species of *Clethrionomys* to be much more closely related to one another than to species of *Microtus, Arvicola* or *Lemmus,* with *C. glareolus* and *C. gapperi* being slightly more similar to one another than either was to *C. rutilus*. Finally, Tegelström (1987) interpreted information derived from mitochondrial DNA restriction endonuclease digestion patterns as evidence for the occurrence of a limited episode of interspecific hybridization between natural populations of *C. glareolus* and *C. rutilus* in Fennoscandia.

The extreme interspecific chromosomal conservatism found here among *Clethrionomys* (only one major interspecific karyotypic difference) is in marked contrast to the patterns seen in other genera of arvicolid rodents such as *Microtus* (Gamperl 1982b, 1982c; Modi 1987a) *Dicrostonyx* (Gileva 1983) and *Ellobius* (Lyapunova et al. 1980). In these genera, interspecific karyotypic differences are often pronounced and attributable to one or more structural rearrangements. For example, Modi (1987a) analyzed G-banded karyotypes for 22 species belonging to eight genera and found a total of 141 euchromatic rearrangements accounting for the extensive interspecific chromosomal variation. The striking homogeneity found in *Clethrionomys* resembles the situation seen among vespertilionid bats of the genus *Myotis* (Bickham et al. 1986), the cat family (Wurster-Hill and Centerwall 1982), and seals (Arnason 1977). Although several factors, such as mutation rates, effective population sizes, fecundity effects due to chromosome segregational behavior at meiosis, and the phenotypic effects of novel homokaryotypes or heterokaryo-

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types are thought to be responsible for the origination and fixation of chromosomal rearrangements (White 1978), there is no empirical support indicating why a group such as *Clethrionomys* should be nearly chromosomally invariant while other related groups exhibit extensive interspecific karyotypic variation. From this, it appears that structural chromosomal differences are not a prerequisite for the attainment of reproductive isolation among *Clethrionomys*.

Silver-staining and rDNA transcriptional activity

It is generally accepted that silver positive staining of nucleolus organizer regions in metaphase chromosomes is indicative of rDNA gene activity (Miller et al. 1976). Results of the present study are interpreted with respect to tissue, individual and species specific differences in rDNA gene expression as evidenced by the silver staining technique.

Significantly greater mean numbers of Ag-NORs were seen in fibroblast cells than in femur bone marrow cells in both specimens of *C. gapperi,* whereas a significant difference was not seen between the femur and spleen tissues in the single specimen of *C. californicus*. This indicates greater rDNA transcriptional activity in cultured cells than in noncultured cells from the same individual, but similar levels of transcriptional activity among the two noncultured tissue types within an individual.

Various results from other studies have been reported regarding intraindividual tissue specific silver staining properties of NORs. Human bone marrow cells have fewer Ag-NORs and demonstrate greater intercellular heterogeneity in silver staining than do cells derived from other tissues (Reeves et al. 1982; Mamaev et al. 1985). Similarly, Merry et al. (1983) found tissue specific differences among the opossums they examined. The basis for tissue specific differences in rDNA transcriptional activity is not understood. However, this variability may be attributable to differential maturation rates of bone marrow cells (Mamaev et al. 1985), differences in cell cycle times or metabolic requirements of the tissues, differential cell growth and/or variation in the availability of necessary transcriptional control factors.

The other two comparisons that were carried out (analyzing similar tissues between individuals of different species) indicated that individual differences in silver staining do exist and that specimens of one species may be more similar to individuals of other species than to other conspecifics. This suggests that intraspecific variability in silver staining is equal to or greater than interspecific differences among *Clethrionomys*, and thus this type of comparison is of limited taxonomic utility.

Sister chromatid exchange

Sister chromatid exchange (SCE) represents recombination of DNA at apparently homologous loci, with such exchange occurring seemingly at random throughout the genome. Although the basis for SCE is not known, the procedure has been widely used as a measure of mutagenicity and genotoxicity (Latt et al. 1979). The two procedures generally used for SCE detection (autoradiography using tritiated thymidine and BrdU incorporation) are both known to increase the frequency of SCE. This observation has led to the question of whether or not SCE occurs spontaneously in living cells. A number of studies has addressed this issue by measuring SCE both in vitro and in vivo by administering various concentrations of BrdU, calculating dose-response curves and extrapolating from a linear region of the curve to predict what the SCE frequency would be in the absence of BrdU. Recently, Tucker et al. (1986) measured SCE frequencies in human and mouse peripheral lymphocytes using monoclonal antibodies and very low (20–30 nM) concentrations of BrdU, and predicted spontaneous frequencies of 7.2 SCE/cell and 4.8 SCE/cell for the two species, respectively.

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A dose response curve was not generated in the present study for *C. rutilus* rather a SCE frequency of 8.0 per cell was determined at a single BrdU concentration of 30 μg/ml. By comparing this result to the curves presented in other studies and interpolating at similar BrdU concentrations, the frequency found here in lung fibroblast cells of *C. rutilus* is consistent with the findings reported for a Chinese hamster fibroblast cell line where a frequency of about 7.5 exchanges per cell was reported (Kato 1974). On the other hand, Kram (1979) reported higher SCE frequencies of about 20 per cell in mouse fibroblast cells.

Meiotic analyses

The presence of a sex vesicle in meiotic pachytene cells has been observed for a number of mammalian species. This structure is thought to function as a means of keeping the X and Y chromosomes in association, since they share limited DNA sequence homology and typically synapse less extensively than do autosomal bivalents. Generally, the sex chromosomes then assume an end-to-end association as the meiotic cycle progresses into diakinesis (Solari 1974).

A conventional sex vesicle and end-to-end association were observed here in the preparations from *C. californicus*. It appears as though the centromeric end of the X synapses with the small-sized Y chromosome in this species. Similar association of the centromeric region of an acrocentric X with the Y was reported in a South American cricetid rodent (Sbalqueiro et al. 1984), while in the mouse *(Mus musculus)* the telomeric region of the acrocentric X pairs with the Y (Hsu et al. 1971). If this synapsis is due to the presence of homologous pseudoautosomal DNA sequences on the sex chromosomes (Pritchard and Goodfellow 1985), then it would appear that these sequences are located at a different chromosomal region of the mouse X compared with the location of the sequences in these two other rodent species. Further, the extreme small size and C-band negative staining property of the Y in *C. californicus* may be the result of o loss of highly repetitive DNA sequences, while the pseudoautosomal sequences and those involved with testis determination and male fertility have been retained.

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Zusammenfassung

Vergleich chromosomaler Bändermuster von amerikanischen und europäischen Rötelmäusen, Gattung Clethrionomys

G-Bänder von Chromosomen folgender fünf *Clethrionomys*-Arten werden beschrieben: *C. glareolus, C. rufocanus, C. gapperi, C. californicus* und *C. rutilus*. Entsprechende Daten stehen auch noch für eine weitere Art, *C. andersoni,* aus der Literatur zur Verfügung. *C. glareolus, C. gapperi, C. californicus* und *C. rutilus* sind durch eine abgeleitete reziproke Translokation eines Autosomenpaares gekennzeichnet, während in *C. rufocanus* und *C. andersoni* der primitive Zustand erhalten geblieben ist. Die Variabilität der C-Bänder ist sowohl zwischen als auch innerhalb der Arten sehr gering. Konvergente Variationen hinsichtlich Form und Länge des Y-Chromosoms kommen bei drei Arten vor. Chromosomale Unterschiede zwischen verschiedenen Arten der Gattung *Clethrionomys* sind wesentlich geringer als in anderen Wühlmaus-Gattungen, d. h. die Evolution in *Clethrionomys* hat stattgefunden ohne gleichzeitige Chromosomenveränderungen. Die Aktivität der ribosomalen DNA (rDNA) wurde in fünf verschiedenen Gewebearten von Individuen dreier Arten mit Hilfe der

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Silberfärbung (NOR-Färbung) untersucht. Dabei ergab sich, daß Fibroblasten eine wesentlich höhere Anzahl von Nukleolusorganisatorregionen (Ag-NOR's) aufweisen als Knochenmarkszellen desselben Tieres. Die intraspezifische Variabilität der Zahl von NOR's pro Zelle innerhalb eines bestimmten Gewebes ist gleich oder größer als Unterschiede zwischen verschiedenen Arten. Die Häufigkeit von Schwesterchromatidaustauschen (SCE's) wurde nach Einbau von 5-Bromdeoxiuridin (BrdU) in einer Zellinie aus Lungenfibroblasten von *C. rutilus* bestimmt. Die durchschnittliche Zahl der SCE's pro Zelle beträgt 8,0 und ist damit gleich hoch bzw. etwas niedriger als bei anderen Nagerarten. Untersuchungen der Meiose von *C. californicus* zeigten, daß zwischen der Zentromerenregion des X-Chromosoms und dem sehr kleinen, C-Band-negativen Y-Chromosom eine End-zu-End-Assoziation in der Diakinese besteht.

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