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Chromosomal evolution in Holarctic ground squirrels *(Spermophilus)*

II. Giemsa-band homologies of chromosomes and the tempo of evolution

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Abstract

Chromosomal morphology within the Holarctic ground squirrels (subgenus *Spermophilus*) was studied by means of Giemsa-banding. Diploid numbers within the subgenus range from 2n = 30–46 in 23 species, with 11 species displaying a modal 2n = 36. Chromosome pairs comprising the 2n = 38

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karyotype were arbitrarily arranged by size and arm length, and the banding patterns of 12 species, representing all diploid numbers, were compared. Pairs one through nine are all large, distinctively banded chromosomes, and were present in all species, either as arms of biarmed elements (2n = 30–38) or as uniarmed elements (2n = 40–46). Among the smaller chromosomes, pairs ten to 15 appear alike in the Nearctic "big-eared" and Holarctic "long-tailed" ground squirrels, and in *S. washingtoni* except that the 2n = 30–32 species *(undulatus, columbianus, beldingi)* lack the largely heterochromatic pair 15, and in the case of *beldingi,* pair 12. Pairs ten to fifteen also appear alike in the Palearctic ground squirrels, in the Nearctic "short-eared" and in *S. brunneus,* but homologies between these groups are more difficult to establish because of the smaller chromosome size and less distinctive banding patterns. In some cases *(S. richardsonii – S. elegans; S. armatus – S. parryii; S. columbianus – S. undulatus)* complete homologies can be established between species, and nearly complete homologies are seen in others *(S. mollis – S. brunneus; S. dauricus – S. relictus).*

Despite the diversity of karyotypes, the large number of shared chromosomal elements within the subgenus *Spermophilus* suggest that these "marker" chromosomes are presumably symplesiomorphic systematic characters. Certain chromosomal divergence events may plausibly be postulated, and existing fossils permit approximate dates to be assigned to these divergences. If chromosomal divergence events are then broadly grouped by age (mid-Pliocene, late-Pliocene, early-, middle-, and late-Pleistocene) and the most parsimonious number of chromosomal changes necessary for the observed divergences counted, rates of chromosomal evolution can be estimated. These vary, in different lineages, from zero to 25 changes/million years, and average, for the subgenus as a whole, 2.3 changes/million years. This rate is much higher than the average reported for rodents.

Introduction

Ground squirrels of the subgenus *Spermophilus* sensu lato are known from the Clarendonian or Hemphillian (late Miocene) in North America (Black 1963; Savage and Russell 1983) and from several Eurasian lineages dating to the Villafranchian (late Pliocene) (Gromov et al. 1965; Kurten 1968). The fossil evidence therefore suggests that ancestral ground squirrels of this group originated within North America. Black (1972) and Moore (1961) postulated that migrations both westward and eastward across the Bering land bridge occurred several times during their evolution, giving rise to different lineages on each continent. These lineages include: 1. the North American "big-eared", "small-eared", and "intermediate" species groups (Davis 1939; Nadler et al. 1976, 1982) which belong to the subgenus *Spermophilus* sensu stricto; 2. Eurasian ground squirrels of subgenus *Spermophilus* sensu stricto; 3. the Eurasian species group sometimes designated as subgenus *Colobotis* (Gromov et al. 1965); and 4. Holarctic long-tailed ground squirrels sometimes ranked as the subgenus *Urocitellus* (Gromov et al. 1965). Despite the morphological diversity of these species groups, their biochemical and chromosomal affinities favor the inclusion of all taxa within a single subgenus *Spermophilus* instead of the several subgenera previously recognized (Corbet 1978; Nadler et al. 1982).

Considerable diversification of chromosome complements has accompanied the evolution of species comprising this subgenus, with diploid chromosome numbers ranging from 2n = 30–46 among North American species (Nadler 1966) and from 2n = 36–42 in Eurasian taxa (Lyanpunova and Vorontsov 1970; Vorontsov and Lyapunova 1970). Some relationships between Eurasian and North American taxa have been ascertained by a combination of morphological, paleontological and chromosomal evidence, as was the case in Holarctic *S. parryii* which share a 2n of 34 and an identical karyotype on both continents despite their isolation by the Bering Strait for 13,000 years (Nadler 1966; Lyapunova 1969). Similarly, the Asian and North American long-tailed ground squirrels *(S. undulatus, S. columbianus)* share identical chromosome complements (2n = 32), including G-banding homology, despite their isolation for more than 100,000 years (Nadler et al. 1975). Understanding of chromosomal evolution between species with longer periods of geographic isolations has been more difficult due to restructuring of both chromosome number and morphology. Nevertheless, Vorontsov and Lyapunova (1976) noted that Middle Asian *S. xanthoprymnus* (2n = 42) and North American *S. vigilis* (= *townsendii*

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vigilis) (2n = 46) appeared to differ by only two Robertsonian chromosome rearrangements and one pericentric inversion, and postulated that these taxa, occurring nearly at the extremes of the geographic distribution for the subgenus and possessing the highest diploid numbers, might be direct descendants of the earliest trans-Beringian ground squirrel migration. Further testing of these postulated chromosomal affinities, and of those between other taxa from both continents possessing 2n = 36 but different karyotypes, was impossible until techniques for assessing homologies of chromosomal arms by means of their banding patterns became available (Seabright 1972).

The present investigation reports comparisons of Giemsa-banding patterns of Eurasian *S. xanthoprymnus* (2n = 42), *S. citellus* (2n = 40), *S. dauricus* (2n = 36), *S. relictus* (2n = 36), and *S. undulatus* (2n = 32); of Holarctic *S. parryii* (2n = 34); and of North American *S. vigilis* (2n = 46), *S. brunneus* (2n = 38), *S. washingtoni* (2n = 36), *S. armatus* (2n = 34), *S. columbianus* (2n = 32), and *S. beldingi* (2n = 30). Homologies identified by comparisons of Giemsa-band patterns are applied to an evaluation of chromosomal evolution in the subgenus with particular emphasis on the tempo of karyotypic change in relation to periods of geographic isolation.

Materials and methods

The following specimens were studied: *Spermophilus xanthoprymnus* (Bennett), USSR, Armyanskaya SSR, Karput, 10 km S Leninakan, 1 male and 1 female; *S. citellus citellus* (Linnaeus), Czechoslovakia, Southern Moravia, 2 females; *S. relictus relictus* (Kashkarov), USSR, Uzbek SSR, Tashkentsk. Obl., Kuramansk. Mts., Angren Plateau, 1 male and 1 female; *S. dauricus dauricus* (Brandt), USSR, RSFSR, Chitinsk. Obl., Amogoitui, 3 males; *S. undulatus eversmanni* (Brandt), USSR, Tuvinsk. Aut. Obl., Mugur-Aksy, 1 male and 1 female; *S. undulatus undulatus* (Pallas), USSR, RSFSR, Irkutsk. Obl., Angarsk, left bank of Kitoi River, 1 male and 1 female; *S. undulatus menzbieri* (Ognev), USSR, RSFSR, Amursk. Obl., Zazeisk. Rai., 1 male; *S. undulatus jacutensis* (Brandt), USSR, Yakutsk. ASSR, vic. of Yakutsk, 1 male and 1 female; *S. parryii tschuktschorum* (Chernyjavskii) (= *leucostictus* [Brandt]), USSR, Chukotsk. Nats. Okr., vic. of Egvekinot, 1 female; *S. parryii janensis* (Ognev), USSR, Yakutsk. ASSR, vic. of Verkhoyansk, 1 male; *S. parryii kodiacensis* (Allen), USA, Alaska, Kodiak Island, 2 males and 1 female; *S. vigilis* (Merriam), USA, Oregon, Malheur County, vic. of Vale, 1 male and 1 female; *S. brunneus* (A. H. Howell), USA, Idaho, Elmore County, 3 mi S, 0.5 mi E of Bear Post Office, 5 males and 3 females; *S. washingtoni* (A. H. Howell), USA, Washington, Franklin County, Scootenay Reservoir, 1 female; *S. armatus* (Kennicott), USA, Wyoming, Lincoln County, vic, of Cokeville, 1 male and 1 female; *S. columbianus columbianus* (Ord), USA, Montana, Madison County, vic. of Harrison, 3 males and 3 females; *S. beldingi beldingi* (Merriam), USA, California, in Inyo County, Rock Lake, 10 mi SW Tom's Place; 1 male; Mono County, 9 mi SW Tom's Place; 1 male and 2 females.

Chromosome and Giemsa-band (G-band) preparations were made from bone marrow cell suspensions following intraperitoneal injections of Velban or Colchicine according to the method of Seabright (1972) and as described previously by us (Nadler et al. 1975).

Results

G-banded karyotypes are compared and illustrated in Figs. 1A and B. The chromosomes are arranged in pairs according to size, morphology, and banding pattern. The arrangement differs from those published previouly (Nadler et al. 1973, 1975) in that it follows the order of decreasing size regardless of arm morphology. Consequently, certain chromosome pair numbers have been changed (see Table).

Chromosome pairs 1–9 were easily recognizable in all species by their larger size and unique banding patterns, and may be considered homologous "marker chromosomes". In *S. brunneus* and *S. washingtoni* the long arms of pair 1 shared homology with the other species (Fig. 1A); while the short arms in both species resembled one another, they appear relatively smaller than those of other taxa except the *townsendii* group, with perhaps some banding differences. *S. vigilis, S. xanthoprymnus* and *S. citellus* have four, two, and one

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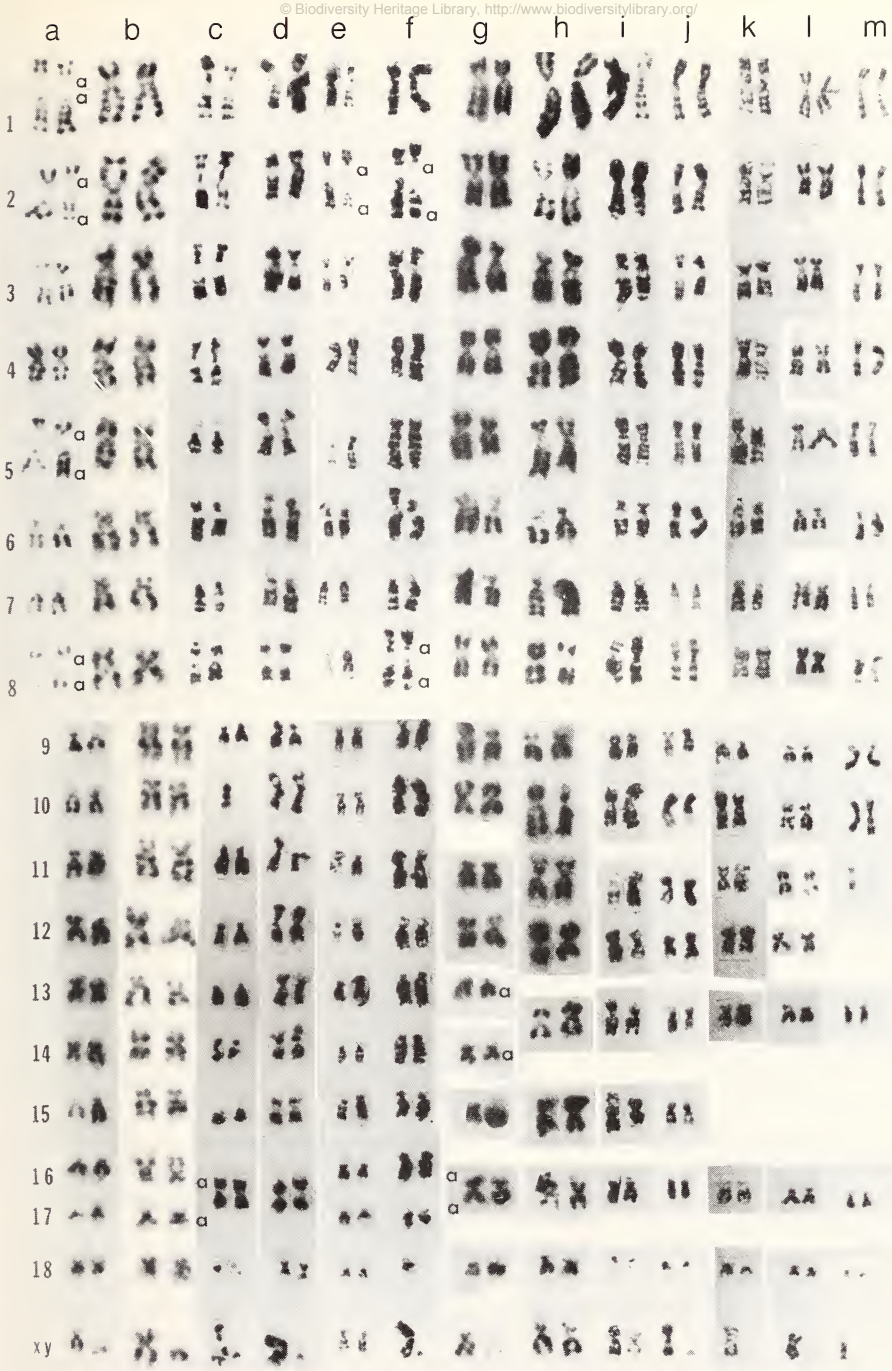

Fig. 1 A. G-band karyotype of chromosome pairs 1–8 from species of Eurasian and North American *Spermophilus*. a: *S. vigilis* (2n = 46); b: *S. brunneus* (2n = 38); c: *S. relictus* (2n = 36); d: *S. dauricus* (2n = 36); e: *S. citellus* (2n = 40); f: *S. xanthoprymnus* (2n = 42); g: *S. washingtoni* (2n = 36); h: *S. armatus* (2n = 34); i: *S. parryii* from Siberia (2n = 34); j: *S. parryii* from Kodiak Island (2n = 34); k: *S. undulatus* from Siberia (2n = 32); l: *S. columbianus* (2n = 32); m: *S. beldingi* (2n = 30). Chromosomes labeled "a" are acrocentrics in species a, e, and f that are presumed homologous to biarmed autosomes and may be involved in fusion or fission events (Fig. 2). – *Fig. 1 B.* G-band karyotypes of pairs 9–18 in the same species of *Spermophilus* listed in Fig. 1 A. The X chromosomes are medium-sized submetacentrics whereas the Y chromosomes vary from small acrocentrics in species, a, b, c, d, f, and j to minute biarmed chromosomes in k, l, and m

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pairs of acrocentric autosomes, respectively, that were homologous with arms of the biarmed members of pairs 1, 2, 5, and 8.

Determination of chromosomal homology was more difficult among pairs 10–18 due to smaller chromosomal size, more contraction of chromosomes by Velban, and fewer visible bands per arm. Greater variation in morphology, or centromere position, also occurred. Nevertheless, *S. parryii* from Siberia and Alaska, *S. armatus*, *S. undulatus*, and *S. columbianus* displayed general homology of pairs 10– 14 or 15. The 15th pair was absent in the latter two species. The banding of pairs 10–14 was quite similar in *S. dauricus* and *S. relictus*, and those pairs also shared closer similarities with those of *S. vigilis*, *S. xanthoprymnus*, and *S. citellus* than with *S. parryii*, *S. washingtoni*, *S. armatus*, *S. columbianus*, and *S. undulatus*. The metacentric pair following 15 of *S. washingtoni*, *S. dauricus* and *S. relictus* (Fig. 1B) may be homologous with acrocentric pairs 16 and 17 of *S. vigilis*, *S. citellus*, and *S. xanthoprymnus*.

Equivalents for autosome pair numbers

This paper	*S. brunneus* (Nadler et al. 1973)	*S. columbianus* (Nadler et al. 1975)
	Pair No.	
1	8	1
2	1	2
3	9	5
4	2	4
5	10	6
6	11	9
7	12	7
8	3	12
9	13	11
10	5	3
11	14	8
12	4	10
13	16	13
14	15	14
15	6	—
16	17	—
17	18	—
18	7	15
$2n_a = 36$	$2n_a = 36$	$2n_a = 30$

The X chromosomes are submetacentric or subtelocentric with 2–4 bands in the long arms and 1–2 bands in the short arms; they often stained indistinctly, but did not appear homologous in all species. The Y chromosomes ranged from minute biarmed chromosomes to medium sized acrocentrics and did not display bands.

The closest interspecific homologies occur between Siberian and Alaskan *S. parryii* (2n = 34) and *S. armatus* (2n = 34) and between Siberian *S. undulatus* and North American *S. columbianus*, both with 2n = 32 (Nadler et al. 1975). The autosomes of these species have identical banding patterns, although the species with 2n = 32 lack pair 15, which Lyapunova (unpublished data) has shown to be composed largely of heterochromatin. Save for the absence of pair 12, the chromosomes of *S. beldingi* are homologous to those of *S. columbianus* and *S. undulatus*.

Relationships between the other species are less clear due to the difficulties in recognizing homologies among the smaller and less distinctly banded chromosomes (pairs 10–18) of submetacentric, subtelocentric, or acrocentric morphology. However, it was possible to show a high degree of affinity between certain species with different chromosome numbers

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such as *S. vigilis* (2n = 46), *S. xanthoprymnus* (2n = 42), and *S. citellus* (2n = 40), and the acrocentric pairs (1, 2, 5, 8) involved in the Robertsonian rearrangements differentiating these and other species were recognized. There are also rather close similarities between the banding patterns of all chromosomes from these three species and Eurasian *S. dauricus* and *S. relictus* (2n = 36).

Relationships between the North American "intermediate" species, *S. brunneus* (2n = 38) and *S. washingtoni* (2n = 36) are established by the similarities of pairs 1–9. Pair 10 in *S. brunneus* is submetacentric rather than metacentric as in *S. washingtoni,* and a tandem fusion in *brunneus* of the small acrocentric pair (13) seen in *S. washingtoni* might account for this difference. However, pair 10 in the big-eared species also appears metacentric, or nearly so, as in *washingtoni,* whereas pair 10 in the small-eared species is submetacentric, as in *brunneus,* and the difference may be due to pericentric inversion of 10 rather than tandem fusion with the small acrocentric (10 + 13). Moreover, pair 15 in the small-eared species and *brunneus* is subtelocentric or acrocentric, but in *S. washingtoni* and in those big-eared species in which it occurs *(armatus, parryii)* it is metacentric. These chromosomal synapomorphies suggest a basic divergence, with *brunneus* allied with the small-eared, and *washingtoni* with the big-eared group. Earlier, *S. brunneus* (2n = 38) and *S. mollis* (2n = 38), with identical gross chromosomal morphology, were shown to have identical G-banding patterns except for small differences in presence or absence of minor bands or in staining intensity of five small chromosomes (pairs 14–18 of this study) (Nadler et al. 1973).

Discussion

Each of the species groups in the subgenus *Spermophilus* has a characteristic range of chromosome numbers. Most species of Palearctic *Spermophilus* have 2n = 36; *S. alashanicus* has 2n = 38; *S. citellus,* 2n = 40; and *S. xanthoprymnus,* 2n = 42 (Vorontsov and Lyapunova 1970; Orlov and Davaa 1975). Most of these differences appear to be due to Robertsonian rearrangements involving either fusion or dissociation of chromosomal arms (fission), except in the case of *S. alashanicus* (see below). Nearctic "small-eared" and "intermediate" *Spermophilus* exhibit a greater range of numbers, 2n = 36–46, but most populations are 2n = 36 *(S. townsendii, S. washingtoni)* or 2n = 38 (*S. mollis, S. brunneus),* and only *S. vigilis* has 2n = 46. One pericentric inversion appeared to distinguish *S. washingtoni* from *S. townsendii,* whereas *S. mollis, S. brunneus* and *S. vigilis* differed from *S. washingtoni* by Robertsonian changes (Nadler 1966; Vorontsov and Lyapunova 1970). However, the pattern of chromosomal evolution may be more complex (see below).

In contrast to these species groups (2n ≧ 36), most Nearctic "big-eared" and Holarctic "long-tailed" ground squirrels have lower diploid numbers, 2n = 30–36. A Robertsonian difference separates *S. richardsonii* (2n = 36) from *S. elegans, S. armatus,* and *S. parryii,* all with 2n = 34. However, chromosomal loss or fragmentation and translocation appear to be involved in evolution of the 2n = 34 karyotype to the 2n = 32 pattern found in *S. undulatus* and *S. columbianus,* and the 2n = 30 complement of *S. beldingi.*

Despite this diversity of diploid numbers, there is a great deal of resemblance among the species of the subgenus *Spermophilus.* As noted above, chromosomal arms of karyotypes with diploid numbers between 34 and 46 can be related to each other by means of Robertsonian fusion or fission, or by pericentric inversion mechanisms. Thus, the karyotype with 2n = 34 consisting entirely of biarmed chromosomes, as in *S. parryii* and others, presumably includes the full complement of genetic material found in the subgenus. Of the 17 pairs of chromosomes in this karyotype (16 autosomal pairs plus a pair of sex chromosomes), a minimum of nine autosomal pairs or paired arms of acrocentrics, appear to be homologous in G-band structure and general size throughout the subgenus. Eight of

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these same "marker" chromosomes can be identified in *Marmota monax* (2n = 38) Nadler et al., unpublished data), a member of a lineage that probably diverged from that of the ground squirrels in the Miocene, and this constitutes strong evidence for the stability of at least some chromosomal configurations in evolving marmotine lineages (cf. Mascarello et al. 1974). Such shared "primitive" chromosomes must be regarded as symplesiomorphic characters in evaluating the phylogenetic relationships of ground squirrels.

Affinities of big-eared and long-tailed *Spermophilus*

Certain species show even greater uniformity of karyotypes. Thus, the karyotypes of Siberian and North American *S. parryii* and *S. armatus*, all 2n = 34, also appear to be entirely homologous except for the X chromosome of *S. armatus* which is larger, which a subtelocentric centromere. *S. columbianus* and *S. undulatus* have entirely homologous G-band patterns (Nadler et al. 1975), and both species differ from *S. parryii* in the loss of small metacentric chromosome 15. Similarly, *S. beldingi* chromosomes are homologous to *parryii* but have lost or translocated an additional small chromosome pair (12).

All of these "big-eared" and "long-tailed" species, including *S. elegans* (2n = 34) and *S. richardsonii* (2n = 36) Nadler et al. 1971) resemble one another not only in karyotype, but also in cranial and external morphology (Davis 1939; Howell 1938; Robinson and Hoffmann 1975), and in biochemical characters (Nadler et al. 1982). It is thus reasonable to assume that they are related. Similarities of external morphology and ecology link the "long-tailed" ground squirrels in group, and the Nearctic "big-eared" species in another. Within these two groups, *S. undulatus* and *S. columbianus* are linked by karyotype and ecology, and form a sister group to *S. parryii*, while *S. armatus – S. beldingi* and *S. elegans – S. richardsonii* are allospecies pairs which have sister group relationship (Hoffmann 1981). We postulate that the 2n = 34 karyotype of *parryii, armatus* and *elegans* may be the primitive complement for this lineage from which 2n = 32 *(S. undulatus, columbianus)* and 2n = 30 *(S. beldingi)* were derived by loss or translocation of one or two pairs of small, probably heterochromatic chromosomes (Fig. 2). This interpretation is preferable to the alternative, whereby a 2n = 32 karyotype (ancestral *columbianus-undulatus*) was derived from "big-eared" ancestor with 2n = 34, and in turn gave rise to *S. parryii* by addition of a pair of chromosomes; it seems improbable that such addition could occur by any known method of chromosomal evolution.

Spermophilus elegans (2n = 34) presently has a wide but disjunct relict distribution in the Rocky Mountain and northern Great Basin, and was even more widely distributed on the Great Plains in the Pleistocene (Neuner 1975). *Spermophilus richardsonii* (2n = 36) occurs on the northern Great Plains; its range is almost entirely within the area covered by the most recent glacial advance, and fossil evidence suggests that it diverged from the ancestral stock at the end of the Pleistocene (Neuner 1975). Therefore, we suggest that the 2n = 36 karyotype of *S. richardsonii* was derived from 2n = 34 by fission of one biarmed chromosome, perhaps pair 8 (Nadler et al. 1971) (Fig. 2).

If the scheme of chromosomal evolution outlined above is valid, it means that Nearctic "big-eared" and Holarctic "long-tailed" ground squirrels shared a common ancestor (Fig. 2). The late Pliocene or early Pleistocene *S. cragini* of North America (Kurten and Anderson 1980) may represent this ancestral lineage, which gave rise to the *S. primigenius – nogaici – polonicus* lineage in Eurasia via trans-Beringian migration in the late Pliocene (Gromov et al. 1965). "Big-eared" species later arose from this ancestral lineage in North America, while ancestral *S. undulatus* diverged from ancestral *parryii* in the Palearctic, perhaps by the early middle Pleistocene, and gave rise to *S. columbianus* by trans-Beringian migration in the middle-late Pleistocene (Nadler et al. 1975).

Of the living species of long-tailed ground squirrels, *S. undulatus* exhibits the greatest

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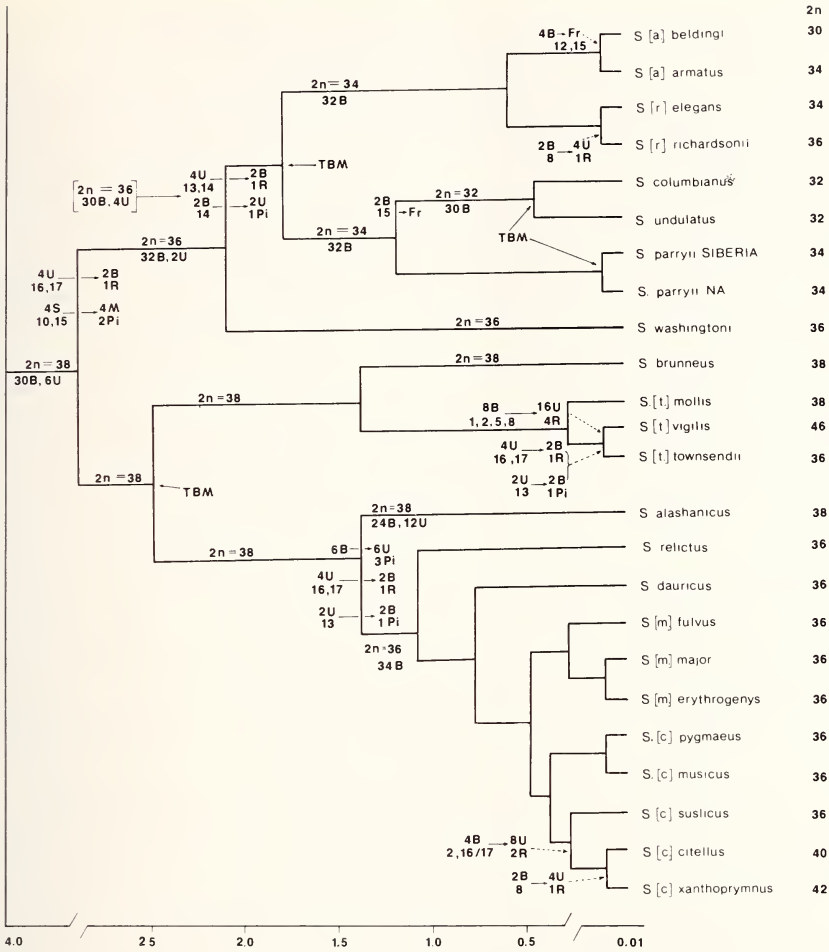

Fig. 2. Hypothetical scheme of chromosomal divergence events within the Holarctic subgenus *Spermophilus*. For an alternative scheme, see VORONTSOV and LYAPUNOVA (1969); LYAPUNOVA and VORONTSOV (1970). Abbrev.: B = biarmed chromosomes; U = uniarmed chromosomes; Pi = pericentric inversion; R = Robertsonian change (fusion, fission); Fr = chromosomal loss (fragmentation, translocation); TBM = transberingian migration

morphological variation, suggesting a longer period of evolution than *S. columbianus*. However, this is confounded by environmental effects; *undulatus* occupies a larger area, and its variability may be merely a product of many local adaptations (VORONTSOV et al. 1980). While their karyotypes are indistinguishable, their long period of divergence is reflected by marked differences in electromorphs and in cranial morphology (NADLER et al. 1982; ROBINSON and HOFFMANN 1975). This is an impressive example of gross karyotypic stability. The arctic ground squirrel, *S. parryii*, in turn arose from the ancestral "long-trailed" stock in Eurasia (NADLER et al. 1975) or in North America (VORONTSOV and LYAPUNOVA 1969, 1970; VORONTSOV et al., 1980); evidence on this point seems contradictory.

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Affinities of Palearctic and Nearctic "small-eared" and "intermediate" ground squirrels

Among most Palearctic ground squirrels, chromosomal resemblances are also great. All of the nine large "marker" chromosomes or equivalent arms appear homologous in all species investigated, and many of the smaller chromosomes are probably also homologous. *S. xanthoprymnus* (2n = 42), *S. citellus* (2n = 40), *S. dauricus* and *S. relictus* (2n = 36) form a Robertsonian series, to which the other species of 2n = 36, NF = 72 ground squirrels of the Palearctic conform (Lyapunova, unpublished data). The single exception to this appears to be *S. alashanicus*, with 2n = 38, NF = 64, and a karyotype consisting of 24 biarmed and 12 uniarmed autosomes (Orlov and Davaa 1975). In addition to a Robertsonian rearrangement, four pericentric inversions must be postulated to derive the *alashanicus* karyotype from either 2n = 40 or 2n = 36 of the Palearctic series.

"Marker" chromosomes (pairs 1–9) and their arms all have homologous banding patterns not only among the Palearctic species, but also among Nearctic *S. brunneus, S. mollis,* and *S. vigilis* (Fig. 1; Nadler et al. 1973), and although slight differences occur, there is also general agreement among the smaller chromosomes (pairs 10–18). This resemblance of karyotypes in 2n≧36 ground squirrels across the Holarctic probably represents the conservation, in different lineages, of portions of the ancestral karyotype of the subgenus *Spermophilus.* In contrast *S. washingtoni,* which morphologically is a small-eared squirrel, differs significantly from other species in that group. Its 2n = 36 is similar, but pairs 10 and 15 are metacentric, like those of big-eared and long-tailed ground squirrels, rather than submetacentric as in the small-eared species. Thus, *washingtoni* is more closely aligned chromosomally with the Nearctic big-eared species, and this resemblance is also seen in biochemical similarity (Nadler et al. 1982).

The oldest fossils of the subgenus are found in North America (Black 1972). The earliest record in Eurasia is that of *S. tologoicus* from the "late Pliocene (Villafranchian)" of Transbaikaliya (Gromov et al. 1965), which was suggested to be the ancestor of *S. dauricus.* Hence, the divergence of Palearctic from Nearctic *Spermophilus* probably dates to one or more trans-Beringian migration during the late Pliocene (Fig. 2), perhaps preceding the migration that resulted in the establishment of the long-tailed ground squirrel *(S. primigenius)* lineage (see above). Subsequent evolution of the Palearctic and Nearctic lines of the "small-eared" and "intermediate" ground squirrels probably proceeded independently, because there is no evidence for any subsequent trans-Beringian migrations in this group. Biochemical and morphological data (Nadler et al. 1982; Hoffmann et al. unpublished data) indicate that *S. brunneus, S. washingtoni, S. dauricus, S. alashanicus,* and perhaps *S. relictus* have retained various primitive characters from the ancestral stock. The pattern of chromosomal evolution proposed (Fig. 2) here indicates that this "intermediate" group is paraphyletic, and defined by shared primitive characters.

The ancestral karyotype can only be inferred. One possibility is that it contained a number of acrocentric chromosomes, as does modern *S. vigilis* (2n = 46) (Vorontsov and Lyapunova 1969, 1970; Lyapunova and Vorontsov 1970), and subsequent chromosomal evolution involved progressive reduction in diploid number. Another possibility is that the primitive karyotype was 2n = 38 (Nadler et al. 1973), as is true in the related genera *Marmota* (Hoffmann and Nadler 1968) and *Tamias* (Nadler et al. 1977), and that chromosomal evolution proceeded to both lower and higher numbers. Support for the first possibility is found in the fact that most cytogeneticists regard fusion of uniarmed chromosomes to form biarmed elements as more probable than the reverse process of chromosomal fission. However, White (1978: 54) cautioned that, other things being equal ". . . in the long run, . . . as many increases as decreases in the number of chromosomes must have occurred in evolution". Support for the second possibility is found not only in outgroup comparisons with other Sciuridae, but also in the karyotype of *S. alashanicus*

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(2n = 38) which, as noted above, does not conform to the Robertsonian series of the other Palearctic *Spermophilus*. The karyotype of *alashanicus* is derivable most parsimoniously not from the 2n = 36 of *S. dauricus* (its closest apparent relative morphologically and geographically), which requires a minimum of one Robertsonian change and four pericentric inversions, but from the karyotype of *S. brunneus* (2n = 38), which requires only 3 pericentric inversions. This suggestion needs to be tested by banding of *S. alashanicus* chromosomes.

The cladogram of chromosomal evolution presented here (Fig. 2) is based on an ancestral karyotype assumed to be 2n = 38, with 30 biarmed and six uniarmed autosomes. The number of autosomal changes postulated in this cladogram ranges from zero to seven in different lineages, with a total of 23 required (including pericentric inversions of pairs 10 and 15). This interpretation also implies four transberingian migrations to establish the Palearctic "short-eared", Holarctic long-tailed, and *S. parryii* lineages. However, it also suggests that the Robertsonian fusion of uniarmed pairs 16 and 17 occurred independently in the Palearctic "short-eared" and Nearctic ancestral *washingtoni* lineages. An alternative interpretation that postulates this change as occurring only once in the ancestral lineage is slightly more parsimonious in terms of chromosomal changes (22 vs. 23), but then requires that an additional transberingian migration be postulated. Given the fact that pairs 16 and 17 have fused independently in other later lineages *(citellus-xanthoprymnus, townsendii)*, we opt for the cladogram presented here as the most probable.

If the other scheme of chromosomal evolution for the subgenus (Vorontsov and Lyapunova 1970), which assumes a primitive karyotype of 2n = 46 and only fusion and no fission in Robertsonian changes, is used a minimum of six to 11 chromosomal changes must be postulated for the five lineages of their scheme (if one includes the pericentric inversion of pairs 10 and 15, which those authors did not consider). The total number of changes required in their cladogram is 38; the present scheme is thus more parsimonious.

The tempo of chromosomal evolution in the subgenus *Spermophilus*

Several chromosomal divergence events within lineages of the subgenus *Spermophilus* can be approximately dated. The earliest event separated the "small-eared" ground squirrels from the "big-eared" and "long-tailed" ground squirrels probably in the mid-Pliocene (~3.4–3.7 m.y. BP) (Black 1972) (Fig. 2). Within the "small-eared" line, Palearctic and Nearctic stocks probably diverged by transberingian migration in the late Pliocene (~2.5 m.y. BP), as did the "long-tailed" "big-eared" ancestor about the same time, or perhaps a bit later; "long-tailed" and "big-eared" lineages diverged about 1.8 m.y. BP. Within the "long-tailed" lineage, the *undulatus-columbianus* ancestor and the *parryii* ancestor probalby diverged in early-middle Pleistocene (~1.2 m.y. BP); *undulatus* and *columbianus* in middle-late Pleistocene (~0.47 m.y. BP), and North American and Siberian *parryii* in the late Pleistocene (~0.01 m.y. BP) (dates conform to transberingian dispersal events of Repenning 1980). Within the "big-eared" lineage, the *armatus-beldingi* ancestor *(S. [armatus])* probably diverged from the *elegans-richardsonii* ancestor *(S. [richardsonii])* in the middle Pleistocene (~.6 m.y. BP), and each of these allospecies pairs diverged in the late Pleistocene (~.01 m.y. BP) (Hoffmann 1981).

Regardless of the direction of chromosomal evolution, it is possible to count the minimal number of chromosomal rearrangements that have occurred since these various divergences. The earliest divergence, between the "small-eared" (2n ≧ 36) and "long-tailed"/"big-eared" (2n ≦ 36) lineages, have a minimum of 0 *(brunneus, mollis)* to 5 *(xanthoprymnus)*, and 3 to 7 chromosomal changes, respectively. The average changes per lineage is 5.4, or about 1.5 changes per million years.

The next series of divergences (2.5–1.8 m.y. BP) includes those between Nearctic and Palearctic "small-eared" *Spermophilus* (0 to 4, and 2 to 5 changes; average 2.7), and

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between "long-tailed" and "big-eared" lineages (0 to 1, and 0 to 2 changes; average 1 change). The overall average for this period is 0.35–1.08 changes per million years.

Next in the temporal sequence (1.2–0.6 m.y. BP) is the divergence of the *parryii* and *columbianus-undulatus* lineages (0 and 1 change; average 0.5), and the *S. [armatus]* and *S. [richardsonii]* lines (2 and 1 changes; average, 1.5). The overall average is 0.42–2.5 changes per million years.

Finally, the most recent divergences (0.1 m.y. BP) of which we have some direct evidence are those between North American and Siberian *S. parryii* (0, and 0 changes) and between *S. [r.] richardsonii* and *S. [r.] elegans* (1, and 0 changes; average, 0.5 changes). The combined average is 25 changes per million years, a much higher rate, if it were to persist. High rates of recent change probably also characterize other lineages with recently evolved sister species (*citellus, xanthoprymnus, townsendii, vigilis,* etc.).

Overage, the rate of chromosomal change is 2.3 to 3.8 changes per million years, depending upon which scheme of chromosomal evolution is employed. This is an order of magnitude above the average for rodents (~0.1/m.y.) reported by Wilson et al. (1975). However, it is probably not atypical of rates of chromosomal evolution within groups undergoing a bout of speciation and radiation into new areas and habitats. Average rates are also misleading if applied to lineages; the rate involved in the divergence of *S. [r.] richardsonii* from *S. [r.] elegans* is 25/m.y., whereas other lineages (*S. brunneus* in the present paper; *S. vigilis* in the model of Vorontsov and Lyapunova), show no chromosomal changes in 3.4 million years.

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Zusammenfassung

Chromosomenentwicklung der holarktischen Erdhörnchen (Spermophilus). II. Homologien der Giemsa-Bandmuster zwischen den Chromosomen und Evolutionsraten

Chromosomenmorphologie der holarktischen Erdhörnchen (Untergattung *Spermophilus*) wurde mittels Giemsa-Bandmuster studiert. Die diploide Anzahl in dieser Untergattung variiert von 2n = 30 bis 2n = 46 bei 23 Arten, wobei 11 Arten einen Mittelwert von 2n = 36 zeigen. Chromosomenpaare mit dem Karyotyp 2n = 38 wurden willkürlich nach Größe und Armlänge angeordnet, und die Bandmuster von 12 diploiden Arten wurden verglichen.

Die Paare 1 bis 9 sind große, deutlich gebänderte Chromosomen. Sie waren bei allen Arten zu finden, entweder als Arme von zweiarmigen Elementen (2n = 30–38) oder als einarmige Elemente (2n = 40–46). Unter den kleineren Chromosomen scheinen die Paare 10 bis 15 bei den nearktischen „groß-ohrigen" und den holarktischen „lang-schwänzigen" Erdhörnchen gleich zu sein, ebenso bei *S. washingtoni,* außer daß den 2n = 30–32 Arten *(undulatus, columbianus, beldingi)* das in der Hauptsache heterochromatische Paar 15 und im Falle *beldingi* das Paar 12 fehlen. Die Paare 10 bis 15 scheinen sich auch bei den palearktischen Erdhörnchen, bei den nearktischen „kurz-ohrigen" und bei *S. brunneus* zu gleichen. Aber Homologien zwischen diesen Gruppen sind schwerer zu errichten wegen der geringeren Chromosomengröße und weniger kennzeichnender Bandmuster. In einigen

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Fällen *(S. richardsonii – S. elegans; S. armatus – S. parryii; S. columbianus – S. undulatus)* können vollständige Homologien zwischen Arten aufgestellt werden, und beinahe vollständige Homologien sind bei anderen zu sehen *(S. mollis – S. brunneus; S. dauricus – S. relictus).*

Trotz der Mannigfaltigkeit der Karyotypen deuten die meisten der gemeinsamen Chromosomenelemente in der Untergattung *Spermophilus* darauf hin, daß diese „Markierungschromosomen" wahrscheinlich symplesiomorphe Merkmale sind.

Gewisse Fälle von Chromosomenabänderungen können glaubhaft postuliert werden, und existierende Fossilien erlauben es, diesen Abänderungen ein ungefähres Entstehungsalter zuzuordnen. Wenn die Fälle von Chromosomenabänderungen dann weitgefaßt nach Entstehungszeit (Mittelpliozän, Spätpliozän, Früh-, Mittel- und Spätleistozän) gruppiert werden und die kleinste Anzahl an Chromosomenabänderungen, nötig für die beobachteten Abweichungen, berechnet wird, können die Chromosomenentwicklungsraten abgeschätzt werden. Diese ändern sich in verschiedenen Entwicklungslinien von 0 bis 25 Änderungen/Millionen Jahre. Sie betragen im Durchschnitt für die ganze Untergattung 2,3 Änderungen/Millionen Jahre. Diese Rate ist viel höher als der Durchschnitt, der für Nagetiere bekannt ist.

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Morphological and physiological characteristics of Muskrats from three different physiographic regions of Maryland, USA

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Abstract

Between 1977 and 1979, 210 muskrats *(Ondatra zibethicus)* were trapped from 3 different physiographic regions of Maryland: Allegheny Plateau, Piedmont Plateau, and coastal plain. Two subspecies are found in Maryland, *O. z. zibethicus* (Western Maryland) and *O. z. macrodon* (Eastern Shore). The muskrats of Central Maryland are considered to be an intergrade, but data from this study show that they closely resemble the Western Maryland subspecies. Seasonal and subspecific changes in metabolic

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